

17th Lowell Wakefield Symposium



Spatial Processes and Management of Marine Populations

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and David Witherell, Editors

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About the Symposium

The International Symposium on Spatial Processes and Management of Fish Populations is the seventeenth Lowell Wakefield symposium. The program concept was suggested by Gordon Kruse of the Alaska Department of Fish and Game. The meeting was held October 27-30, 1999, in Anchorage, Alaska. Eighty presentations were made.

The symposium was organized and coordinated by Brenda Baxter, Alaska Sea Grant College Program, with the assistance of the organizing and program committees. Organizing committee members are: Martin Dorn, U.S. National Marine Fisheries Service, Alaska Fisheries Science Center; Susan Hills, University of Alaska Fairbanks, Institute of Marine Science; Gordon Kruse, Alaska Department of Fish and Game; and David Witherell, North Pacific Fishery Management Council. Program planning committee members are: David Ackley, U.S. National Marine Fisheries Service; Bill Ballantine, University of Auckland, New Zealand; Nicolas Bez, École des Mines de Paris, France; Tony Booth, Rhodes University, South Africa; John Caddy, Food and Agriculture Organization, Italy; Nick Caputi, Western Australian Marine Research Laboratories, Australia; Jeremy Collie, University of Rhode Island; Rom Lipcius, Virginia Institute of Marine Science; Jeff Polovina, U.S. National Marine Fisheries Service, Hawaii; Claude Roy, ORSTOM, Sea Fisheries Research Institute, South Africa; Stephen J. Smith, Department of Fisheries and Oceans, Canada; Gordon Swartzman, University of Washington; and Sigurd Tjelmeland, Institute of Marine Research, Norway

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The Lowell Wakefield Symposium Series

The University of Alaska Sea Grant College Program has been sponsoring and coordinating the Lowell Wakefield Fisheries Symposium series since 1982. These meetings are a forum for information exchange in biology, management, economics, and processing of various fish species and complexes as well as an opportunity for scientists from high latitude countries to meet informally and discuss their work.

Lowell Wakefield was the founder of the Alaska king crab industry. He recognized two major ingredients necessary for the king crab fishery to survive—ensuring that a quality product be made available to the consumer, and that a viable fishery can be maintained only through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played important roles in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaska waters, and in drafting international agreements for the high seas. Toward the end of his life, Lowell Wakefield joined the faculty of the University of Alaska as an adjunct professor of fisheries where he influenced the early directions of the university's Sea Grant Program. This symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries. Three Wakefield symposia are planned for 2002-2004.

Spatial Modeling of Fish Habitat Suitability in Florida Estuaries

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Abstract

Spatial habitat suitability index (HSI) models were developed by a group of collaborating scientists to predict species relative abundance distributions by life stage and season in Tampa Bay and Charlotte Harbor, Florida. Habitat layers and abundance-based suitability index (S_i) values were derived from fishery-independent survey data and used with HSI models

that employed geographic information systems. These analyses produced habitat suitability maps by life stage and season in the two estuaries for spotted seatrout (*Cynoscion nebulosus*), bay anchovy (*Anchoa mitchilli*), and pinfish (*Lagodon rhomboides*). To verify the reliability of the HSI models, mean catch rates (CPUEs) were plotted across four HSI zones. Analyses showed that fish densities increased from low to optimum zones for the majority of species life stages and seasons examined, particularly for Charlotte Harbor. A reciprocal transfer of S_i values between estuaries was conducted to test whether HSI modeling can be used to predict species distributions in estuaries lacking fisheries-independent monitoring. The similarity of S_i functions used with the HSI models accounts for the high similarity of predicted seasonal maps for juvenile pinfish and juvenile bay anchovy in each estuary. The dissimilarity of S_i functions input into HSI models can account for why other species life stages had dissimilar predicted maps.

Introduction

Understanding and predicting relationships of the dynamics between fish stocks and important habitats is fundamental for the effective assessment and management of marine fish populations. Managers of commercial and recreational fisheries now recognize the importance of habitat to the productivity of fish stocks (Rubec et al. 1998a, Friel 2000), and accurate maps of habitats and fish populations are becoming important tools for the management and protection of essential habitats and for building sustainable fisheries (Rubec and McMichael 1996; Rubec et al. 1998b, 1999; Ault et al. 1999a, 1999b). However, mathematical models that describe spatial relationships between habitats and fish abundance are not available for most species, generally because it is not clear what constitutes "habitat" or how it relates to the spatial and temporal variations in abundance of fish stocks. Rather than a simple relationship, areas of higher or lower population abundance are typically complex functions of several environmental and biological factors.

Some early attempts to quantify linkages between fish stocks and habitat were developed by the U.S. Fish and Wildlife Service (FWS) habitat evaluation program. The most visible product of those efforts was the Habitat Suitability Index (HSI) (FWS 1980a, 1980b, 1981; Terrell and Carpenter 1997). The central premise of the HSI approach derives from ecological theory, which states that the "value" of an area of "habitat" to the productivity of a given species is determined by habitat carrying capacity as it relates to density-dependent population regulation (FWS 1981). Empirical suitability index (S_i) functions were derived by relating population abundance to the quantity and quality of given habitats (Terrell 1984, Bovee 1986, Bovee and Zuboy 1988). Suitability indices are generally continuous functions of environmental gradients, but they can be scaled to a fixed range or made dimensionless. Higher suitability index values *de facto* mean that areas

with higher relative abundance in terms of numbers or biomass are “more suitable habitat.” Suitability indices have been multiplied against the amount of area constituting the index score to create habitat units that quantify the extent of suitable habitats (FWS 1980b, 1981; Bovee 1986). Historically, spatial calculations were limited by computational capabilities. Today, geographic information systems operating on powerful desktop computers make such spatially intensive analyses tractable.

Florida is undergoing rapid human population growth and development in the coastal margins, and this explosive growth is believed to be detrimental to the sustainability and conservation of coastal fisheries resources. Intensive fishery-independent monitoring programs have been established in 5 of 18 major estuaries spread throughout Florida (McMichael 1991). In the management of the state's extensive and valuable marine fishery resources, one of the principal questions that has arisen is: Is it possible to use the empirical functions developed for one estuary and transfer them to another where abundance data are not available, but environmental regimes are known, to predict the likelihood of species occurrences, relative abundance, and spatial distributions? To address these issues, scientists from the Florida Fish and Wildlife Conservation Commission, the National Oceanic and Atmospheric Administration (NOAA), and the University of Miami have been collaborating on suitability model development and implementation using geographic information systems (GIS). A primary research goal is to predict the spatial distributions of given fish species by estuary, life stage, and season from empirical functions derived from similar aquatic systems. In this paper, we show how the dependent variable “relative abundance” can be related to a suite of independent environmental variables to examine two main hypotheses: (1) that relative abundance increases with habitat suitability, and (2) that predicted species spatial distributions produced from S_i functions and habitat layers in one estuary will be similar to the predicted maps derived from S_i functions transferred from another estuary.

Methods

In the present study, we adopted an analytical approach previously described in Rubec et al. (1998b, 1999), that follows methods published by FWS and NOAA (FWS 1980a, 1980b, 1981; Christensen et al. 1997, Brown et al. 2000). This methodology links HSI modeling to GIS visualization technologies to produce spatial predictions of relative abundance of selected fish species by life stages and seasons.

CPUE Data and Standardization

Since 1989, the Florida Marine Research Institute (FMRI) has conducted fishery-independent monitoring (FIM) in principal Florida estuaries (Nelson et al. 1997). In this study, we used FIM random and fixed-station data collected from 1989 to mid-1997 in Tampa Bay (6,286 samples) and Charlotte

Harbor (3,716 samples). Data were collected using a variety of gear types and mesh sizes during the survey's history. To use all survey data in a comprehensive analysis, we standardized sample CPUEs across gears for each species' life stage using a modification of Robson's (1966) "fishing power" estimation method (Ault and Smith 1998). Gear-standardized data sets for Tampa Bay and Charlotte Harbor were created for the following species and species life stages: early-juvenile (10-119 mm SL), late-juvenile (120-199 mm SL), and adult (≥ 200 mm SL) spotted seatrout (*Cynoscion nebulosus*); juvenile (10-99 mm SL) and adult (≥ 100 mm SL) pinfish (*Lagodon rhomboides*); and juvenile (15-29 mm SL) and adult (≥ 30 mm SL) bay anchovy (*Anchoa mitchilli*).

Habitat Mapping

The FMRI-FIM program in Tampa Bay and Charlotte Harbor provided the bulk of the data used in these analyses. At each sampling site, environmental information on water temperature, salinity, depth, and bottom type, and biological data on species presence, size, and abundance were collected (Rubec et al. 1999). Surface and bottom temperature and salinity data from the FIM database were supplemented with temperature and salinity data from other agencies, including the Southwest Florida Water Management District (SWFWMD), Florida Department of Environmental Protection, Shellfish Environmental Assessment Section (SEAS), and the Hillsborough County Environmental Protection Commission (EPC). Submerged aquatic vegetation (SAV) coverages were created using the Arc/Info GIS from SWFWMD 1996 aerial photographs of both estuaries. Areas with rooted aquatic plants (e.g., seagrass) or marine macro-algae were coded as SAV, while remaining areas were coded as bare bottom. Bathymetry data for both estuaries were obtained from the National Ocean Service, National Geophysical Data Center (NGDC) database. To deal with temporal and spatial biases, the combined datasets derived from 8.5 years of sampling were then used to determine mean temperatures and mean salinities by month within cells associated with the 1-square-nautical-mile sampling grid. The mean values were associated with the latitude and longitude at the center of each cell. Universal linear kriging associated with the ArcView GIS Spatial Analyst was used to interpolate monthly mean temperatures and mean salinities across the cells using a variable radius with 12 neighboring points (ESRI 1996). Shoreline barriers were imposed to prevent interpolation between neighboring data points across land features, such as an island or peninsula. Rasterized surface and bottom temperature or salinity habitat layers (each composed of 18.5-m² cells) were created for each estuary (24 monthly layers for each environmental factor). Monthly layers for each estuary were then averaged to produce seasonal habitat layers for spring (March-May), summer (June-August), fall (September-November), and winter (December-February). Depth layers for each estuary were derived by interpolation of NGDC bathymetry data using inverse distance weighting with 8 neighboring points and a power of 2 (ESRI 1996).

HSI Models and Parameter Estimation

HSI modeling for each species life stage has two main steps. First, a function was derived that relates a suitability index S_i to a habitat variable X_i for each i -th environmental factor,

$$S_i = f(X_i) \quad (1)$$

Suitability functions are expressed in terms of species relative density (CPUE) related to a particular environmental factor (i.e., temperature, salinity, depth, or bottom type). Second, HSI values for each map cell were computed as the geometric mean of the S_i scores for n environmental factors within each cell (Lahyer and Maughan 1985):

$$HSI = (\prod S_i)^{1/n} \quad (2)$$

A smooth-mean method was used for deriving equation 1 for continuous environmental "habitat" variables (Rubec et al. 1999). For each species life stage, mean annual CPUEs (number/m²) were determined at predefined intervals for temperature (1°C), salinity (1 g/L), and depth (1 m). These data were then fit with single independent-variable polynomial regressions (JMP software, SAS 1995). Anomalies in the tails of the S_i functions for two species life stages (juvenile pinfish, early-juvenile spotted seatrout) were adjusted based on expert opinion. Mean CPUEs for each bottom type were calculated (bare and SAV). Values from predicted S_i functions were divided by their respective maxima and then scaled from 0 to 10.

Each computed HSI value (equation 2) used all four environmental factors. Suitability indices for each species life stage were assigned to the habitat layers in ArcView Spatial Analyst (ESRI 1996), and used in the model to create predicted HSI maps (Fig. 1) for each season of the year. Bay anchovy, a pelagic species, was modeled using surface-habitat layers for temperature and salinity, whereas bottom temperature and salinity layers were used for spotted seatrout and pinfish. The final predicted HSI values were further classified into quartile ranges to create four HSI zones: low (0-2.49), moderate (2.50-4.99), high (5.00-7.49), and optimum (7.50-10.00).

Model Performance

The models presented above are heuristic and qualitative in nature, thereby precluding any formal statistical testing of model efficacy. We therefore developed two simple measures of model performance. The first evaluates the within-estuary correspondence between predicted seasonal HSI zones and the means of actual CPUE values that fall within the predicted zones. If histograms of mean CPUE values increased across "low" to "optimum" HSI zones, then model performance was judged to be adequate, and we scored the result with a YES. Performance was also scored a YES if the differences between sequential mean CPUEs were small (<10% difference) but an overall

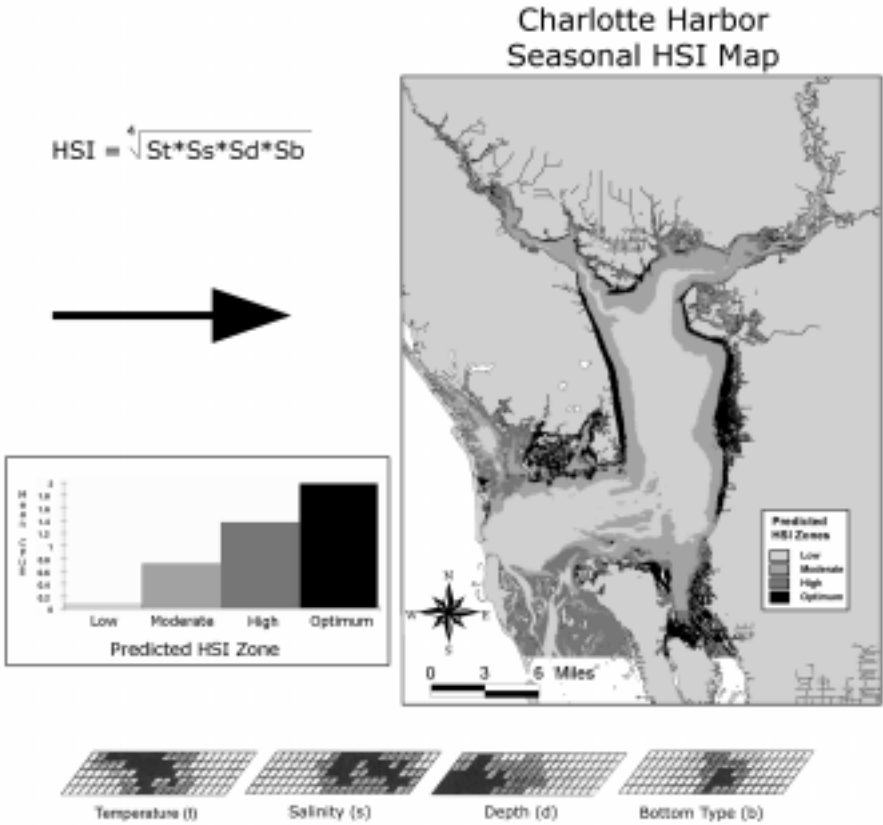


Figure 1. Raster-based GIS modeling process used to produce seasonal Habitat Suitability Index (HSI) maps of fish species life-stages.

increasing trend was apparent across zones. Performance was scored as NO when an increasing trend in CPUEs was not apparent across the zones.

Another test of performance evaluated the efficacy of using predictor relationships developed for one estuary, in a blind transfer of the model to a set of environmental conditions in a second estuary. This test had two attributes: (1) that CPUEs increase across HSI zones as defined above, and (2) that zones defined by the independent models (transferred S_i functions) appear similar to those defined by functions derived from within each estuary. In the latter tests, HSI zone values (1-4) associated with within-estuary HSI maps were compared on a cell-by-cell basis with zone values of the corresponding seasonal HSI map for the same estuary derived from transferred S_i functions. Each pair of predicted seasonal HSI maps were considered to be similar if $\geq 60\%$ of the cells by zone were scored the same in the

majority (2 out of 3 or 3 out of 4) of the HSI zones. To evaluate whether the maps minimally identified the most suitable habitats associated with higher species life stage abundances, we also computed differences between predictions of the "optimum" zones by the two models. Agreement (at the $\geq 60\%$ no difference level) in the optimum zone indicated that the two independently derived maps qualitatively reflected areas of similar critical importance to stock productivity.

Results

Suitability Functions

With pinfish, the S_i functions for juveniles were similar between Tampa Bay and Charlotte Harbor (Fig. 2). The highest S_i values occurred near 25°C, at 34-35 g/L salinities, less than 1 m depths, and over SAV. The highest S_i values for adults occurred between 28 and 33°C, at salinities of 31 g/L in Tampa Bay and 37 g/L in Charlotte Harbor, at 1 m depth in both estuaries, and over SAV in both estuaries. The S_i functions were quite broad across the temperature and salinity gradients for both juvenile and adult life stages. The depth curves from the two estuaries overlapped for juveniles but were more divergent (not closely overlapping) for adults across the entire depth range and were found to occur in deeper water (10 m) in Tampa Bay than in Charlotte Harbor (7 m).

With spotted seatrout, early-juvenile S_i functions were similar between Tampa Bay and Charlotte Harbor, with the highest peaks at 30-35°C, 17-23 g/L salinity, over SAV, and in shallow water (<1 m). The early-juvenile seatrout occurred in deeper water in Tampa Bay (6 m) than in Charlotte Harbor (4 m). The temperature curves for late-juvenile seatrout were markedly different. A broad peak occurred near 22°C in Tampa Bay, and a narrow peak near 28°C occurred in Charlotte Harbor. The late-juvenile S_i functions for salinity were broad in both estuaries, peaking near 20 g/L in Charlotte Harbor and 27 g/L in Tampa Bay. Both S_i functions for depth peaked in the 1-2 m range, but the one for Tampa Bay diverged markedly and extended into deeper (8 m) water than the function for Charlotte Harbor (4 m) did. The S_i values for late-juvenile seatrout were highest over SAV in both estuaries but were also high over bare bottom. The highest S_i values for adult spotted seatrout in both estuaries (Fig. 3) occurred near 25°C, at 26-34 g/L salinity, and within the first meter depth along the shoreline. The depth functions diverged markedly and extended into deeper water in Tampa Bay (8 m) than in Charlotte Harbor (4 m). Adult seatrout S_i values were high over SAV and low over bare bottom.

Both juvenile and adult bay anchovy in Tampa Bay and Charlotte Harbor were found over broad ranges of temperature and salinity and predominated in shallow water. With juvenile bay anchovy, the S_i functions peaked at 28°C in Tampa Bay and 33°C in Charlotte Harbor, at 5-10 g/L salinity, near 1 m depth, and over bare bottom in both estuaries. The functions overlapped closely for temperature, salinity, and bottom type but

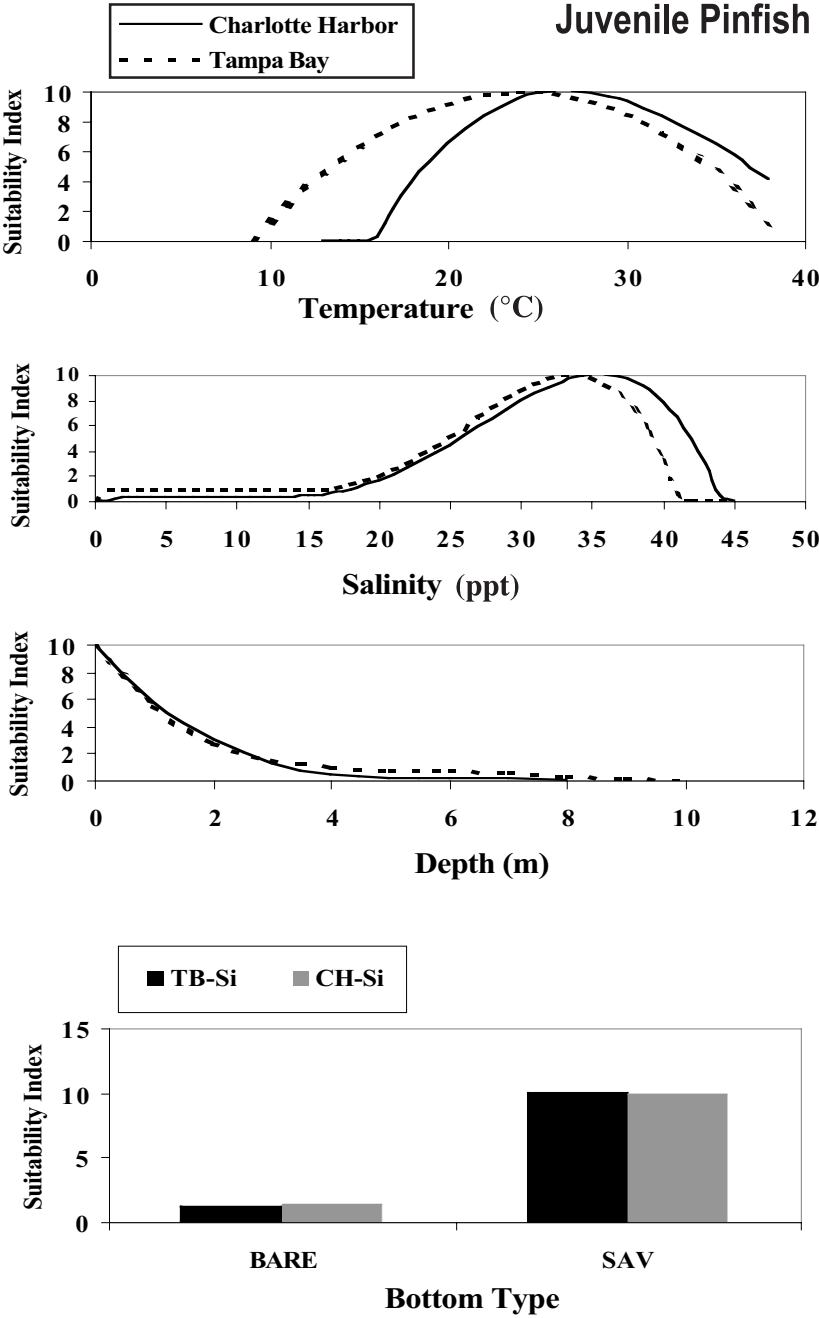


Figure 2. Suitability index (S_i) functions for juvenile pinfish across gradients of temperature, salinity, depth, and bottom type.

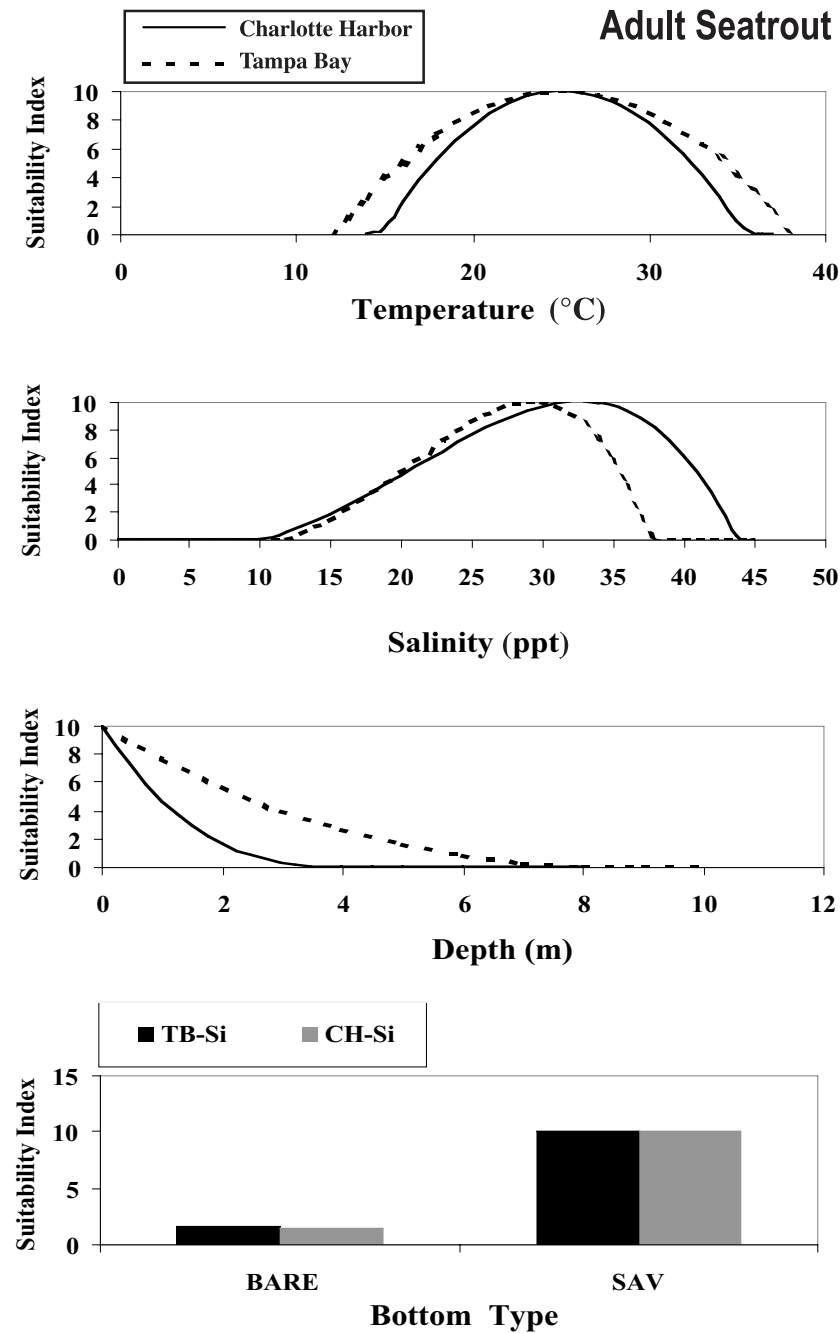


Figure 3. Suitability index (S_i) functions for adult spotted seatrout across gradients of temperature, salinity, depth, and bottom type.

diverged to some degree for depth. The adult bay anchovy S_i functions peaked at 28–33°C, and the peak salinity ranged from 6 to 8 g/L in Charlotte Harbor and 8 to 15 g/L in Tampa Bay. The highest S_i values occurred over bare bottom (but were also high over SAV) and at <1 m depth in both estuaries.

Habitat and HSI Maps

One bottom type, 1 bathymetry, 4 surface salinity, 4 bottom salinity, 4 surface temperature, and 4 bottom temperature seasonal habitat layers were created for each estuary for a total of 36 habitat maps for Tampa Bay and Charlotte Harbor. To test the reciprocal transfer of S_i functions between the two estuaries, we produced 56 predicted HSI maps using S_i functions derived from within each estuary (28 per estuary) and 56 maps with S_i functions transferred from the other estuary.

Increasing CPUE Relationship by HSI Zones

Many species' life stages showed increasing mean CPUEs across HSI zones (Table 1). For Charlotte Harbor, mean CPUEs increased across low to optimum HSI zones for 78.6% of the 28 predicted HSI maps produced using Charlotte Harbor habitat layers and S_i functions. Similarly with S_i functions transferred from Tampa Bay, 82.1% of 28 cases showed increasing mean CPUEs using Charlotte Harbor habitat layers. In Tampa Bay, increasing mean CPUEs occurred in 42.9% of 28 cases using habitat layers and S_i functions from within Tampa Bay. Increasing mean CPUEs occurred in 50% of 28 cases for predicted HSI maps created from Tampa Bay habitat layers and S_i functions transferred from Charlotte Harbor.

Similarity of Predicted HSI Maps

In Tampa Bay, juvenile pinfish met the similarity criterion across zones for all four seasons (Table 2). None of the adult pinfish seasonal HSI maps in Tampa Bay were similar across zones. In Charlotte Harbor, the predicted HSI maps for juveniles were similar across zones for summer, fall, and winter (Table 3). Adult pinfish maps were only similar across zones during the spring and winter seasons. With the optimum zone analysis for pinfish, the criterion was met in Tampa Bay with juveniles for all seasons and not met for any season with adults (Table 2). In Charlotte Harbor, the optimum zone criterion was met for all four seasons for juveniles and for 2 out of 3 seasons for adult pinfish (Table 3).

When we compared HSI maps by season for spotted seatrout for Tampa Bay only maps for early-juveniles in the winter exceeded the $\geq 60\%$ no difference criterion across the zones (Table 4). This was also the case in Charlotte Harbor (Table 5). None of the maps for late-juveniles and adults met the similarity criterion across zones for any of the four seasons in either estuary (Tables 4 and 5). For the optimum zone comparison with early-juvenile seatrout in Tampa Bay, the 60% criterion was exceeded for spring, summer, and fall (Table 4). No optimum zone occurred during the winter.

Table 1. Number of cases across seasons where increasing mean CPUE versus mean HSI relationships were found.

Species	Life stage	Ratio (yes) scores across seasons			
		Charlotte Harbor		Tampa Bay	
		CH- S_i	TB- S_i	TB- S_i	CH- S_i
Spotted seatrout	Early-juvenile	3/4	4/4	2/4	1/4
	Late-juvenile	3/4	1/4	1/4	0/4
	Adult	2/4	3/4	1/4	3/4
Bay anchovy	Juvenile	3/4	4/4	0/4	1/4
	Adult	4/4	4/4	3/4	3/4
Pinfish	Juvenile	3/4	3/4	2/4	2/4
	Adult	4/4	4/4	3/4	4/4
Total		22/28 (78.6%)	23/28 (82.1%)	12/28 (42.9%)	14/28 (50.0%)

TB- S_i = Suitability indices from Tampa Bay.
CH- S_i = Suitability indices from Charlotte Harbor.

Table 2. Percent similarity by grid cells for pinfish between Tampa Bay predicted HSI maps.

Life stage	Season	Percent no difference "0" cell counts by zone				Similarity scores If count "0" \geq 60%	
		Low	Moderate	High	Optimum	In majority of zones	In the optimum zone
Juvenile	Spring	100.0	66.8	99.9	97.2	Yes	Yes
	Summer	99.6	69.6	94.5	100	Yes	Yes
	Fall	99.4	72.2	99.9	98.7	Yes	Yes
	Winter	100.0	61.5	69.1	68.7	Yes	Yes
Adult	Spring	36.0	69.2	92.0	15.4	No	No
	Summer	41.9	65.7	83.7	16.7	No	No
	Fall	16.3	68.5	95.1	17.8	No	No
	Winter	58.4	85.9	9.1	—	No	—

Table 3. Percent similarity by grid cells for pinfish between Charlotte Harbor predicted HSI maps.

Life stage	Season	Percent no difference "0" cell counts by zone				Similarity scores If count "0" ≥ 60%	
		Low	Moderate	High	Optimum	In	In the
						majority of zones	optimum zone
Juvenile	Spring	13.9	99.6	50.4	100	No	Yes
	Summer	69.8	96.1	84.2	95.9	Yes	Yes
	Fall	64.2	96.4	72.0	100	Yes	Yes
	Winter	19.7	99.1	61.2	100	Yes	Yes
Adult	Spring	95.0	79.1	41.2	84.0	Yes	Yes
	Summer	96.9	44.9	35.5	55.0	No	No
	Fall	97.6	46.5	37.9	89.3	No	Yes
	Winter	96.1	66.9	12.0	—	Yes	—

Table 4. Percent similarity by grid cells for spotted seatrout between Tampa Bay predicted HSI maps.

Life stage	Season	Percent no difference "0" cell counts by zone				Similarity scores If count "0" ≥ 60%	
		Low	Moderate	High	Optimum	In	In the
						majority of zones	optimum zone
Early-juvenile	Spring	100	52.4	51.9	100	No	Yes
	Summer	100	31.6	31.9	78.4	No	Yes
	Fall	100	35.8	43.1	99.8	No	Yes
	Winter	93.8	75.9	—	—	Yes	—
Late-juvenile	Spring	99.1	0.2	3.4	47.0	No	No
	Summer	99.5	0.4	27.9	36.9	No	No
	Fall	99.7	0.7	4.1	56.4	No	No
	Winter	99.4	1.8	2.4	1.9	No	No
Adult	Spring	99.8	1.9	38.7	97.5	No	Yes
	Summer	99.8	11.4	30.4	87.2	No	Yes
	Fall	99.8	11.0	40.2	95.7	No	Yes
	Winter	99.9	10.8	29.6	91.1	No	Yes

Table 5. Percent similarity by grid cells for spotted seatrout between Charlotte Harbor predicted HSI maps.

Life stage	Season	Percent no difference "0" cell counts by zone				Similarity scores If count "0" ≥ 60%	
		Low	Moderate	High	Optimum	In	In the
						majority of zones	optimum zone
Early-juvenile	Spring	18.5	65.8	99.4	49.3	No	No
	Summer	7.3	26.7	54.6	100	No	Yes
	Fall	11.7	48.3	99.3	78.8	No	Yes
	Winter	97.6	96.9	1.7	—	Yes	—
Late-juvenile	Spring	1.6	32.2	5.6	98.6	No	Yes
	Summer	1.7	46.3	38.4	87.5	No	Yes
	Fall	1.6	24.6	13.4	94.2	No	Yes
	Winter	1.7	4.2	2.5	99.9	No	Yes
Adult	Spring	8.0	17.9	95.1	100	No	Yes
	Summer	13.8	50.3	38.3	100	No	Yes
	Fall	18.6	42.7	83.8	100	No	Yes
	Winter	9.1	28.2	78.0	100	No	Yes

Table 6. Percent similarity by grid cells for bay anchovy between Tampa Bay predicted HSI maps.

Life stage	Season	Percent no difference "0" cell counts by zone				Similarity scores If count "0" ≥ 60%	
		Low	Moderate	High	Optimum	In	In the
						majority of zones	optimum zone
Juvenile	Spring	100	67.8	78.5	64.4	Yes	Yes
	Summer	100	65.3	76.9	93.8	Yes	Yes
	Fall	100	58.5	65.0	61.2	Yes	Yes
	Winter	99.9	71.9	89.7	53.4	Yes	No
Adult	Spring	100	16.0	36.5	6.3	No	No
	Summer	100	0.7	27.1	15.1	No	No
	Fall	100	—	30.7	20.8	No	No
	Winter	100	15.0	18.4	1.1	No	No

Table 7. Percent similarity by grid cells for bay anchovy between Charlotte Harbor predicted HSI maps.

Life stage	Season	Percent no difference "0" cell counts by zone				Similarity scores If count "0" ≥ 60%	
		Low	Moderate	High	Optimum	In majority of zones	In the optimum zone
Juvenile	Spring	20.1	90.8	91.7	97.9	Yes	Yes
	Summer	25.0	—	91.7	96.1	Yes	Yes
	Fall	23.8	64.6	87.2	96.5	Yes	Yes
	Winter	27.8	91.4	83.8	91.3	Yes	Yes
Adult	Spring	17.6	2.8	52.7	100	No	Yes
	Summer	28.1	—	—	100	No	Yes
	Fall	16.5	—	25.2	100	No	Yes
	Winter	6.3	2.1	49.4	100	No	Yes

Table 8. Number of cases across seasons where predicted HSI maps (within and transferred) agree based on the percent similarity of grid cell scores.

Species	Life stage	Grid cell (yes) scores across seasons			
		Charlotte Harbor		Tampa Bay	
		In majority of zones	In optimum zone	In majority of zones	In optimum zone
Spotted-seatrout	Early-juvenile	1/4	2/3	1/4	3/3
	Late-juvenile	0/4	4/4	0/4	0/4
	Adult	0/4	4/4	0/4	4/4
Bay anchovy	Juvenile	4/4	4/4	4/4	3/4
	Adult	0/4	4/4	0/4	0/4
Pinfish	Juvenile	3/4	4/4	4/4	4/4
	Adult	2/4	2/3	0/4	0/3
Total		10/28 (35.7%)	24/26 (92.3%)	9/28 (32.1%)	14/26 (53.8%)

None of the late-juvenile maps met the criterion for any season. With adults, all seasons met the optimum zone similarity criterion. Hence, the zone of highest abundance in Tampa Bay was predicted for early-juvenile and adult, but not for late-juvenile seatrout. In Charlotte Harbor the optimum zones were similar for most seasons (10 of 11 cases) for all seatrout life stages (Table 5).

For bay anchovy in Tampa Bay (Table 6), the percent similarity criterion across zones was met for juveniles but not for adults for all four seasons. The same results were found in Charlotte Harbor (Table 7). The optimum zone criterion was met for spring, summer, and fall for juvenile bay anchovy in Tampa Bay (Table 6). None of the adult maps met the optimum zone criterion by season in Tampa Bay. In Charlotte Harbor, both juvenile and adult anchovy met the criterion for all four seasons (Table 7). Hence, the optimum zones by season were similar for juveniles in Tampa Bay (Table 6) and similar for juveniles and adults in Charlotte Harbor (Table 7).

Overall, 10 of 28 (35.7%) of the HSI maps in Charlotte Harbor were similar when comparing pairs of predicted seasonal HSI maps (Table 8). Similarly, 9 of 28 (32.1%) maps produced for Tampa Bay were similar across zones, using S_i values from within Tampa Bay and transferred from Charlotte Harbor. Better results were obtained in comparing the similarity of only the optimum zones. In 24 of 26 (92.8%) cases, the zones of highest abundance agreed in Charlotte Harbor. In Tampa Bay, optimum zones were similar in 14 of 26 (53.8%) cases.

Discussion

We have described the first phase of our research to develop and evaluate habitat suitability models for predicting spatial distributions of fish from data on species relative abundance indices and environmental "habitat" layers. In the course of our explorations, we adopted the geometric-mean HSI modeling methods used in several previous studies (Terrell and Carpenter 1997, Christensen et al. 1997, Brown et al. 2000). In terms of within-estuary model performance, 22 of 28 cases (78.6%) showed increasing mean CPUEs across HSI zones in Charlotte Harbor, whereas mean CPUEs increased in 12 of 28 cases (42.9%) when we used S_i values from Tampa Bay in Tampa Bay (Table 1). In terms of cross-transferability, Tampa Bay S_i values transferred to Charlotte Harbor yielded a higher proportion of increasing CPUEs across HSI zones (23 of 28 cases; 82.1%) than S_i values transferred from Charlotte Harbor to Tampa Bay (14 of 28 cases; 50%). However, map comparisons for both estuaries were successful for only about one third of the cases when transferring suitability indices from one estuary to predict the spatial distributions and relative abundance of fish in the other (Table 8).

Generally, when S_i functions for the same environmental variable were similar for the two estuaries, transferability was for the most part successful. This occurred for both juvenile bay anchovy and juvenile pinfish.

Likewise, when S_i functions for even a single variable differed between the two estuaries, the lack of transferability was exacerbated. For example, suitability functions dependent on salinity for adult spotted seatrout abundance showed out-of-phase modal peaks (Fig. 2), and in both cases, the cross-transferability failed (Tables 4 and 5). The divergence of suitability functions between estuaries was most apparent for depth. Marked differences in overlap of the S_i functions across the depth gradients were found with late-juvenile spotted seatrout, adult pinfish, adult bay anchovy, and adult spotted seatrout. Differences in fitted suitability functions incorporated into HSI models strongly determine the outcomes for predicted HSI maps.

Suitability functions were intrinsically determined by use of aggregated "annual" data. However, differences in life histories and seasonal environmental patterns can produce substantial differences in the estimated HSIs. Further analyses indicate that early-juvenile spotted seatrout in Tampa Bay were most abundant in deep waters during winter (low HSI zone) but most abundant in shallow waters during the rest of the year. Adult bay anchovy appear to switch their habitat affinities from bare bottom in fall through spring to SAV during the summer in both Charlotte Harbor and Tampa Bay. Improvements in habitat-animal association models may be realized by the creation of seasonal suitability functions.

One might conclude that differences in the S_i functions indicate that there are different habitat affinities by species life stage between estuaries. However, we believe that the differences are likely attributed to the HSI model-building process. HSI models were originally developed to support rapid decision-making in data-poor situations. Many of the published models were created using suitability index values derived from the literature and/or expert opinion (Terrell and Carpenter 1997). The HSI algorithm in its present format is thus a heuristic model useful for qualitative interpretations and may be inadequate for quantitative analysis and as a prediction tool. Comparison of HSI methodologies with more formal statistical models (i.e., multiple regression) highlights some of these inadequacies. For example, a major problem of HSI models is the ad hoc procedure of giving equal weight to any and all environmental variables. In addition, standard methods of statistical model-building are rarely employed for variable selection, evaluation of model form, etc. (e.g., Neter et al. 1996). Many of these problems with HSI model-building arise from a somewhat strict focus on prediction of "average" phenomena rather than evaluating the statistical variation contained in the basic data, which is central to the development of parametric statistical models.

We conclude that HSI models may be very useful in data-poor situations where some type of rapid management response is required. However, with fish and environmental "habitat" data of high spatial and temporal resolution, we believe that significant improvements in the development of predictive models of fish-habitat associations may be obtained by using more contemporaneous regression-based methods.

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Recent Approaches Using GIS in the Spatial Analysis of Fish Populations

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Abstract

Geographical information systems (GIS) are information systems that can store, analyze, and graphically represent complex and diverse data with spatial attributes. Considering that GIS are rapidly emerging as the analytical tool of choice for investigating spatially referenced fish population dynamics and assisting in their management, it was deemed appropriate to review the state of research within this field and provide examples of current applications. Areas of research that we investigated included databases, visualization and mapping, fisheries oceanography and ecosystems, georeferenced fish population dynamics and assessment, space-based fisheries management, and software. The enhanced analytical functionality offered by GIS, coupled with their optimized visualization capabilities, facilitates the investigation of the complex spatiotemporal dynamics associated with fish, fisheries, and their ecosystems. This paper reviews current GIS research and its application to spatially oriented fisheries management, and illustrates the necessity of carefully evaluating and selecting appropriate GIS approaches for different fishery resource scenarios.

Introduction

There is an increasing awareness by fisheries scientists of the importance of the spatial component within their data. Spatially referenced information is highly dimensional ($\geq 3D$) and the data voluminous, often impeding

investigation and analysis. This difficulty has been somewhat relieved by increases in computing performance, data storage capacities, and database management systems, and also by new computationally intensive spatial analysis tools. As a consequence, geographical information systems (GIS) are now recognized as the tool of choice in a variety of disciplines when addressing spatially referenced problems (Star and Estes 1990, Maguire et al. 1991). Geographical information systems differ from traditional information systems because they present the opportunity to store, process, analyze, and graphically represent complex and diverse data with spatial attributes within a problem-solving environment (Dueker 1979, Smith et al. 1987, Maguire 1991).

Geographical information systems are frequently used by various disciplines and it is, therefore, not surprising that GIS technology is now being incorporated into the fishery sciences (Giles and Nielsen 1992, Simpson 1992, Li and Saxena 1993, Meaden 1996). For this reason, we review current GIS research and its application to spatially oriented fisheries management, and illustrate the necessity of carefully evaluating and selecting appropriate GIS approaches for different fishery resource scenarios. This paper outlines the background and history of GIS in fisheries management, and describes recent developments in databases, applications, and software. Prospects for the future are discussed, as well.

Background and History

Geographical information systems were developed in the 1960s in terrestrial management fields when sufficient spatially referenced information became available. Geographical information systems are now widely applied in primary and secondary industry, engineering, town planning, and waste management (Marble et al. 1984, Smith et al. 1987, Star and Estes 1990, Maguire et al. 1991). From both fisheries resource research and management perspectives, the application of GIS has been slow, only being adopted in the 1980s. Early applications focused on the management of inland, nearshore, and coastal fisheries (Caddy and Garcia 1986, Simpson 1992, Meaden 1996, Meaden and Do Chi 1996) and aquaculture (Kapetsky et al. 1987, 1988; Meaden and Kapetsky 1991). This was mainly due to the availability of spatial information in these zones obtained mainly from satellite imagery. Although fisheries applications gradually expanded to offshore waters, covering all of the oceans by the 1990s, the number of marine applications is still limited when compared to the terrestrial realm (Table 1).

Caddy and Garcia (1986), Meaden and Kapetsky (1991), Simpson (1992), Meaden and Do Chi (1996), Meaden (1996), and Booth (2000a) outline three issues that have hampered the growth and implementation of fishery GIS. The first is financial, associated with the costs to collect aquatic biological, physicochemical, and sediment data. These costs, together with extra costs related to synthesizing large spatial databases into a useable format, have

Table 1. Stages in the growth of GIS applications to spatial-oriented fishery research and management (adapted from Meaden 2000).

Stage	Characteristics	Dates	Motivation
1	Tentative emergence; very slow growth; mainly used in inland water fisheries management and aquaculture site selection (inland to inshore).	1984-1990	Developments in remote sensing; GIS work at FAO; imitation of other terrestrial GIS activities.
2	Accelerating growth into a wider range of fishery fields (inshore to off-shore).	1991-1997	Increased opportunities through the development of more powerful PCs and certain publications.
3	Consolidation and expansion into more fields. Wider interest base (offshore to distant waters).	1997 →	Data availability and storage; increasing publicity and needs for recognition.

Note: It is too early to determine whether Stage 3 is simply an extension of Stage 2, though there appears to be a leveling off in the publication rate.

hindered the development of aquatic, and in particular marine, GIS. These costs alone (ignoring the costs associated with the training and employment of personnel) are often prohibitive, restricting GIS to developed countries or large commercial concerns. The second reason concerns the dynamics of aquatic systems. Aquatic systems are more complex and dynamic than terrestrial domains and, therefore, require different types of information, both in terms of quality and quantity. The aquatic environment is typically unstable and needs to be recognized as a 3D (spatial) or even a 4D (spatiotemporal) domain. Mapping 4D information (3D + time) is difficult and is often not tackled for this reason. Third, while many commercial software developers have incorporated advanced statistical tools into their packages, there has always been a terrestrial bias, particularly with regard to systems developed for commercial applications. As a result, no effective GIS software is available for handling both fisheries and oceanographic data as it involves resolving problems associated with database storage and graphical representation of heterogeneous vector and raster data sets.

Current Situation

Databases

Meaden (2000) compared the existing problems and inherent complexities of fisheries and oceanography databases to terrestrial systems. Most ter-

restrially developed GIS are 2D and fewer are 3D (at most 2.5D when surface modeling), thus lack true spatiotemporal (4D) capabilities required for marine applications. As a result, we therefore need to develop 3-4D oriented GIS for fisheries and oceanographic applications. Ocean-based data are usually extremely expensive to collect, thus large agencies are required to collect and share data. Additional funding is required for fisheries/ocean mapping (GIS) and monitoring. There is a clear need to standardize and consolidate data collection structures and database design to adjust for discrepancies in space and/or time. User-friendly and accessible tools are required to convert analog data to digital data, and to process matrix (raster) information. Easier access to oceanographic and satellite information is required together with the establishment of 3-4D database links to GIS.

Application

In order to assess the current situation and progress in GIS, recent applications were carefully reviewed and classified into following four categories: visualization and mapping of parameters related to fisheries resources, fisheries oceanography and their ecosystems, georeferenced fish resource analyses, and space-based fisheries management. Figure 1 illustrates the relationships among these categories.

Visualization and Mapping

Mapping to study habitat and biodiversity is the most basic and common research area to which marine GIS work has been applied. It has been proposed that basic mapping does not constitute a GIS (Booth 2000a), rather it is the generation of secondary data and their analysis that sets it apart from computer mapping or computer-aided design. In a broad sense, univariate mapping is a basic GIS component because advanced GIS analyses are conducted by integrating variables into a multivariate analysis. Geographical information systems have been developed that focus on mapping, atlasing, and exploratory data analysis to obtain a better understanding of the correlations between the distribution and abundance of fish, other species, abiotic and biotic covariates (Skelton et al. 1995, Booth 1998, Fisher and Toepfer 1998, Scott 2000). These analyses are used in further analyses within the system that include generalized additive and linear modeling and coverage overlaying (Booth 1998) and correlation analysis (Waluda and Pierce 1998). Geographical information system overlays of water bodies and road systems are also being used to expedite identification of accessible stream reaches in river basins for biological sampling (Fisher et al. 2000).

Understanding habitat, distribution, and abundance are important issues in fisheries management, especially in the United States, due to the 1996 reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act requiring amendments of all U.S. federal fisheries management plans to describe, identify, conserve, and enhance essential fish

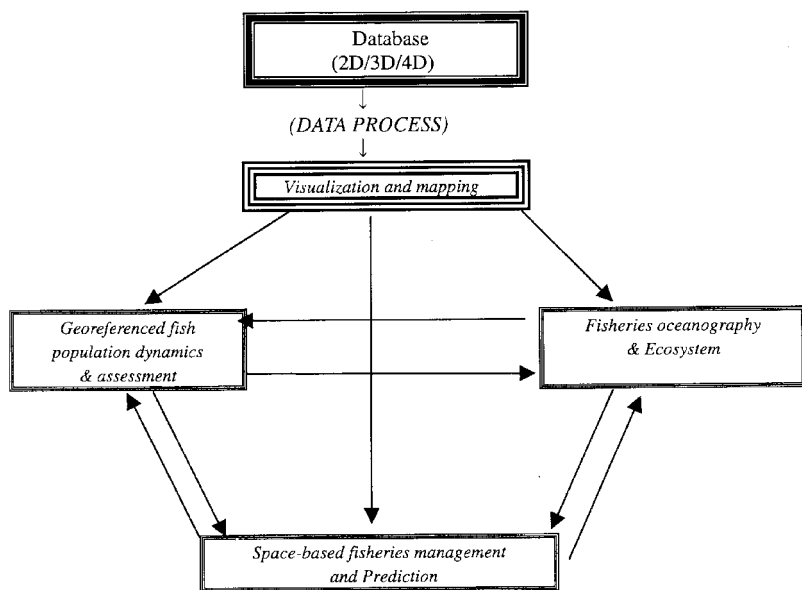


Figure 1. Relationships among four types of spatial analyses of fish populations using GIS. (Note: These four areas frequently overlap.)

habitat (EFH). The designation of an EFH will involve the characterization and mapping of habitat and habitat requirements for the critical life stages of each species. In addition, threats (including damage from fishing gear) to EFHs need to be identified, and conservation and enhancement measures promoted. Geographical information system technologies are essential for the successful implementation of this new fisheries management target, particularly in the initial characterization of habitat, the spatial correlation of potential threats with habitat, the evaluation of cumulative impacts, and the monitoring of habitat quality and quantity. Habitat mapping, modeling, and the determination of EFH are now commonly addressed within a GIS framework (Booth 1998, Fisher and Toepfer 1998, Parke 1999, Fisher et al. 2000, Nishida and Miyashita 2000, Ross and Ott 2000).

Fisheries Oceanography and Ecosystems

Fisheries oceanography and ecosystem science refer to that research area relating to spatial relationships among fish, fisheries, oceanography, and ecology. Knowledge obtained through these studies will, therefore, be critical in achieving an ethos of "responsible fishing" and facilitate optimal fisheries management practices (FAO 1995). Since its adoption, the world's fishing

nations are gradually promoting sustainable fisheries, protecting their resource bases, and attempting to maintain ecosystem health.

The development of GIS to understand the functional relationships between fisheries and ecosystems is still in the pilot or planning stages. Edwards et al. (2000) addressed ecosystem-based management of fishery resources in the northeastern U.S. shelf ecosystem. The objective of their research was to determine whether the management of marine fisheries resources in the northeastern region of the United States was consistent with ecosystem-based management for an aggregated sustainable yield of commercially valuable species. In their study, a GIS was used to display and analyze spatial data for investigating ecosystem-based management of fisheries resources. Distributions of species, fishing effort, and landing revenues based on 10-minute squares over Georges Bank during a 3-year period were spatially analyzed. Similar maps of fishing effort by gear (fish trawls and scallop dredges) suggest the scope for likely bycatch. An indication of the economic importance of the groundfish areas closed to other fisheries, especially to the Atlantic sea scallop (*Placopecten magellanicus*) fishery, is suggested by revenue coverages. As a result, GIS could well handle the spatial analysis of ecological, technological, and economic relationships and could facilitate reviews of management plans for their consistency with ecosystem requisites. An essential component of this study is a clear understanding of the spatial distribution of interactions among species, fishing effort, and technologies, and markets for fisheries products. Edwards et al. (2000) concluded that GIS will be the only tool for such complex spatial analyses and the research is now progressing with this particular objective.

An interesting GIS area that has scope for development is the linkage of ecosystem-fisheries research with the use of the model ECOPATH (Pauly et al. 1999). ECOPATH can handle numerical evaluations of ecosystem impact of fisheries and can conduct simulations of dynamics among ecosystem elements (trophic interactions in the food web) to provide an overview of the mechanism of marine ecosystem changes depending on fishing effort. If the results of the simulations could be visualized by GIS, more comprehensive spatiotemporal changes of ecosystem members could be portrayed; e.g., changes of biomass, consumption and production rates, diet composition, habitat preferences, and movement rates. With the addition of spatial analytical methods, "ECOSIM/ECOSPACE" has been developed and is being used to investigate a marine ecosystem study off the west coast of Florida (Ault et al. 1999).

Little research has been published concerning migration dynamics using GIS. Saitoh et al. (1999) studied the migration dynamics of the Japanese saury (*Cololabis saira*) by investigating the relationships between oceanic conditions and saury migration patterns through the observation of the movement of pursuing fishing vessels obtained from satellite imagery. The results of overlaying of sea surface temperature (SST) data with fishing

boat movement along the Oyashio front clearly indicated the migration dynamics of the Japanese saury.

Kiyofuji et al. (2000) studied the spatial and temporal distribution of squid fishing boats using visible images from the Defense Meteorological Satellite Programs (DMSP) and from the Operational Linescan System (OLS). The relationship between SST obtained from Advanced Very High Resolution Radiometer (AVHRR) developed by the National Oceanic and Atmospheric Administration (NOAA) and fishing boat distribution was also investigated. The preliminary conclusion was that by applying marine GIS, visible images using DMSP/OLS could provide both the position where fishing boats gather and the relationship between fishing boat location and SSTs.

A GIS can easily analyze remote-sensed data. Sampson et al. (2000) provided a numerical assessment of two types of kelp (*Ecklonia maxima* and *Laminaria pallida*) biomass off the West Cape coast of South Africa. High concentrations of kelp occur along this coast in relatively pristine conditions. In recent years, the importance of this resource has been emphasized in relation to its use in alginate extraction and as a commercially highly valuable food source for abalone. Therefore, there is a distinct need to manage this resource, including obtaining estimates of absolute biomass. Sampson et al. (2000) compared past photographic (qualitative) and new quantitative GIS methods. Results showed that the biomass of surface kelp had been overestimated, on average, by 230% using the old methodology. The GIS method based on remote sensing inputs, proved to be a more successful tool in mapping and estimating the biomass of the kelp and it is being modified to model the amount of alginate and abalone that can be produced per year.

A similar system developed by Long et al. (1994b) used aerial photography to identify and delineate seagrass beds, and to estimate seagrass biomass after digitization. Welch et al. (1992) approached coastal zone management using data from image analysis and aerotriangulation to build up a time series of changes in salt marshes. Their GIS, using thematic overlaying and Boolean logic, quantified and visualized changes induced through human impact over a 40-year period. Exciting progress is also being made using 3D GIS to improve our understanding of fish distribution and abundance using hydroacoustics and echo-integration (Wazenböck and Gassner 2000).

Warning et al. (1999) used a GIS to investigate the basic ecological characteristics of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) habitats in shelf-edge and deeper waters off the northeastern United States. Using sighting data and corresponding information on bathymetry, slope, oceanic fronts, and SST, logistic regression analyses was conducted to determine that the distribution of sperm whales was more dependent on depth and slope, while that of beaked whales was more dependent on SST.

Georeferenced Fish Resource Assessment

The need to manage fisheries from a spatial perspective is clear (Hinds 1992). Few attempts, however, have been made to incorporate the spatial variability of stocks' age-structure, maturity, and growth patterns together with catch and effort data into an assessment framework. Commercial catches are georeferenced, with fish being harvested at specific geographic locations as a function of the fishing effort and stock abundance at that location. By neglecting this spatial component, existing assessment models evaluate the status and productivity of the stock based on pooled catch-at-age data, fisheries-independent survey indices, and key population parameters.

Spatially referenced stock assessment has only recently been attempted. Currently, there is a growing interest in the development of marine GIS, both to visualize these spatial data sets and to provide a platform for further stock assessments and forecasting. As a result, a GIS incorporating spatially referenced fisheries data and assessment models would contribute significantly toward integrating this with other data sources and providing quantitative and qualitative management advice, and therefore to consequently improving integrated resources management.

Booth's (1999, 2000b) studies correlated fishing effort with observed age-structured fishing mortality to present a spatial perspective of the status of the resource. Yield-per-recruit modeling was expanded in Maury and Gascuel's (1999) study providing insight into spatial problems inherent to the delineation of marine protected areas and how these might affect fishing operations. These models encapsulate three fundamental aspects to fisheries modeling, all of which are spatiotemporally explicit: the environment, the fish stock, and the fishing fleet.

Corsi et al. (2000) applied an equilibrium biomass production modeling approach to assess the abundance of the Italian demersal resources as a function of spatially distributed fishing effort. Peña et al. (2000) further simplified the stock dynamics model and used a GIS to estimate the nominal yield of jack mackerel (*Carangidae*) using fishing ground information, and observed yield and sea surface temperature gradients. Using real-time fishing catch and location data, together with near-real-time satellite imagery, a transition probability matrix was used to calculate nominal yields at various thermal gradients. A low-level GIS used by Cruz-Trinidad et al. (1997) conducted a cost-return analysis of the trawl fishery of Brunei Darussalam, south of the Philippines, where optimal fishing patterns were determined using profitability indicators under various economic and operational scenarios. Walden et al. (2000) also developed a simple, yet real-time, GIS for the New England groundfish fisheries. This GIS evaluated various possible fine-scale time-area closures to assess the projected mortality reductions and losses in revenue of three principal demersal fish species: Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Pleuronectes ferrugineus*).

Several studies have addressed the estimation of population size from fisheries-independent surveys using GIS. Nishida and Miyashita (2000) estimated age-1 southern bluefin tuna (*Thunnus maccoyi*) recruitment, using information obtained by omni-scan sonar. In their study, a linear relationship was estimated between the strength of the Leeuwin Current into the survey area and the average school size as recorded by the sonar. They noted that young southern bluefin tuna schools were transported to the survey area depending on the expansion (strength) of the Leeuwin Current into the survey area. Therefore, they suggested that recruitment abundance should be estimated by standardization with respect to the expansion (strength) the Leeuwin Current. Similarly, Ali et al. (1999) used scientific echo sounders to investigate fish resource abundance in the South China Sea. They used marine GIS software, Marine Explorer (Itoh 1999), and its built-in kriging procedures were applied to quantify biomass of fish resources.

Space-Based Fisheries Management

Unfortunately, space-based fisheries management is the most poorly represented area in the GIS literature. This is principally due to the "in-house" use of this approach by management agencies and, in many instances, the applications are not suitable for publication in the peer-reviewed literature. It is these systems that have the largest potential as management tools within the public sector, including management and government agencies, as they can incorporate real-time spatially referenced data capture (Hinds 1992). Because the enforcement of fishing effort is a direct way to mitigate fishing impacts on the marine ecosystem as well as fish resources, fisheries managers have been giving some priority to monitoring the locations of fishing vessels. With this in mind, GIS software, which allows for global positioning system (GPS) integration to an onboard computer has been developed and was demonstrated during the Fishery GIS Symposium in 1999 (Simpson and Anderson 1999). Some GPS capability is used by fishermen for relocation to good fishing grounds by analyzing historical data using GIS (Simpson and Anderson 1999).

Data sources include vessel monitoring systems, catch-reporting/logging (Meaden and Kemp 1996, Kemp and Meaden 1998, Long et al. 1994a), and remote-sensed imagery of fishing areas (Kiyofuji et al. 2000, Peña et al. 2000). Foucher et al. (1998) described a prototype GIS that uses simple overlaying tools to quantify areas of conflict between competing fisheries for the octopus (*Octobrachiata*) and groundfish stocks off Senegal. Unfortunately the data used by many of these systems is often entered from handwritten or hard copy catch return reports. This implies a lag from event to the time at which it could be used as information. There is a definite move toward collecting the data in a digital format and transmitting it from vessels still at sea, increasing the adaptability of the GIS (Meaden 1993, Pollitt 1994, Meaden and Kemp 1996).

Caddy and Carocci (1999) described a GIS for aiding fishery managers and coastal area planners in analyzing the likely interactions of ports, inshore stocks, and local nonmigratory inshore stocks. This tool provides a flexible modeling framework for decision making on fishery development and zoning issues and has been applied to the scallop (*Pectinidae*) fishery in the Bay of Fundy, Canada, and the demersal fishery off the northern Tyrrhenian coastline of Italy.

Research using GIS as a bycatch mitigation tool is in its formative stages. Commercial software programs have been cited as a stumbling block to progress. Hopefully, when this issue is resolved a large number of applications could be expected, as bycatch management is arguably one of the most urgent and serious issues in world fisheries. Published results illustrate that GIS can specify (even pinpoint) the habitat areas of bycatch species on a fine spatiotemporal resolution. Mikol (1999) has investigated vessels targeting Pacific hake (*Merluccius productus*) off the Pacific Northwest U.S. coast, off Washington and Oregon. Ackley (1999) assessed Alaska's groundfish bycatch problem with GIS tools. He investigated time-area closures necessary to minimize bycatch of king crab (*Paralithodes camtschaticus*), Chinook salmon (*Oncorhynchus tshawytscha*), and chum salmon (*Oncorhynchus keta*) in the eastern Bering Sea as part of the groundfish fishery management plan for the North Pacific Fishery Management Council.

Software

Whereas most GIS platforms contain 2D database functionality and high quality graphical output, few progressed beyond 2-D databases, simple geostatistical analysis, and Boolean logic-based overlaying and buffering procedures. These platforms have terrestrial origins and do not have the capacity of handling or analyzing highly spatiotemporally variant data sets. As a result there is no generic commercial software that can efficiently handle fisheries information and its analytical demands. This limits fisheries GIS. Terrestrial GIS have tackled the problems with specialized analysis through customized modules. Fisheries GIS equivalents have been noted in this review.

More than 95% of the papers presented during the First International Symposium on GIS in Fishery Science, held in Seattle in March 1999, used terrestrial 2D or 2.5D GIS software. These software platforms could only handle fisheries and oceanography data to a limited extent, specializing in only a few specific functions such as simple presentation, navigation systems (electrical charts), satellite data processing, contour estimation, database, vertical profiling for oceanographic information, and bathymetry mapping. Although these systems were functional they could not incorporate all of these specific functions into one system. The development of integrated GIS software is required. In addition, such software needs to be used for conducting spatial numerical analyses and modeling with links to stock assessments, simulations, and ecosystem management. Furthermore, such software must be user-friendly and ideally would run without requir-

ing any programming, as fishery scientists in many countries have limited funding to hire GIS specialists and they cannot spend time on programming themselves. Several systems are in the developmental stages (Itoh 1999, Kiefer et al. 1999) and we anticipate their release. Itoh's (1999) menu-driven GIS software (Marine Explorer) is suited to store and manipulate fisheries and oceanography data. Details on Marine Explorer can be found at <http://www.esl.co.jp>.

Prospects and Summary

Our assessment of the current status on application of GIS in spatial analyses of fish populations is summarized in Fig. 2. As noted, there are few applications in numerical analyses and predictions, which will be the challenging area for the future.

GIS development in any discipline evolves over time, with different emphasis being placed on the results that are produced. Crain and McDonald (1983) noted this development cycle, stating that most GIS started as inventory tools, then progressed to handle a range of analyses before being used extensively to integrate data for management. Fisheries GIS are no exception. Meaden (2000) outlines various fisheries specific challenges to GIS development (Table 2). These hurdles need to be addressed to ensure rapid fisheries GIS development in the future.

There is an urgent need to develop spatially oriented management methodologies due to the limitations of the traditional concept of the pooled single-stock maximum sustainable yield or total allowable catch. Management measures need to be applied in space and time along with considering ecosystem implications, bycatch, multispecies interactions, and the socioeconomic importance of fisheries. In this manner, responsible fishing practices can be pursued while securing protein sources that may be able to mitigate food crises expected in the beginning of the twenty-first century. It is certain that such ecosystem management schemes for responsible fisheries will be complex, prompting the use of GIS as suitable management and assessment tools.

Integrated ecosystem fisheries management is the most important and challenging area in fisheries resources research. The facets are numerous and need careful consideration if GIS technology is to be used. Some prospects are achievable in the immediate future while the rest will occur in the long term. Clearly, some of the challenges are intrinsically interrelated and therefore difficult to separate and it is of little relevance to attempt to compartmentalize challenges between inland, coastal, and marine fisheries. Obviously there is a hierarchy of challenges such that some of them will only affect a minority of activists in this field, and some are likely to be more or less easily overcome. It is the authors' hope that this paper can contribute to promoting fisheries scientists, biologists, managers, fishers, and educators to apply fisheries GIS for optimal utilization and management of our fisheries resources within their wider ecosystems.

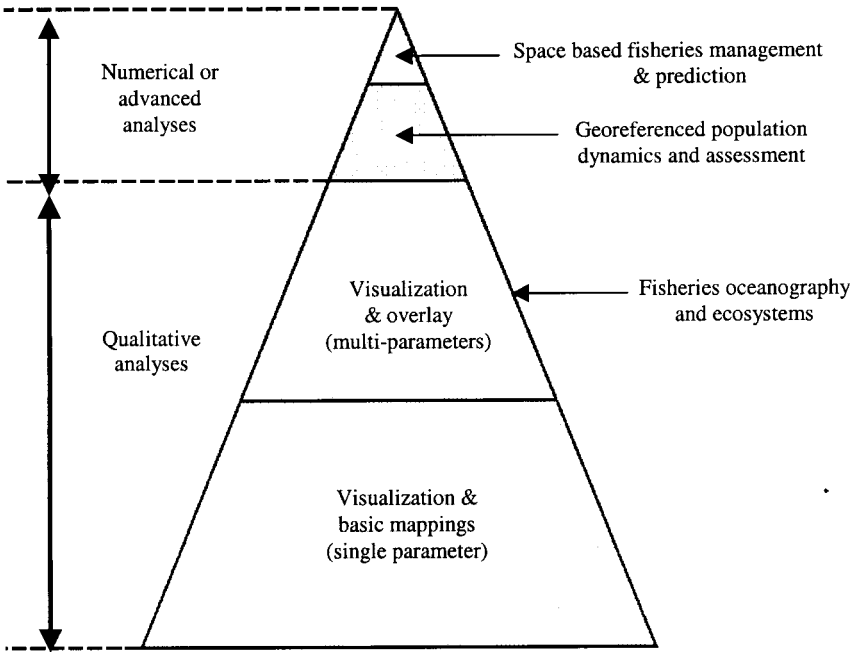


Figure 2. Summary of the current situation of GIS applications in spatial analyses of fish populations. (There are only limited numbers of applications in numerical or advanced spatial analyses, whereas the majority of applications are for qualitative analyses.)

Table 2. Major challenging areas, listed by subject, that can be considered prospects for future GIS application in fisheries resource research (adapted from Meaden 2000).

Data

- Standardization of data collection structures with adjustment for discrepancies in space or time
- Conversion of analog data to digital data
- Consolidation of data gathering and databases
- Automation of data collection
- Establishment of simple database linked to GIS platform
- Consideration of 3D or 4D database for the GIS
- Development of easy method to access oceanography and satellite information
- Development of easy method to process matrix (raster) information

Presentation

- Application of enhanced visualization to fisheries GIS
- Effective and easy way to present 3D and 4D parameters of fisheries and oceanography information such as catch, CPUE, temperature, and salinity

Stock assessment, prediction, and spatial numeral analyses

- Development of linkage between GIS and stock assessment
- Applying GIS methods, models, simulations, and geostatistics in a fluid, dynamic 3D environment
- Development of space-oriented prediction methods for fishing and oceanographic conditions

Fisheries management using GIS

- Space-oriented fisheries management
- Ecosystem-based fisheries management
- Essential fish habitats and marine reserves
- Fishing effort monitoring system using GPS and VMS (vessel monitoring systems)
- Fisheries impact assessment (development of space-based stock assessment)
- Spatial allocation of results of stock assessments such as MSY and TAC
- Monitoring and modeling of quota arrangements

Software

- Development of user-friendly and high performance fisheries GIS software that can handle simple parameters and also satellite information and that can perform simple mappings as well as complex integrated spatial numerical analyses

Human interaction

- Establishment of the international fisheries GIS association for networking to exchange ideas and information
 - Collaborative and interactive GIS activities in fisheries resources research by fisheries scientists, oceanographers, fishers, and fisheries managers for effective, meaningful, and realistic achievements
 - Fostering a trustful relationship between researchers, fishers, and politicians
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Using GIS to Analyze Animal Movements in the Marine Environment

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Abstract

Advanced methods for analyzing animal movements have been little used in the aquatic research environment compared to the terrestrial. In addition, despite obvious advantages of integrating geographic information systems (GIS) with spatial studies of animal movement behavior, movement analysis tools have not been integrated into GIS for either aquatic or terrestrial environments. We therefore developed software that integrates one of the most commonly used GIS programs (ArcView®) with a large collection of animal movement analysis tools. This application, the Animal Movement Analyst Extension (AMAE), can be loaded as an extension to ArcView® under multiple operating system platforms (PC, Unix, and Mac OS). It contains more than 50 functions, including parametric and non-parametric home range analyses, random walk models, habitat analyses, point and circular statistics, tests of complete spatial randomness, tests for autocorrelation and sample size, point and line manipulation tools, and animation tools. This paper describes the use of these functions in analyzing animal location data; some limited examples are drawn from a sonic-tracking study of Pacific halibut (*Hippoglossus stenolepis*) in Glacier Bay, Alaska. The extension is available on the Internet at www.absc.usgs.gov/glba/gistools/index.htm.

Introduction

Studies investigating patterns of movement in aquatic species can be very informative regarding many fisheries management concerns, including population regulation, local depletion, migration, marine reserve design, and habitat selection (Freire and Gonzalez-Gurriaran 1998, Hooge and Taggart 1998, Kramer and Chapman 1999). However, little of the advanced field of analyzing movement patterns, developed for the terrestrial environment (see White and Garrott 1990), has been applied to aquatic species. A literature review of scientific papers about fish and crabs referenced in the BIOSIS Previews® bibliographic database since 1994 indicates that, of 374 articles investigating movement, only 48 examined home range patterns, no study calculated probabilistic home ranges, and none rigorously examined patterns of site fidelity, serial autocorrelation, or sample size effects. This record is in sharp contrast to studies of terrestrial species, in which these analytical methods have been broadly applied, and can partly be attributed to the difficulty of obtaining large sample sizes in the aquatic environment. However, these analytical methods have not been applied even in many movement studies of aquatic species that did have adequate sample size.

Use of analytical methods for studies of movement within a geographic information system (GIS) context has been hampered by a lack of tools. A GIS provides a rich environment within which to analyze movement patterns; it allows the integration of multiple layers of habitat data into a framework capable of complex two- and three-dimensional analysis. In response to this lack of tools, we wrote a program that implements a suite of movement analysis functions within a GIS environment. In this paper we discuss the program and examine methods to prepare data, conduct exploratory data analysis, perform home range and habitat selection analyses, and test other hypotheses. Discussion about much of the methodology is brief, as many of the details are beyond the scope of this paper. We have, however, referenced a wide variety of literature, which workers should peruse before utilizing the program. Data used in examples have been taken from a sonic-tracking study of Pacific halibut (*Hippoglossus stenolepis*) in Glacier Bay, Alaska between 1991 and 1996 (Hooge and Taggart 1998).

The Animal Movement Analyst Extension to ArcView® GIS

Multiple criteria need to be met by software synthesizing movement analysis with GIS. The program must integrate completely with a widely used GIS available on multiple operating systems. It should be able to work with any point data that are otherwise usable by the GIS and to create both raster (grid) and vector (polygon) results in the output data structures of the chosen GIS. It should have a full suite of analysis routines, including

data exploration and animation, home range analysis, spatial statistics, habitat selection, modeling, and hypothesis testing. Ideally this program would be written in an object-oriented programming language that can be extended easily with additional code; it should also make each of its routines available for calling by other parts of the GIS so they can be used in new and unforeseen ways.

The Animal Movement Analyst Extension (AMAE) was written as an ArcView® extension. ArcInfo/ArcView® (Environmental Systems Research Institute, Inc., Redlands, California) is the most widely used GIS throughout the world at this time. The extension capability of ArcView® allows code written in the object-oriented programming language Avenue (and Visual Basic in the near future) to be loaded and unloaded at will from the GIS. While the AMAE would run much faster if written in a language capable of producing compiled dynamic link libraries, doing so would make the program processor-specific. Keeping the code in the scripting language Avenue allows the code to work on multiple operating systems and processors as well as to be modified easily for other uses. By employing as many compiled routines built into ArcView® as possible, the speed of the program on newer computers is quite reasonable. The AMAE is capable of utilizing any point data usable by ArcView® and produces completely compatible raster and vector outputs. It can work on any selected subset of data resulting from queries in ArcView® or other ArcView® extensions. More than 50 functions are implemented in the AMAE (Table 1). All the major functions are written as callable routines that can be integrated into other Avenue programs. The AMAE is in the public domain and is available from the principal author or on the Internet at www.absc.usgs.gov/glba/gistools/index.htm.

Preparation of the Data

Preparing data for the AMAE is relatively easy. The program directly utilizes point shape files, which can import point data from delimited text, dBase files, structured query language (SQL) databases, and many computer-aided design (CAD) and GIS file structures. Data can also be directly digitized onto the screen or through a digitizer tablet. Utilizing the Tracking Analyst Extension® (ESRI) with the AMAE allows the real-time collection of data from GPS units or other data sources. The only fields required for data analysis are X and Y coordinates. The AMAE will work in any projection, but the theoretical underpinnings of some routines require coordinate systems with equal X and Y units; geographic coordinates, which have unequal axis units, can be handled by re-projecting them in the View Window. The AMAE's time-based functions require dates in the dBase standard of yyyyMMdd and time of day in the 24-hour clock format of hours:minutes:seconds. Any attribute data that can be brought into ArcView® can be joined, linked, or embedded within the the AMAE point files and can also be utilized by those functions of the AMAE that employ attribute data.

Table 1. Functions implemented in the Animal Movement Analyst Extension.

1	2	Name of function	Description
V	M	Create Polyline from Point File	Creates a polyline theme connecting points in the order of the records
V	M	Animate Movement Path	Animates the movement path with the user-selected values
V	T	Display Movement Path	Moves through the movement path one position at a time via mouse clicks
V	M	Set Movement Path Variables	Allows user to set the graphics and field display for the two path functions
V	M	Static Interaction*	Analyzes spatial correlation between two individuals without regard to time
V	M	Dynamic Interaction*	Analyzes the simultaneous spatial correlation between two individuals
V	M	Location Statistics*	Generates 38 location statistics and graphical output from point themes
V	M	Nearest Neighbor Analysis*	Conducts a nearest neighbor analysis for CSR in the specified polygon
V	M	Cramer-Von Mises CSR*	Conducts a C-VM test for CSR within the specified polygon
V	M	Circular Point Statistics*	Determines the mean angle, significance, and creates a graphic histogram
V	M	Harmonic Mean Point Theme*	Conducts a harmonic mean home range analysis, producing a point theme
V	M	Spider Distance Analysis*	Conducts multiple types of distance analysis for habitat selection
V	M	Availability Analysis*	Conducts an availability analysis of habitat selection
V	M	Classify Points by Polygons	Classifies each point by the polygon or line on or within which it lies
V	M	Random Selection*	Randomly selects a user-specified number of points
V	M	Outlier Removal*	Removes the user-specified % of points via the harmonic mean method
V	M	Generate Random Points*	Generates several types of random distributions within a Polygon
V	M	Add XY Coordinates to Table	Adds X and Y coordinate fields to the attribute table
V	M	Calculate Successive Distances	Calculates the distance between sequential points
V	M	Calculate Distance	Calculates the distance between a point and all objects in another theme
V	M	Summarize Attributes	Aggregates the attribute table based on the user-specified requests
V	M	Sort Shape File	Permanently sorts the point shape file
V	M	Histogram	Creates a histogram based on a theme's legend classification

Table 1. (Continued) Functions implemented in the Animal Movement Analyst Extension.

1	2	Name of function	Description
V	M	Create Bootstrap File	Iteratively subsamples data (with replacement) using specified sample sizes
V	M	Batch Home Range Processing	Performs the selected home range analysis on multiple point themes
V	M	Minimum Convex Polygon*	Calculates the minimum convex polygon home range
V	M	Kernel*	Calculates a fixed kernel home range with multiple options
V	M	Jennrich-Turner*	Calculates a Jennrich-Turner bivariate normal home range
V	M	Harmonic Mean*	Calculates a harmonic mean home range, but no area
V	M	Delaunay Triangulation*	Generates a TIN between points for a distribution-free home range
V	M	Dirichlet Tessellation*	Generates polygons around points for a distribution-free home range
V	M	MCP Sample Size Bootstrap	Bootstrap test examining the effect of sample size on MCP home range area
V	M	Site Fidelity Test*	Performs a site fidelity test with or without a constraining polygon
V	B	Recalculate Area, Length...	Updates area, length, and circumference in the units of the View projection
V	B	Point Buffer	Creates a buffer shape file of the specified distance around each point
V	B	Delete Graphics	Deletes all graphics in the View
V	T	Display Coordinates	Displays the geographic and UTM coordinates at the specified location
V	T	Nearest Neighbor*	Allows the user to draw a rectangular extent and conduct an NN test
V	T	Random Normal Points	Allows the user to draw a circle and generate a random normal distribution
T	M	Field Properties	Displays the properties of the selected field in the active Table
T	M	Add Record Numbers	Adds the record numbers in either the Table or Vtab order
T	M	Selection to DBF	Exports the selected records to a new .dbf-formatted table
T	M	Create Cumulative Field	Creates a new field with the cumulative total from the selected field
T	M	Histogram	Creates a histogram based on a selected field in a Table

Column 1 indicates whether the function is found within the View document (V) or the Table document (T). Column 2 indicates whether the function is presented as a Menu (M), Tool (T), or Button (B). An asterisk (*) indicates routines with functions that can easily be called by other Avenue programs.

Exploratory Data Analysis

One of the first exercises after entering or importing data into the GIS is to explore some of the general movement patterns of the tracked animals. The point to polyline creation tool produces travel paths (see Fig. 1A), which can then be used in the AMAE's display and animation tools. A movement path can be displayed either one point at a time via mouse clicks or as an automated animation. The user can choose to display the attribute fields associated with each point at the bottom of the screen or in a window next to each point. If there is a date field, distance traveled as well as speed and average speed are also displayed. Animation can be set to run either forward or backward and at various speeds with different types of lines and point symbols. Simple or complex attribute queries can be applied so that travel paths are restricted to certain types of events, such as daylight movements or positions within a particular depth range. Attribute sorting or summarizing routines in the AMAE can also be used to restructure these travel paths. This type of exploratory analysis is helpful for generating hypotheses to be tested and for observing patterns in the data not evident from the point distributions alone.

Home Range

Home range calculation is often performed next. However, a home range is an analytical construct that has biological meaning only when the assumptions of the individual home range model are met and the limitations of the model understood (White and Garrott 1990). For a home range to exist at all the animal must exhibit site fidelity (Spencer et al. 1990, Hooge 1995). We have implemented a robust and powerful test for site fidelity in the AMAE (Fig. 1B). This test is an extension of the Monte Carlo random walk test developed by Spencer et al. (1990). The test has been modified to use the actual sequence of distances traveled by the animal during each observation interval and has also been extended to work within a more realistic world of constrained movements (Hooge 1995). A polygon representing the space within which the random walk test is to occur can be created from any type of spatial data that can be brought into ArcView® (e.g., bathymetry, oceanographic conditions, or substrate; see Fig. 1B). After generating the user-specified number of random walks, the AMAE calculates for each walk both the mean squared distance from the center of activity and the linearity of the path, measures of, respectively, the data dispersion and directed movement. The actual movement path's values are then compared to the ranked values of the random walks to determine significance. To be site-faithful the animal's actual locations should not exhibit significant dispersion. This test can be used, even with small sample sizes, to discern changes in behavior between site fidelity and random or directed explorations by choosing a "time window" and then iterating this test along the entire set of points.

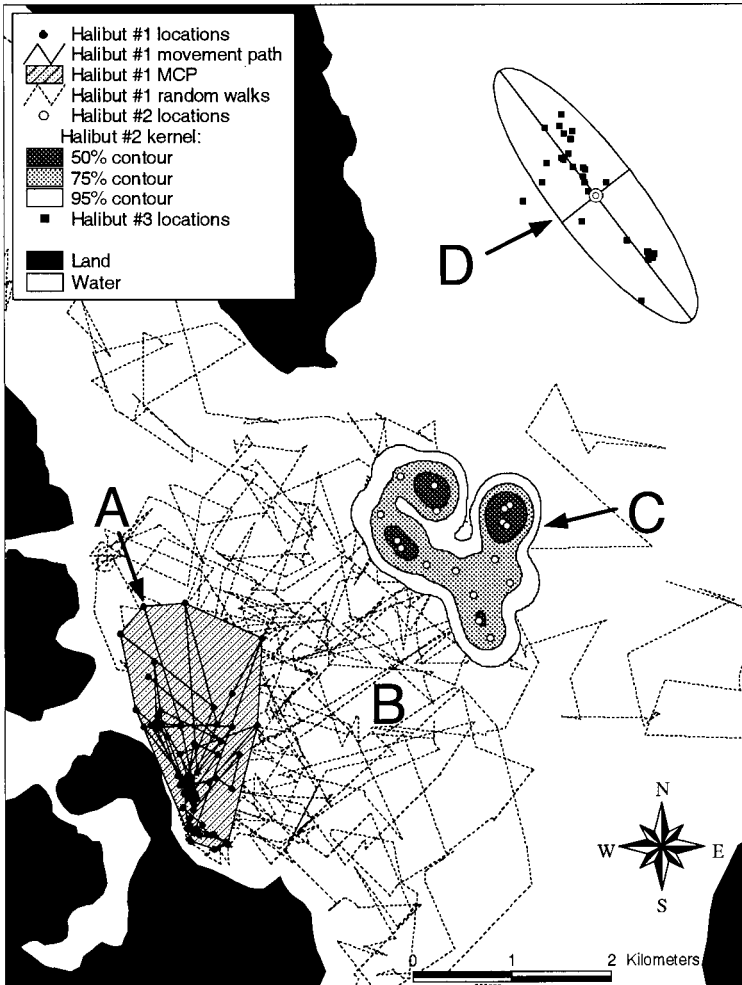


Figure 1. A test for site fidelity (B), with land as a constraining polygon for 10 random walks; and three different home range models: a minimum convex polygon (A), here shown enclosing the actual movement path of the animal tested in (B); a fixed kernel home range (C) with least-squares cross-validation of the smoothing factor, showing the 50%, 75%, and 95% utilization distribution contours; and a Jennrich-Turner 95% ellipse home range (D) with the centroid and the major and minor axes of the data shown. Data are from a sonic-tracking study of Pacific halibut in Glacier Bay, Alaska. Three-year sonic tags were internally implanted into 97 halibut captured on longlines. Individual fish were tracked by a vessel between 1991 and 1996. The points plotted in A, C, and D constitute the positions of three different sonic-tagged halibut in the west-central part of Glacier Bay, tracked daily or weekly over a 5- to 7-month period during the summer of 1992.

If the preliminary analysis indicates that site fidelity exists, the next step is to analyze the animal's home range. A full discussion of the home range concept and of the advantages and disadvantages of different home range methods is beyond the scope of this paper. For details see Burt (1943), Worton (1987), Boulanger and White (1990), and White and Garrott (1990). An assumption common to all home range models is adequate sample size, a criterion that nonetheless varies considerably with the varying methods (Worton 1987, Boulanger and White 1990, White and Garrott 1990). One approach for assessing sample size adequacy is to examine the correlation between home range area and number of location points. Alternatively, the AMAE's bootstrap file creator can be used; the bootstrap generates numerous data subsets by selecting a specified number of points (the selected sample size) randomly and with replacement from the actual observed locations (Efron and Tibshirani 1993). The home ranges of the bootstrapped files can be used to discern the underlying sampling distribution and whether sample size affects home range area. Some other assumptions do exist for certain home range models and are discussed later.

We chose to incorporate several home range models based on their robustness and common usage, and discuss these briefly. The most basic is the minimum convex polygon (MCP, Fig. 1A), which is the area described by the smallest convex polygon that encloses all location points for an animal (Burt 1943). The MCP can be considered as the space that the animal both uses and traverses. We include it primarily to allow comparisons with the many previous studies using MCPs, since it is the oldest and simplest method. However, the MCP is extremely sensitive to sample size, is greatly affected by outliers, and contains much area never used by an animal. Because of the severe sample size effects, the AMAE includes an automated bootstrap test for the MCP to examine the mean and variance of home range area with varying sample size. The outlier effect can be mitigated by removing a certain percentage of points, such as 5%. The AMAE utilizes a harmonic mean outlier removal method, which calculates a distance measure from each point to all other points, removes the point with the largest harmonic mean value, and recalculates after the removal of each point (Spencer and Barrett 1984). Also, with knowledge of habitat relationships, areas can be clipped out of the MCP by ArcView® functions to more accurately represent the areas actually used. However, in order to avoid circular reasoning, habitat analysis should not then be conducted on the resulting altered home range.

Probabilistic home range techniques are better than MCPs for describing how animals actually use the area within their home ranges (Jennrich and Turner 1969, Ford and Krumme 1979, Anderson 1982, Worton 1989). These are often also called utilization distributions; each cell within a probabilistic home range has an associated probability that the animal is at that location. Probabilistic models can be sensitive to serial autocorrelation, and the point statistics function in the AMAE will generate a serial autocorrelation value (the t^2/r^2 ratio, Swihart and Slade 1985). However,

the corrections for autocorrelation may lead to more bias than the autocorrelation itself (see Future Additions). All the home range functions described here allow the user to select the desired probability contours and to produce either vector or raster output. Probability contours enclose the smallest area (as determined by each probabilistic home range method) that encompasses the specified percentage of location points. Larger probability contours (e.g., 95%) more accurately describe the area that the animal actually uses, whereas smaller contours (e.g., 50%) are less affected by deviations from the assumptions of the home range models and therefore are better for statistical comparisons. To expedite analysis, all of the home range methods can be batch-processed in the AMAE using multiple attribute fields to separate different home ranges.

One of the most robust of the probabilistic techniques is the kernel home range (Fig. 1C; Worton 1989), which is based on a nonparametric density estimator. The AMAE implements a fixed kernel with the smoothing factor calculated via least squares cross validation (LSCV), which is widely considered the most robust technique (Seaman and Powell 1996). However, especially with large sample sizes, the ad hoc smoothing factor is often quite close to the value obtained by LSCV, despite its dependence on a normal distribution of the kernels created around each point. The ad hoc value may offer a smoothing factor that is more comparable between studies.

The AMAE also includes the Jennrich-Turner home range (Fig. 1D; Jennrich and Turner 1969), a utilization distribution that is parametric and uses an ellipse to estimate home range. While having the advantages of speed and simplicity, this algorithm assumes the data follow a bivariate normal distribution, a requirement that is often not met by animals in the wild. The random normal point generation tool in the AMAE does allow the user to test the actual point pattern against a random normal distribution with the same axis and variance. The Jennrich-Turner method, like the MCP, is principally useful for comparison with older studies as well as for generating the principal axis of the location data.

The harmonic mean home range method, a nonparametric approach based on the distances from observed locations to a grid of points (Dixon and Chapman 1980), is also included. This technique is especially useful in determining animal activity centers. The AMAE does not calculate area values for the harmonic mean home range, though, as this method is considered less robust than the kernel (Worton 1987).

When sample sizes are very large (thousands of points per individual) and serial autocorrelation is a significant issue, the AMAE provides triangulation and tessellation as two alternative home range models (Silverman 1986). Both techniques calculate the density of location points without any assumptions about the underlying distribution of the data. The Delaunay triangulation builds a triangulated irregular network (TIN) from each point to all other points possible without intersecting such lines from other points. The Dirichlet tessellation creates a polygon around each location such that

all parts of the polygon are closer to the enclosed point than to any other point. To determine density, the output from these routines can be run through AMAE's area calculation tool and then contoured based on inverse area of the triangles or polygons. The triangulation routine is also useful for looking at slope relationships, and the tessellation routine for examining spatial relationships between points and nearest features.

Hypothesis Testing

The ultimate goal of most movement studies is to compare the patterns of observed movement against a null hypothesis to elucidate such processes as habitat selection, relationships between individuals, population dispersion patterns, or marine reserve efficacy. There are multiple hypothesis-testing tools within the AMAE but there are only limited statistical capabilities, with some additional functions available through Spatial Analyst®. However, attribute data created in the AMAE can easily be exported to stand-alone statistical applications, particularly those that readily accept delimited data or dBase files such as SPSS® (SPSS Inc., Chicago, Illinois), SAS®, and StatView® (SAS Institute Inc., Cary, North Carolina). Also, many of the functions in the AMAE can easily be called from Avenue, allowing the creation of hypothesis-specific bootstrapping or Monte Carlo tests.

One of the primary advantages of integrating a GIS with the study of animal movements is the powerful environment available for examining species-habitat relationships. Several functions have been programmed into the AMAE to aid in examining habitat selection. The first of these is the classification tool, which allows animal locations to be classified by the polygon, line, or grid cell on which the points lie. These classified attribute tables can then be exported to a statistical package to conduct the appropriate test (Allredge and Ratti 1992). Not all the habitat that exists in the study area or home range is available to an organism at any particular time. To address this issue we have implemented a modification and extension to the habitat selection algorithm used by Arthur et al. (1996). This availability function uses the movement patterns of the animal to determine the area that could be utilized at each location and then compares these possibilities to the choice made at the next movement. This method is especially relevant when the home range is much larger than the animal's daily movements.

The two methods described above are prone to the loss of both power and robustness when there are significant errors in either the animal locations or habitat polygon mapping (Nams 1989), and such errors are common. For these situations, habitat analysis techniques that utilize either probabilistic home ranges or univariate distance measures are appropriate. The probabilistic home ranges generated by the AMAE can be used to determine habitat selection by comparing the probabilities associated with each habitat type. Alternatively, converting the spatial relationship between the location points and habitat into a univariate distance measure decreases the effect of small locational errors by converting categorical data into a

continuous variable. This distance analysis, named "spider" for the shape of the graphics produced, calculates the distance either between points and the nearest habitat (to either the edge or center of a polygon or line) or between the points and all habitats (Fig. 2). These distance tables can then be exported to a statistical package for parametric or nonparametric analyses of variance.

There are two functions in the AMAE to evaluate hypotheses about directed movement. For movements that appear directed but occur both to and from locations, the site fidelity function can examine either attachment to those locations (with mean squared distance values) or directed movements toward them (with linearity values). To test the significance of one-way movements, circular statistics can be applied; the AMAE produces a graphical circular histogram with mean vector and employs a test for significant circular angle (Batschelet 1981).

Movements of one individual may affect the movements of others through such processes as territoriality, competition, or reproduction. The relationship between the movements of two individuals can be examined for both dynamic and static interaction (Doncaster 1990). Dynamic interaction is the spatial relationship between the simultaneous movements of two individuals. The AMAE implements a moving time-window bootstrap test (Hooge 1995) to determine whether two movement paths exhibit either positive or negative dependence or are random with respect to each other. Static interaction is the comparison of the movements of two individuals without regard to time. This test is accomplished by calculating the correlation between two individuals' probabilistic home ranges (Hooge 1995). For the null hypothesis, random points are generated within the area of MCP home range overlap and are then compared with the actual correlation.

Many spatial hypotheses that users may wish to investigate do not have specific tests available in the literature. The AMAE has multiple tools to create Monte Carlo or bootstrap tests; these can either be used manually at the graphical user interface or they can be strung together by calls in Avenue scripts to build complex analyses. These tools include random point generation functions (utilizing several different distributions; see Fig. 2), random walk functions, and random selection functions, in addition to aggregation and summarizing functions. There are also two tests for complete spatial randomness (CSR) in the AMAE, a nearest neighbor analysis (Clark and Evans 1954), and a Cramer-Von Mises test of CSR (Zimmerman 1993). The point statistics function also produces 38 different statistical values for point patterns, including graphical output of many values (e.g., principal axis, harmonic mean, and geometric mean).

Future Additions

In future versions of the AMAE we hope to provide several commonly requested functions that are not yet available. These include triangulation capability to build point location files from multiple bearings, additional

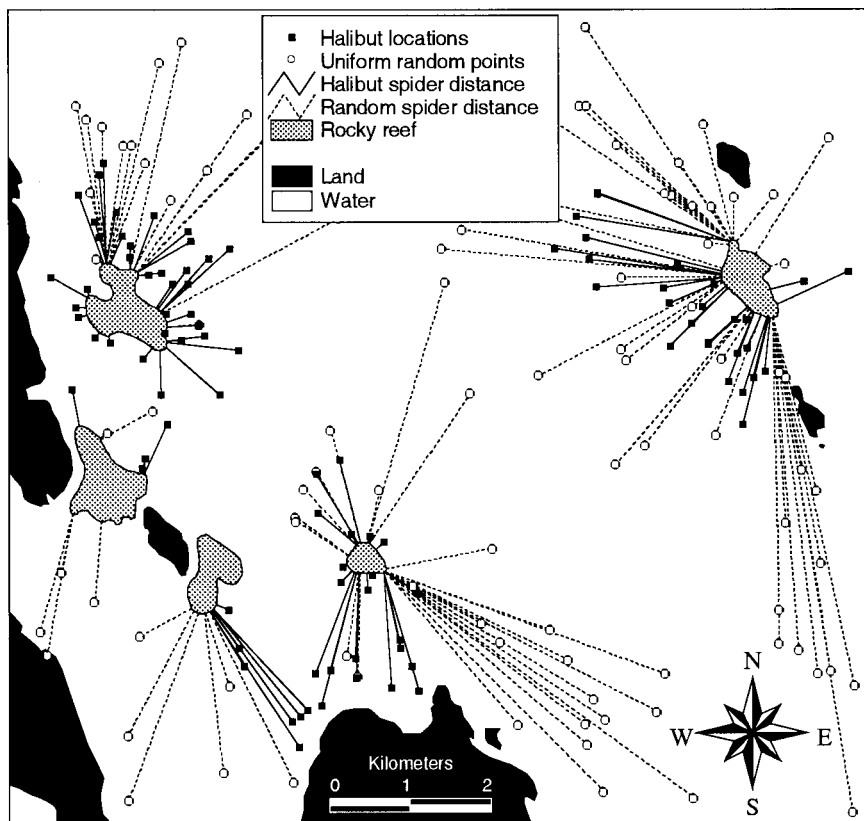


Figure 2. Distance analysis between Pacific halibut locations and rocky habitat found on reef tops in central Glacier Bay, Alaska. The points plotted in this figure consist of 96 randomly selected locations from 24 separate halibut tracked bimonthly for approximately 1 year between 1994 and 1995. Sonic-tagged halibut were located using a grid-search method that covered all of Glacier Bay. The points used in this analysis are not taken from the entire set of points for each individual, but rather include only the points occurring within the selected analysis area. The distance to edge (spider) function was first run on the 96 randomly selected halibut locations; an equal number of random points was then generated uniform-randomly within the study area (in water only), and the spider distance function was run between these random points and the rocky-reef habitat. There was a significant association of halibut positions with these reefs compared to the random locations (Mann-Whitney U, $Z = 6.23$, $P < 0.001$).

habitat selection routines, Fourier home range analysis, more modeling tools, more flexible time formats, tests for serial autocorrelation, and three-dimensional home range methods. We also hope to expand our separate population viability analysis module with spatially specific individual-based modeling tools, in order to integrate individual movement analysis with population-level modeling in the AMAE. We have purposefully omitted a test for serial autocorrelation from the AMAE other than calculating the overall t^2/r^2 ratio. We did so because we believe that such tests, as currently constructed, are flawed and produce a greater bias by excluding points from analysis than that caused by autocorrelation (Andersen and Rongstad 1989, Reynolds and Laundré 1990, Otis and White 1999). We are currently working on more robust methods to detect and address serial autocorrelation. We are also working on extending the home range methods implemented in the AMAE into three dimensions; however, this effort is hampered by the limitations of present three-dimensional GIS systems such as ArcView's® 3D Analyst® (ESRI), which lack the true volumetric capabilities of other programs such as PV-Wave® (Visual Numerics, Inc., Houston, Texas).

Conclusion

The Animal Movement Analyst Extension significantly expands the capabilities of ArcView® GIS into the study of movement patterns and habitat selection. It permits the user to conduct a wide range of spatial analyses and hypothesis testing on movement data taken from observation and from radio-, sonic-, and satellite-tracking data. The AMAE is completely integrated within the GIS environment, allowing complex animal-habitat relationships or movement hypotheses to be examined. The use of a non-compiled language can result in significant processing times for large data sets or for the more numerically intensive routines that cannot take advantage of built-in compiled code. However, the Avenue language permits the program to run on multiple platforms and operating systems and to be extended easily by the user. In addition, the use of batch routines allows processing of large data sets to occur without user input. We hope that the AMAE will help encourage other workers also to produce GIS extensions rather than stand-alone code.

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A Conceptual Model for Evaluating the Impact of Spatial Management Measures on the Dynamics of a Mixed Fishery

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Abstract

While the need for spatial models of fisheries dynamics is widely acknowledged, few such models have been developed for mixed fisheries. This paper presents the approach used to develop a simulation tool that allows exploration of, among other things, the impact of spatial and seasonal management measures. The project involves both fisheries scientists and computer scientists. The simulation model mimics the dynamics of a mixed fishery exploiting demersal and/or benthic resources, and aims at being as generic as possible for broad applicability to different types of fisheries. The dynamics of each population is described by biological parameters and a spatio-seasonal distribution with possible migration between patches. The dynamics of fishing activity is modeled through “métiers” and fishing strategies. Métiers describe the fishing practices at the scale of the fishing operation and are characterized by target species, gear, fishing location, and fishing season. A wide variety of management measures may be explored from this simulation tool; e.g., classical TACs, effort controls, and marine protected areas. The simulator allows for flexibility in several model assumptions; e.g., stock-recruit relationship and selectivity models. Generic functionality is facilitated by the use of an object language.

Introduction

Most fisheries are mixed; i.e., they consist of a number of species (multispecies) exploited either simultaneously or sequentially by fishing units using distinct gears and resorting to different types of fishing activity (multifleets), depending on the time of the year. This results in so-called technical interactions that make it difficult to evaluate the dynamics of both resources and fishing activity. The diversity of fishing activity, associated catch level and catch composition, arises evidently from the variety of fishing grounds exploited, species targeted, and gears used, but also from other factors like individual fisherman behavior, economic considerations, or environmental conditions. Fishermen are generally aware of the large-scale spatiotemporal variation of resources and may allocate fishing effort accordingly. Such spatiotemporal variations include concentrations of some age groups in some areas at certain seasons due to specific events of the life cycle of the species (reproduction, feeding, etc.), and oriented migrations between those areas. In this context, the spatial and seasonal allocation of fishing effort among fishing grounds is of particular relevance to evaluate the dynamics of the fishery. These aspects are all the more important in mixed fisheries since fishermen may switch not only fishing grounds, but also target species and fishing gears. In light of this overall complexity, simulation tools are indispensable for evaluating the dynamics of mixed fisheries, particularly under alternative management scenarios.

Several models of mixed fisheries were published in the last two decades. Murawski (1984), Pikitch (1987), and Mesnil and Shepherd (1990) built diagnostic models to assess the medium-term consequences of an initial fixed allocation of fishing effort per métier. Murawski and Finn (1986) and Marchal and Horwood (1996) developed optimization models to find the fishing effort allocation between métiers or gears that ensures a sustainable exploitation of populations. In the case of an artisanal fishery, Laloë and Samba (1991) used fishing tactics (i.e., métiers) and fishing strategies to describe fishing activity. Laurec et al. (1991) also used métiers, but modeled interannual changes in fishing effort allocation depending on fisherman adaptability to changes in revenues. With the exception of these last two papers, these are equilibrium models in that they evaluate the impact of a fixed allocation of fishing effort, keeping all other parameters constant. Furthermore, they either ignore spatial aspects altogether, or only consider implicitly nonhomogeneous fishing mortalities when computing mortalities per métier for instance. Models that explicitly account for the spatial dynamics of both populations and exploitation are needed to properly explore the dynamics of resources and to assess the impact of spatial management measures. However, few such models may be found for mixed fisheries. Allen and McGlade (1986) modeled the dynamics of the ground-fish fishery of Nova Scotia, but did not use real data. Based on predator-prey relationships, their model is more a theoretical and heuristic tool to investigate the implications of fisherman behavior upon a fishery's dy-

namics. Sparre and Willman (1993) developed BEAM 4, a bioeconomic model initially designed for sequential shrimp fisheries. It is based on two submodels: the first dealing with biological and technical components, which serves to compute the relationship between fishing effort and yield; the second for the economic component to compute various measures of economic performance. The biological and technical model is first run and its outputs form the inputs of the economic model. Given an initial allocation of fishing effort among fleets, the model computes equilibrium projections. Effort-based management measures may be tested by modifying fleet size, fleet selectivity, or the spatial allocation of fishing effort of fleets. Walters and Bonfil (1999) presented a multispecies spatial stock assessment model for the groundfish fishery of British Columbia to test management measures like global TACs, global effort limitation, and permanent closures of fishing grounds. The model considers a number of fishing grounds characterized by their species composition. These stocks are exploited by a single fleet, for which allocation of fishing effort is dynamically determined by the gravity model of Caddy (1975). The population dynamics are made spatial in that subpopulations in distinct fishing grounds mix with one another as a function of species dispersal rate and distance between grounds. There are no oriented large-scale migrations, nor seasonality in the model.

In this paper, we present a simulation tool based on three submodels, namely populations, fishing activity, and management measures. Submodels are coupled through fishing effort and overlaid in space and time. The population dynamics component focuses on seasonal variations in the spatial distribution of resources rather than local mixing. These variations are tied to the life cycle of the species. Fishing activity also exhibits seasonal patterns. It is described as depending on the selection of target species, fishing gear, and fishing ground. The simulation model can be used to assess the relative performances of a range of management measures including TAC, effort limitation, and gear restrictions, defined at either global scale or locally. In addition, the impact of local and temporary closures of some zones may also be evaluated.

The Models

Spatial and Temporal Aspects

The fishery simulator must be able to assess the performance of local management measures as well as global measures. It must include a realistic description of fishing activity within the context of a mixed fishery. A structure and a dynamics that are explicitly spatial and incorporate seasonality are needed for each component of the fishery; i.e., populations, fishing activity, and management measures. This enables us to consider spatial and seasonal control variables for regulating exploitation, e.g., fishing effort and catches.

Models based on patches and migrations between these patches are appropriate to describe dynamics accounting for seasonal and spatial variations. The description of spatiotemporal aspects relies on defining seasons within a year, and zones within a region. A monthly time scale is chosen, hence every parameter is constant within a month. A season is a set of successive months. A region is the area where the fishery takes place. Based on a map of this region, a regular grid is constructed using a spatial step separately chosen for latitude and longitude scales. Each zone is a set of contiguous cells. Seasons and zones are defined independently for each entity of the fishery; i.e., each population, each fishing activity, and each management measure. At a given month, each population or fishing activity is present in one or several zones, and this spatial distribution is specific to a season. Management measures may be applied to specific zones during certain seasons. Within each zone, processes are assumed to be homogeneous. Hence, a population is uniformly distributed over the cells of a zone in a given month. Similarly, fishing effort exerted by a fishing activity at a given month is uniformly allocated over the cells corresponding to its fishing grounds at that time. Because population zones may not entirely match fishing zones, it is necessary to account for the intersection between those zones. Hence, we assume that for a given population, the fishing mortality in a given population zone, induced by the effort allocated in a fishing zone intersecting that population zone, is proportional to that effort prorated by the area of the intersection between these two zones. An analogous assumption is made to calculate the impact of a spatial management measure upon fishing effort. To be able to make corresponding computations, any information relative to a zone is also associated to each cell of this zone.

The spatial resolution of the model may be initially chosen according to the spatial scale at which scientific and commercial data are available, and depending on existing knowledge about the fishery.

Population Dynamics

To allow for the existence of several populations of the same species in a given region (which may for instance occur in the case of shellfish stocks), the concept of metapopulation (Pulliam 1988) is introduced. In this version of our model, a metapopulation is a set of populations of the same species inhabiting the region of the fishery. In contrast to the usual metapopulation terminology in which populations are coupled by larval dispersion, the dynamics of each population are independent. This restriction may be relaxed in future versions. For each metapopulation, the model is either age- or length-structured. Each population has specific biological parameters; i.e., minimum and maximum ages or lengths, age or length at maturity, natural mortality, growth and length-weight parameters, and individual fecundity coefficient. Maturity is assumed to be knife-edge. A “stock-recruit” relationship describes the number of juveniles produced by the

mature stock. Seasons are defined separately for reproduction and for recruitment.

The model considers large-scale oriented migrations that happen seasonally. Populations may migrate either between zones within the region, or outside of the region (emigration). Immigration from abroad is also possible. These migration events delimit population seasons and are supposed to occur instantaneously at the beginning of each season. Age- (or length-) specific migration coefficients are defined for each season. Thus, given an initial spatial distribution for each age or length class, the spatial distribution varies seasonally. Reproduction is assumed to occur instantaneously, after possible migrations, at the start of each month of the reproductive season. Natural mortality and fishing mortality take place each month after migrations and reproduction. In this paper, catchability per zone and season is the probability that a fish present in the zone at that season will be caught by a standardized unit of effort, sometimes called availability. The seasonal catchability of a population is thus a vector of average age-specific coefficients (averaged over the zones relative to that season). It is further assumed that a fish present in a set of zones at a given season may be caught in any of the corresponding cells with equal probability. This implies that the catchability in each zone is the average catchability reweighted by the surface of the zone. This assumption enables us to account for concentration effects in small zones. The catchability of juveniles is zero from birth until the recruitment season.

Finally, in the age-structured case, a population undergoes each month the following succession of events (Fig. 1):

1. Change age class (if the month is January).
2. Migrate and emigrate (if the month is the beginning of a season), and recruit (if the month belongs to the recruitment season).
3. Immigration.
4. Reproduce (if the month belongs to the reproduction season).
5. Survive natural and fishing mortality.

Survival rates to natural and fishing mortalities are modeled using the exponential decay model. Animals are counted at the beginning of the time step.

Fishing Activity

Each fishing gear is characterized by a parameter (either numerical or categorical) with an associated range of values and a selectivity model for each population that can be caught by the gear. The selectivity parameters depend on the gear parameter. In the case of mesh gears, a selectivity factor allows calculation of selectivity parameters as a function of mesh

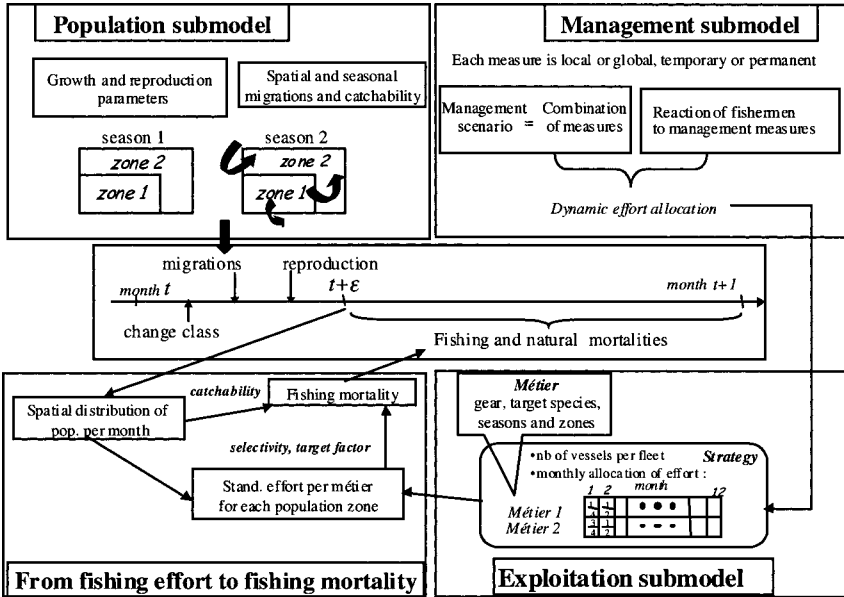


Figure 1. Structure of the model with the three submodels: population dynamics, fishing activity, and management.

size. The gear is also characterized by the unit of effort and a standardization factor. This factor is particularly relevant for mixed fisheries, since it is necessary to calibrate fishing effort among gears. Note that the value of the gear parameter can change according to management measures.

Fishing activity is modeled at several scales. At the fishing operation scale, the "métier" (Biseau and Gondeaux 1988) is usually defined by the combination of target species, fishing gear, and fishing ground, at a period of the year. In our model, a métier is hence characterized by a gear with an initial value of its parameter, one or several target species, a maximum number of fishing operations per day, and seasons. Each season corresponds to a specific spatial allocation of fishing effort, which means that at a given month the métier is only practiced in certain zones. A travel time directly impacting the time spent fishing is associated with each zone. When there are several zones at a given season, an average travel time is associated with the season. To distinguish target species from incidental species, a target factor is defined per population for each métier. It quantifies the fact that a métier usually targets some species more than others. The target factor is assumed to depend on the season, but it does not depend on the age class of the species.

At the scale of the year, the fishing strategy is characterized by the succession of métiers used throughout the year. Structuring fishing activity by strategies follows from the observation that, in mixed fisheries, fishermen often participate in several métiers during the year to take advantage of seasonal variations in the abundance of certain species. In our model, each strategy is characterized by a list of métiers for each month, and by a vector of proportions that yields the effort distribution of fishing units between these métiers. Each strategy is practiced by a number of fishing units of each fleet, and in each strategy, a proportion of fishing units in each fleet is allowed to change fleets. Individual fishing units are not identified, but arranged in fleets according to the duration of fishing trips which results in a maximum monthly fishing effort per fishing unit for each fleet. The fleet roughly describes the spatial range of exploitation through the duration of fishing trips. Since fishing units are assumed to be equivalent, no individual fishing power is considered, and fishermen are assumed to be working at full capacity all year long.

Relationship between Fishing Effort and Fishing Mortality

At a given month, catch and abundance in numbers for a given population are computed from the fishing mortality per age (or length) class and per population zone. This mortality is directly deduced from the standardized fishing efforts calculated per métier and per population zone, for all the métiers catching the population (Fig. 1). Indeed, fishing mortality results from multiplying catchability by the average mean of these efforts weighted by the product of the gear selectivity and the target factor for this population.

Standardized fishing effort per métier and population zone for a given month is computed as follows:

- For each fleet, compute time spent at fishing in hours per fishing unit, in each métier zone associated to that month, subtracting the travel time corresponding to that métier zone from the maximum monthly fishing effort of the fleet.
- For each fleet, compute fishing effort per fishing unit in each métier zone, in standardized effort units corresponding to the métier gear.
- For each strategy, compute fishing effort in each métier zone, accounting for the proportion of each fleet's effort that practices this métier during this month, and for the number of fishing units of each fleet in the strategy.
- Calculate fishing effort per cell for each métier zone.
- Deduce fishing effort per population zone according to the intersection between the population zone and the métier zone at this month.

Management Measures and Associated Fisherman Behavior

A range of management measures is considered in the model. Any measure may be defined either for the entire region (global measure), or for a specific zone (local measure). Measures include total allowable catch (TAC), total allowable effort (TAE), maximum fleet size, limitation of the number of permits per métier, limitation of trip duration, gear restriction, and gear prohibition. In the case of local management measures, there are three additional cases: total closure of the zone and prohibition of fishing for some populations or for some métiers. Every kind of management measure is defined by the zones and the seasons of application, and by an implementation procedure specifying which variables are affected by the management measure and how they are affected.

Exploring the impact of management measures is likely to go wrong if the reaction of fishermen to these measures has not been included in the model. Obviously, identifying these reactions is a difficult question. They could, for instance, be modeled as a function of previous catch, effort, or species profitability. Or they might be assessed from the analysis of real data. In the prototype version of the model, we tried to implement reactions that are as neutral as possible. For instance, in the case of a global TAC, a possible consequence of reaching the TAC could be to generate discards if the species is not the main target of the métier. However, if it is a main target, then the fishing units practicing that métier should switch to another one. In the case of a local closure, any métier such that the intersection of its zone with the closed zone is not empty will be affected by the management measure. These reactions result in a dynamic allocation of fishing effort (Fig. 1).

Input Information for the Model

Given the complexity of the model, it is unlikely that the simulation tool will include any fitting procedure. Therefore, model parameters are to be taken either from the literature, or from side studies directed at parameter estimation. The simulator is thus a tool for integrating data and existing knowledge about a fishery. A first step in applying the simulator to a given fishery thus consists in gathering available parameter estimates for the model. Classical biological parameters, as well as gear parameters and selectivities, are usually available in the literature. Other parameters must be estimated from additional data analyses. For instance, the spatio-seasonal distributions of populations and associated migration parameters will need to be quantified. Methods are currently being developed to evaluate such distributions from commercial and scientific data (M. Verdoit, Lab. MAERHA, IFREMER, Nantes, France, pers. comm. [Ph.D. thesis preparation]). Regarding fishing activity, Pelletier and Ferraris (2000) proposed an approach to determine métiers from commercial logbook data. Once métiers are defined, fishing strategies may be deduced from the analysis of yearly time series of fishing

operations. Standardization factors and target factors per métier may also be evaluated from the analysis of logbooks or landing data, for instance using linear models (Stocker and Fournier 1984, Pascoe and Robinson 1996). The design of appropriate statistical models for this purpose is under study (Biseau et al. 1999). Note that as far as possible, we tried to define the components of our model so that model parameters may be estimated from the types of data generally available in fisheries; i.e., commercial logbook data, scientific surveys, observer data, and fishermen interviews.

Software Aspects

Development Constraints

A number of specifications were imposed regarding the use of the fishery simulator and its design.

First, the simulator should be both rapidly configurable by expert users, and accessible to non-modelers. The former will use it as an exploration tool to gain some insight in the dynamics of mixed fisheries and evaluate its outcomes under alternative management scenarios. For the latter, it may be a tool to help decision-making through simulation gaming. Therefore, the simulator may be utilized either from input files containing the data and the parameters of the simulation, or from a user-friendly interface based on dialog boxes. In both cases, the outputs of the simulation may be viewed on a map of the region or as time series plots. Several graphics may be visualized at the same time, and the user may choose a range of variables to map or plot, e.g., catch or effort per métier. The main parameters of the simulation may also be recalled in a control panel.

Second, entering the data requires an efficient graphical user interface. Given the models presented above, the amount of information required to properly describe a mixed fishery is substantial. In addition, even in well-known fisheries, there always remain uncertainties about some parts of the dynamics, so that several alternative hypotheses have to be considered. Investigating a single management scenario thus requires several simulations. To avoid repetitive inputs for successive simulations, the simulation tool is coupled with a database that is permanent, modifiable, and updatable. This database (the main database) comprises several subdatabases, each of which contains all the information relative to a fishery (fishery database). These include not only the parameters relative to each element of the fishery, but also equations to model, for example, growth, selectivity and the stock-recruit relationship. The main database also comprises a reference database which contains information that may be shared by fishery databases.

Third, the simulator must provide flexibility in the equations modeling the dynamics and allow for the integration of new equations and new models to the extent possible. The tool may then be generic and applicable to many groundfish fisheries. This flexibility also makes it possible to

interactively modify the description of the dynamics, as further knowledge and information about the components of the fishery become available. Note that the knowledge of the dynamics of the populations and even more so the dynamics of mixed fisheries are constantly evolving, due to increases in available information, new research, and technological and economic changes. The objective of a generic and flexible tool leads us to choose a language and to develop an editor and an interpreter of equations associated with the simulator. The interpreter should accept mathematical equations as well as algorithms, i.e., decision rules, and stochasticity. New equations are to be stored in the reference database. This option is available for the growth model, the length-weight relationship, the relationship between female fecundity and individual length, the stock-recruitment relationship, the selectivity model, and the reaction of fishermen to management measures. An object language makes it easier to add new entities to the fishery, like populations, métiers, or management measures. Thus, the simulator allows for an arbitrary number of populations, fishing activities, and management measures to be modeled.

A last important specification for the simulator is the ability to evolve at the same time as the underlying dynamics are modified and new processes are considered. Note that the choice of an object language avoids to some extent major redefinitions of the computer code. In addition, it seems desirable that every user of the simulator may access its most recent version rapidly, should not need other software to run it, and may use it from any platform. The solution found to meet these constraints is to store the simulator tool in the place where it is developed and to allow a remote access via internet or intranet. All these reasons motivated us to develop the simulator with the Java language. Another advantage in using Java is the availability of numerous standardized libraries, in particular regarding graphics and interface.

Current Status of the Software

A simplified version of the software was implemented using the Java Development Kit version 1.2. The development of the fishery dynamics (populations and fishing activities) is based on matrix equations. Only age-based population dynamics were implemented. The present version of the tool comprises an interpreter of equations supporting usual mathematical functions. Regarding the interface, all the dialog boxes relative to the region, the metapopulation (population, biology, migration), and the fishing activity (fleet, gear, métier, strategy) were coded, but their connections with the input database are not totally finished. However, a parser was constructed to allow direct inputs through a data file.

Several simplifications of the model had to be done in the prototype due to a limited time for developing the software. Population dynamics were not coded for length-based equations. Management measures were not integrated yet, nor the reaction of fishermen to these measures. The interpreter of equations does not yet accommodate algorithms nor

stochasticity. At this stage and given the different priorities of development, the tool is not yet available on the web.

The simulation tool was tested and validated using the saithe fishery for which the dynamics were modeled by Pelletier and Magal (1996). This example is very simple in that it is a single species exploited by two métiers. However, the dynamics of population and fishing activity are spatial and seasonal, which is the main feature of our model. The validation step required us to reparameterize the initial model using the variables and the time step of the mixed fishery model, so that the results could be reproduced with the simulator.

Discussion and Conclusion

No real application to a mixed fishery was yet entered in the prototype, so that the interest of the tool for testing management measures in such a context cannot be displayed to date. Nevertheless, the model may be compared with models that are available for mixed fisheries, in particular those of Walters and Bonfil (1999) and BEAM 4 (Sparre and Willman 1993).

Comparison of Fisheries Models

Concerning population dynamics, BEAM 4 also models seasonal migrations at a large scale, and in addition, implicitly considers depth and vertical migrations by defining particular zones. In contrast, Walters and Bonfil (1999) are interested in modeling nonoriented dispersion-like movements. In the latter, seasonal aspects are not taken into account. None of the models account for stochasticity in the equations and the dynamics may not be interactively modified.

Fishing activity is not structured in the model of Walters and Bonfil (1999), who consider a global fishing effort distributed between fishing grounds. But, at each time step, effort is reallocated between fishing grounds as a function of the cost and gross income associated with each ground. On the contrary, in BEAM 4, fishing activity is composed of fleets that differ through their selectivity and their spatial allocation of effort. In BEAM 4, the spatiotemporal allocation of fishing effort is fixed. In its present version, our software is similar to BEAM 4 in that it computes projections from an initially fixed spatiotemporal allocation of fishing effort. In the next version, the implementation of fisherman reactions to management measures will result in temporal changes in this allocation.

With respect to spatial aspects, these two models assume that fishing grounds match population zones exactly, which are thus common to all populations. In our approach, zones are defined independently for each population and for each activity. We believe this is more appropriate for mixed fisheries since populations do not have the same spatial and seasonal distributions. In addition, the spatial allocation of fishing effort for a given métier may not be tied to a single target species: it may depend on other species and other factors as well.

With respect to management measures, our model allows for free specification of management zones, which makes it possible to design areas with partial or total restrictions to fishing that may or may not match fishing grounds. Besides, several management measures may be applied simultaneously to the fishery. A combination of several management measures is indeed more realistic, and is more likely to be efficient at regulating exploitation in mixed fisheries.

Software Aspects

We believe the specifications set on the development of the software are quite innovative in fisheries science, and in population dynamics in general. Often, simulation tools are developed for a given context and may not be adapted to other fisheries. Alternatively, the description of the fishery may not be changed without rewriting parts of the code. Our prototype is flexible, thus quite generic. This is made possible by the object language, and the editor/interpreter of equations, but also because the fishery model comprises three relatively independent components which are coupled at a given time step of the simulation by the spatial support, i.e., the cell.

Perspectives

We presented a preliminary prototype, to which several features obviously need to be added. The first step in this process is the coding of management measures and fisherman reaction to these measures. Fisherman reactions will be modeled under the form of decision rules based on catches, métiers, gear, and strategies. They may be diverse and fishery-specific. Simple decision rules will be first coded. For a given fishery, additional reactions may be inferred from the analysis of commercial data, fisherman interviews, and other sources. Regarding population dynamics, sex-specific and length-based models need to be coded. Also, within-year growth should be made possible as it is indispensable for fast-growing species. In addition, the next version will allow for maturity ogives in the computation of reproduction. From the software standpoint, forthcoming developments will be based on Enterprise Java Beans, which enable a utilization of the software on the Web. The second step is the application to a mixed fishery. Most of the information relative to the Celtic Sea groundfish fishery has already been compiled, and analyses for the spatial and seasonal distribution of populations and fishing effort are under way. An application to a French coastal fishery is in preparation too.

In later versions of the software, we also contemplate adding new features in the fishery model. First, it seems desirable to incorporate a stock assessment module that will allow for feedback management strategies to be tested. This module could be a standard model like VPAWIN (Darby and Flatman 1994), that may be called by the software. Second, we would like to account for fishing units, so as to consider fishing powers, and to refine effort dynamics to allow for the dependence of effort upon variables like

previous catches for example. This would make effort dynamics closer to that of Walters and Bonfil (1999). It follows from previous extensions that it would be necessary to introduce some economic considerations, e.g., seasonal variations in species prices, since they strongly influence fisherman decisions. Last, other types of population movements may be included. The present model is mainly valid for demersal and benthic populations. For instance, dispersion and shorter-term movements would yield another insight in the dynamics. Note, however, that such nonoriented movements somehow blur the dynamics induced by the dependence of fishing effort allocation upon the spatiotemporal distribution of targeted populations.

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Evaluating the Scientific Benefits of Spatially Explicit Experimental Manipulations of Common Coral Trout (*Plectropomus leopardus*) Populations on the Great Barrier Reef, Australia

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Abstract

A simulation approach is used to evaluate the likely scientific benefits of experimental manipulation of fishing mortality on the Great Barrier Reef, Australia. The Effects of Line Fishing (ELF) Project commenced in 1994, with the first round of manipulations conducted during 1997-1998. The experimental design involves 24 reefs arranged in four clusters of six reefs spanning 7 degrees of latitude. The experiment includes spatial replicates of individual reefs and explicitly manipulates fishing mortality at the level of individual reefs to be able to distinguish fishing from natural effects. The benefits of the experiment are measured in terms of the bias and variance of estimates of quantities needed to develop a model to evaluate alternative spatially explicit management strategies for common coral trout, *Plectropomus leopardus*, on the Great Barrier Reef. The estimator considered is a variant of the Deriso (1980) delay-difference estimator. The benefits of the 1997 manipulations and future data collection in terms of the ability to estimate biomass and fishing mortality are demonstrated clearly.

The magnitude of the benefits of additional manipulations in 1999 are smaller and depend on whether it will be possible to encourage fishers to increase fishing pressure for 12 months on the northernmost reefs and the reefs that are already open to fishing.

Introduction

The Great Barrier Reef (GBR) extends over approximately 15 degrees of latitude and ranges from 10 to 120 nautical miles off the mainland coast of Queensland, Australia (Fig. 1). The bulk of the area is a declared Marine Park and World Heritage Area comprising approximately 350,000 km² and over 3,000 reefs and shoals. The primary conservation management strategy is one of zoning areas for different levels and types of human use. Zones range from no-access and “look but don’t touch” to fishing and harvesting. Fishing, including line fishing, is a long-standing activity in Great Barrier Reef waters. Line fishing in the region comprises extensive commercial, recreational, and tourist (charter vessel) sectors, all using roughly similar gear (single baited hooks on handline or rod and reel). Management of line fishing on the GBR has, however, been hampered by a shortage of information about fishing activities and their effects (Mapstone et al. 1997).

A simulation model for the coral trout, *Plectropomus leopardus*, fishery on the GBR is being developed that includes biological, economic, and management components. This model will have to be spatially as well as temporally explicit to capture the essential dynamics of the coral trout resource and its harvest. This development follows the trend elsewhere towards the use of simulation models to evaluate the implications of changed management arrangements, including the use of feedback control harvest regimes (Walters et al. 1992, Smith 1994, Walters 1994, Punt and Smith 1999). The simulation model will be used to evaluate management strategies based on effort controls, spatial closures, etc. Although the line fishery on the GBR is based on over 125 species, common coral trout makes up at least 45% of the catch by commercial fishers, and probably slightly less of the recreational catch (Mapstone et al. 1996a, 1997). Attention has therefore been focused solely on developing a simulation model to assist with management of this species only. In time, attention may be paid to including other key target species (e.g., red throat emperor, *Lethrinus miniatus*) and broader ecosystem factors in the simulation model.

It is generally straightforward to develop the mathematical specifications for a simulation model. For standard fisheries applications, such models can be parameterized from the results of stock assessments (e.g., Butterworth and Bergh 1993) although it is common for the values for many of the parameters of a fisheries simulation model to be simply guesses based on “expert judgement” (e.g., Starfield and Bleloch 1991, Walters 1994). The parameterization problem can become particularly severe for situations when there are many fleets, the fishery is based on many stocks, and there are few data on which to base parameter estimates, as was (and to a

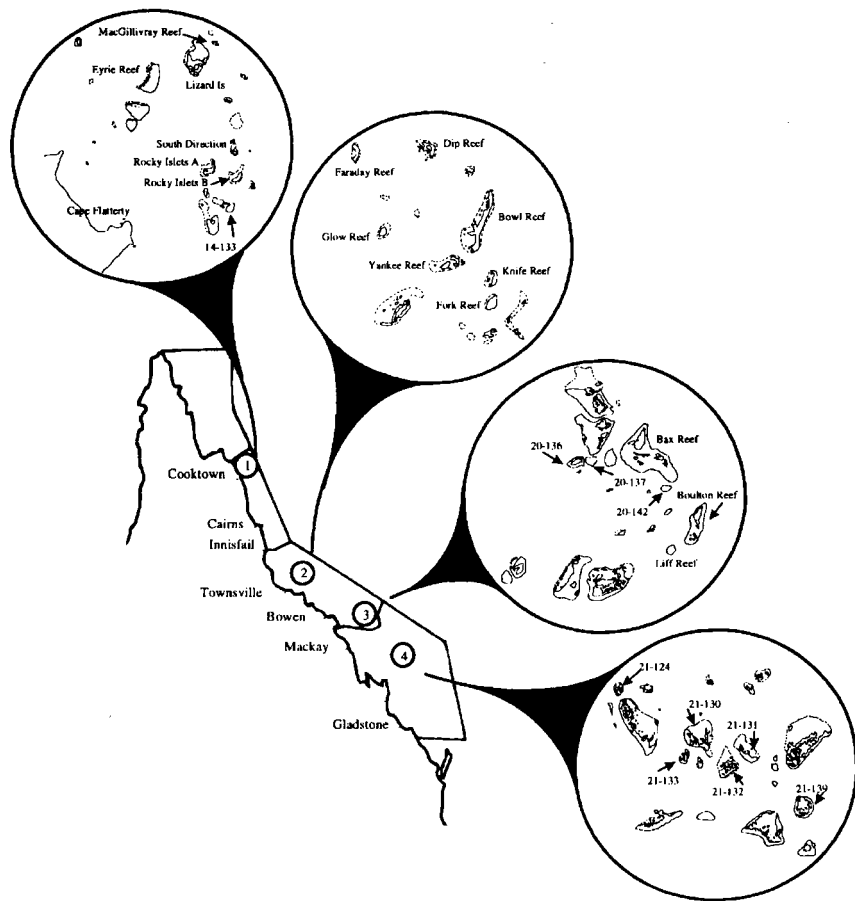


Figure 1. Map of eastern Australia, showing the Great Barrier Reef and the locations of the four experimental clusters of coral reefs.

large extent remains) the case for coral trout on the GBR. To assist in the parameterization of the coral trout model, a large scale manipulative experiment (the ELF Experiment) was designed (Walters and Sainsbury 1990, Mapstone et al. 1996b) to provide, through deliberate manipulation of fishing pressure and reef closures (to fishing), field data from which estimates could be derived for the following quantities:

1. Reef-specific population size.
2. The catchability coefficient.
3. Fishing mortality and natural mortality.

Estimates for these quantities could then be extrapolated spatially using ancillary data to provide values for some of the key parameters of the simulation model for the entire Great Barrier Reef. These estimates are, of course, not the only source of information for parameterizing the simulation model, there being extensive data on growth (Brown et al. 1994, Ferreira and Russ 1994), gear selectivity (Fulton 1996), movement (Davies 1995, James et al. 1997), and maturity (Brown et al. 1994, Ferreira and Russ 1994, Russ et al. 1996, Adams et al. 2000).

The paper explores the likely ability of the ELF experiment combined with a specific method of analyzing its results (referred to as an estimator) to estimate the above three quantities. Uncertainty about the estimated quantities will have to be reflected in the final simulation model outcomes, the precautionary principle implying that the greater the uncertainty, the more precautionary management should be. In this paper we explore this approach by developing a simulation testing framework to address a number of key questions regarding estimation ability. Although several estimators were considered, the paper reports results for one class of estimator only to enable general principles to be highlighted. The choice of estimator is explained later in the paper.

The paper proceeds by outlining the ELF experiment and the basic simulation framework. The details of the model used in the simulation framework, the approach used to measure estimation ability, and the questions which the framework is used to address are described next. Finally, the estimators considered in the study are described and the basis for the choice for the class of estimators that is the focus of this paper is provided.

Methods

Overview of the ELF Experiment

The experiment is facilitated by the spatially fragmented structure of the Great Barrier Reef and the use of spatial closures for conservation management in the region. The experiment involves 24 individual platform reefs spanning 7 degrees of latitude or approximately half the length of the GBR (Mapstone et al. 1996b). The 24 reefs are grouped into four "clusters" (Liz-

ard, Townsville, Mackay, and Storm Cay), each consisting of six reefs (Fig. 1). Four reefs within each cluster have been closed to fishing for 10-12 years, as part of the Great Barrier Reef Marine Park's spatial zoning system (closed reefs) while two have always been open to fishing (open reefs). Two of the closed reefs in each cluster remain closed to fishing (except for research line fishing surveys) throughout the experiment to serve as controls for the experimental treatments. The other two closed reefs in each cluster are opened to "at will" bottom line fishing for 1 year (pulse fishing) and are then closed again. The two open reefs in each cluster are subject to increased fishing pressure (pulsing) for 1 year each, and then closed to further fishing for a period of 5 years. The geographic scope of the experiment and replication of treatment reefs within each cluster should allow estimation of regional variation in the biological characteristics of several main and secondary target species and regional variation in the responses to changed fishing practices (Mapstone et al. 1996b, 1998). Replicate treatments have been implemented in a step-wise fashion in order to incorporate, as far as possible, interannual variation in response. Applying different treatments (closed, open, pulsed) in different years (see Table 1) should allow the impact of fishing-induced effects to be distinguished from natural impacts while also controlling for the perversities of interannual variation in ambient conditions. The first round of experimental manipulations occurred from March 1997 to March 1998, following two years of "baseline" monitoring of all experimental reefs (Mapstone et al. 1998). The second round of manipulations commenced in March 1999 and will be complete in March 2000.

Simulation Protocol

Monte Carlo simulation is used to compare scenarios in terms of the ability to estimate several key model quantities. This evaluation process has a long history in fisheries (e.g., Hilborn 1979, de la Mare 1986, Punt 1989) and involves the following basic steps:

1. Construction of a number of operating models. An operating model is a mathematical/statistical model of the fishery. Each operating model reflects, *inter alia*, an alternative (yet plausible) representation of the status and productivity of the resource. Linhart and Zucchini (1986) define an operating model to be "the nearest representation of the true situation which it is possible to construct by means of a probability model." The operating model is used to generate the simulated experimental data sets.
2. Running the simulations; 500 simulations were run for each scenario, with each simulation involving the application of an estimator to one of the artificial data sets.
3. Summarizing the results of the simulations.

Table 1. The experimental design used for the “ideal” scenarios.

Treatment	1995/6	1997	1998	1999	2000	2001	2002	2003	2004	2005
Closed Control-1 (CC ₁)	C/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C
Closed Control-2 (CC ₂)	C/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C
Closed Fished-1 (CF ₁)	C/C	C/P	P/C	C/C	C/C	C/C	C/C	C/C	C/C	C/C
Closed Fished-2 (CF ₂)	C/C	C/C	C/C	C/P	P/C	C/C	C/C	C/C	C/C	C/C
Open Pulsed Fished-1 (OPF ₁)	O/O	O/P	P/C	C/C	C/C	C/C	C/C	C/O	O/O	O/O
Open Pulsed Fished-2 (OPF ₂)	O/O	O/O	O/O	O/P	P/C	C/C	C/C	C/C	C/C	C/O

Table entries are C: reef closed to fishing; O: reef open to fishing; P: reef pulse fished. The first symbol in each cell represents the management regime for January to March in the year indicated in the column header and the second symbol reflects the management regime for April to December in the same year.

Overview of the Operating Model

The operating model (Appendix A) is based on that developed by Mapstone et al. (1996b), which was in turn based on that used by Walters and Sainsbury (1990). This model is similar to that which will form the basis for the simulation model to be used to provide management advice but has been tailored for the specific problem of testing estimators. It represents the population dynamics of several “stocks” of common coral trout, each associated with a specific reef. The population dynamics model is age-, sex- and size-structured, assumes that the number of 0-year-olds is related to the size of the reproductive component of the population according to a Beverton-Holt stock-recruitment relationship, and allows for larval movement among reefs. Post-settlement movement is assumed to be zero as adult coral trout do not appear to move large distances or between neighboring reefs (Davies 1995, Zeller 1997).

The animals of each age are divided into “groups” at birth and all animals within a group are assumed to grow according to the same growth curve. This allows variability in growth and population size structure to be modeled reasonably parsimoniously. The age and size structure of the population on each reef at the start of the simulated experiments is determined by projecting the population forwards for 30 years from unexploited equilibrium with random variation in recruitment and natural mortality. During the experiment, fishing mortality on each reef depends on its “open,” “closed,” or “pulsed” status (equation A.13). The data generated for each experimental reef (Appendix B) are: catches (by mass), fishing effort, indi-

Table 2. The sampling strategy for each cluster.

Treatment	1995	1996	1997	1998	1999	2001- 2005
CC ₁	0 0 0 2	0 1 0 2	0 1 0 2	0 1 0 2	0 1 0 2	0 1 0 2
CC ₂	0 0 0 2	0 1 0 2	0 1 0 2	0 1 0 2	0 2 2 2	0 1 0 2
CF ₁	0 0 0 2	0 1 0 2	2 2 2 2	0 1 0 2	0 1 0 2	0 1 0 2
CF ₂	0 0 0 2	0 1 0 2	2 2 2 2	0 1 0 2	0 2 2 2	0 1 0 2
OPF ₁	0 0 0 2	0 1 0 2	2 2 2 2	0 1 0 2	0 1 0 2	0 1 0 2
OPF ₂	0 0 0 2	0 1 0 2	0 1 0 2	0 1 0 2	0 2 2 2	0 1 0 2

The four sampling times are taken to be mid-March, mid-May, mid-August, and mid-November. A zero implies no sampling, a 1 represents that only an underwater visual survey was done, and a 2 indicates that both an underwater visual survey and a research line fishing survey occurred. The surveys planned for March 1997 were cancelled due to the presence of Cyclone Justin. The research line fishing surveys on MacGillivray Reef (CF₂), Lizard Island cluster, in November 1997 did not take place because of bad weather.

ces of relative abundance from underwater visual surveys (UVS) and research line fishing surveys, and estimates of the age composition of the catch from the research line fishing surveys. Account is taken of the apparently variable success of attempts to pulse the “manipulation” reefs during 1997-1998 (Mapstone et al. 1998). In particular, all of the analyses assume that the attempt to “pulse” the reefs CF₁ and OPF₁ (Table 1) for the northernmost (Lizard) cluster failed and this was also the case for the attempts to pulse the OPF₁ reefs for the three other clusters. This represents a “worst case” interpretation of the available data because there is some evidence that the OPF₁ reefs did receive slightly greater fishing effort than other open reefs (i.e., there was a small “pulse” effect).

Table 2 lists the sampling strategies applied in the simulations (which mimic those used in reality in 1995-1997). The sample sizes for the determination of the age composition of the catch (based on research fishing) are set to the actual (realized) sample sizes for the surveys that have already taken place and to the average of these past sample sizes (by reef) thereafter.

Measuring Estimation Performance

The quality of the estimates of seven quantities is used to evaluate the performance of estimators:

- Biomass available to fishing (legal fish only: the target species has a minimum legal size-limit) at the start of 1996.
- Biomass available to fishing (legal fish only) at the start of 2004 (i.e., after 6 years of “recovery” following pulse fishing).

- c. Ratio of the biomass available to fishing at the start of 2004 to that at the start of 1996.
- d. Fishing mortality rate during April 1997 (the first month of the first round of manipulations).
- e. Rate of natural mortality for animals aged 5 years and older.
- f. Catchability coefficient for commercial fishing (\tilde{q} - Equation B.2).
- g. Exponent of the relationship between abundance and catch rates from commercial fishing (δ - Equation B.2).

The results of the simulations are summarized by the median relative errors (MREs) and the median absolute relative errors (MAREs). The MRE is the median across the 500 simulations of the quantity:

$$100(\hat{Q}^U / Q^{True,U} - 1) \quad (1)$$

where $Q^{True,U}$ is the true value of quantity Q for simulation U , and

\hat{Q}^U is the estimate of Q for simulation U .

and the MARE is the median across the 500 simulations of the quantity:

$$100|\hat{Q}^U / Q^{True,U} - 1| \quad (2)$$

The MRE and MARE are preferred to the bias (average relative error) and the root-mean-square-error (the square root of the average of the squared relative errors) because they are much less sensitive to occasional outlying estimates. The sign of the MREs indicates the direction of bias in the estimator and the magnitude indicates the relative size of error. The magnitude of the MAREs reflect the overall degree of difference between the estimator and the true value of the parameter, with lower values being better. For example, an MRE of 10 indicates the estimates are “on average” 10% larger than the true value while an MARE of 10 indicates that the “average” difference in absolute terms between the estimates and the true values is 10%.

The simulation framework is used to examine a variety of key questions:

1. The extent to which experimental data will allow estimation of the seven quantities under ideal (but operationally realistic) conditions.
2. The impact of the possible failure to impose the treatment effect in the northernmost cluster.

3. The impact of the possible failure to impose adequate treatment effects on any of the open reefs.
4. The consequences of apparent wide spread environmental perturbations unrelated to the experiment in March 1997 on catchability.
5. The value, in terms of improved accuracy and precision of quantities a) – c), of the first and second round of manipulations and the post-manipulation monitoring program.

The first of these questions provides a baseline against which the results for the other questions can be compared. The second and third questions are considered because it appears that there was no obvious impact on fishing effort of the attempt to pulse the northernmost closed reef and only a slight impact on the manipulated open reefs during the 1997-1998 manipulation (Mapstone et al. 1998). Environmental conditions (e.g., water temperature) in the central and southern GBR were substantially altered following the presence of Cyclone Justin in the Coral Sea throughout March 1997. It is unclear whether these conditions were due solely to Cyclone Justin, the concurrent reversal of the El Niño Southern Oscillation, other (unknown) phenomena, or a combination of several such events. Catch rates of coral trout fell sharply for the remainder of 1997 throughout the central-southern GBR following these events. The final question was motivated by a mid-term review of the ELF experiment during 1998 which focused on the benefits, in terms of increased certainty in key parameter estimates, of a second round of manipulations in 1999 and the planned ongoing monitoring (Mapstone et al. 1998).

Estimators

The data available for estimation purposes are information from both twice-annual underwater visual surveys (UVS) and annual research line fishing surveys of all reefs, additional research line fishing surveys of half of the reefs approximately quarterly during 1997-1998 (see Davies et al. [1998] for details of the sampling methodology/design), and age-composition data for each reef from each research line fishing survey (ELF Project, unpubl. data). The choice for the estimator examined in detail in this paper is based on a variety of considerations. In particular, the chosen estimator needs to be able to produce the types of information required for parameterizing the simulation model (i.e., the seven quantities listed in the previous section), should be able to make use of the types of data available from the experiment (and elsewhere), and should perform adequately in the simulation trials. Four classes of estimator were considered initially: biomass dynamics (or production) models (Hilborn and Walters 1992), delay-difference models (Deriso 1980, Schnute 1985), full age-structured models (Hilborn 1990), and methods based on Sequential Population Analysis (Fournier and Archibald 1982; Deriso et al. 1985; Pope and Shepherd 1985; Methot 1989, 1990).

Biomass dynamics models were rejected immediately as they have no ability to make use of age-composition data (hence provide no basis for estimating the rate of natural mortality) and the meaning of fishing mortality from such models is often unclear (Punt and Hilborn 1996). In contrast, SPA approaches are clearly capable of using age-composition data and providing estimates for the quantities of interest. However, these approaches would require estimation of very many parameters (minimally, the age structure (by reef) at the start of 1995 and the annual recruitments thereafter) so would almost certainly have been highly imprecise. The performance of SPA approaches is also generally relatively poor when the level of fishing mortality is low (e.g., Pope 1972, Lapointe et al. 1989, Rivard 1990) as would be the case during the recovery period following closure of reefs. While it may be worthwhile to explore the performance of SPA approaches in the future, it was decided for this study to explore the performance of estimators based on full age-structured models and delay-difference models. These two types of estimators are capable of using the data available from the experiment, providing estimates for the quantities of interest, and do not have many estimable parameters (generally 2-4 key and several nuisance parameters (e.g., catchability coefficients) per population depending on how the estimator is constructed). The full age-structured approach is slightly more general than the delay-difference approach. However, simulation testing of a full age-structured estimator is computationally much more intensive than for a delay-difference estimator. It was decided therefore to base the evaluations of this paper on a delay-difference model and defer evaluation of estimators based on full age-structured models.

Appendix C outlines a generalized delay-difference model and its associated estimator. The model operates on a monthly time-step to be able to make full use of the experimental data, and uses information from different reefs within a cluster to distinguish the impact of observational error (which may be common to some extent across reefs within a cluster) on changes in the indices of abundance from the impact of actual changes in abundance caused by the experimental treatments. The estimator is applied to data for each cluster of six reefs, principally because demographic variables such as natural mortality are likely to differ among clusters. Applying the estimator to all reefs in a cluster simultaneously means that some parameters (e.g., natural mortality and some part of the annual environmental variation in catchability) can be assumed common across reefs. Table C.2 lists several variants of this estimator. The choice of the estimator for application to the full range of simulation tests is based on applying each of these variants (which are all special cases of the general (base case) estimator) to a base case simulation trial. The variants differ in terms of the number of estimable parameters, whether the data from catch surveys are used, whether an attempt is made to estimate the annual observation error component common to all survey types, etc. The variants have been constructed to be relatively general and do not use information that could

not possibility be available to them (e.g., the estimators do not know that catchability declined as a result of Cyclone Justin, merely that systematic changes in catchability may occur).

Results and Discussion

Base Case Scenario

The base case scenario represents the (relatively) ideal scenario in which future pulse fishing is successful on all intended reefs (previously open and previously closed) in all clusters and in which the environmental perturbations in 1997 impacted catchability. The MREs and MAREs for the base case estimator and the five quantities that are reef-specific are given in Table 3 while Table 4 provides results for M and δ , the quantities that depend on cluster rather than on reef.

The estimates of biomass are positively biased. The extent of bias is smallest for reefs CF_1 and CF_2 for which the median relative errors are close to 10% for the majority of reefs. The estimates of depletion (B_{04}/B_{96}) are less biased than the estimates of biomass. The only notably biased estimates of B_{04}/B_{96} are those for the "Open Hard Fished" reefs. This is a consequence of large positive biases associated with B_{96} . Not surprisingly given the biases for B_{96} , the estimates of fishing mortality in April 1997 (F_{97} in Table 3) are negatively biased (although seldom notably so for the "Closed Fished" (CF) reefs). Corrections for the bias associated with the estimates of biomass will have to be applied when these estimates are used to parameterize any simulation model used for the evaluation of management actions.

The estimates of natural mortality are unbiased (Table 4). The estimates of catchability for the commercial fishery and δ are very poor and indicate that the ELF experiment is unlikely to estimate the relationship between commercial fishing effort and fishing mortality reliably. The main difficulty associated with estimating the relationship between fishing mortality and (commercial) fishing effort is that commercial catch rates are only available for those years during which reefs are open to fishing. For the majority of years, the reefs are closed to legal fishing so reliable commercial catch rate data are unavailable, since fishing in these years represents infringements of the closures. Although ample commercial catch rate data are available over a number of years for other reefs not involved in the experiment, the abundance and catch rate data for those reefs generally lack contrast and so provide a very poor basis for estimation. Estimation of M , catchability and of δ is not considered further in this paper because M is estimated reliably in all trials while catchability and δ are never estimated reliably. The result that the relationship between catch rates and abundance will be very poorly determined by the experiment highlights the need to consider a wide variety of possible relationships during any evaluation of alternative management regimes that use catch rates as an indicator of abundance.

Table 3. Median relative errors (MREs) and median absolute relative errors (MAREs) (expressed as a percentage) by reef and quantity of interest for the base case trial and the base case estimator.

Treatment	Median relative error				Median absolute relative error			
	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}
Lizard – CC ₁	7.4	6.4	1.1	N/A	32.1	33.0	10.1	N/A
Lizard – CC ₂	7.5	6.5	2.0	N/A	33.3	34.3	10.8	N/A
Lizard – CF ₁	12.2	12.3	2.4	-14.0	34.8	42.0	12.6	35.7
Lizard – CF ₂	10.5	11.9	0.7	N/A	26.3	37.7	15.9	N/A
Lizard – OPF ₁	27.2	18.9	-8.7	-27.0	30.4	29.7	17.4	34.1
Lizard – OPF ₂	23.5	7.5	-13.2	-22.4	26.9	29.1	19.8	30.5
Townsville – CC ₁	22.6	21.1	2.0	N/A	38.1	36.2	10.4	N/A
Townsville – CC ₂	22.3	21.2	-0.6	N/A	36.4	37.2	10.9	N/A
Townsville – CF ₁	8.0	10.9	1.2	-12.7	21.2	32.7	15.5	26.9
Townsville – CF ₂	19.0	28.6	2.1	N/A	27.5	36.1	13.8	N/A
Townsville – OPF ₁	3.0	-0.5	-1.1	-9.9	23.4	24.4	12.0	30.3
Townsville – OPF ₂	19.9	0.3	-14.6	-19.1	24.3	28.9	17.9	27.6
Mackay – CC ₁	21.7	18.9	-0.6	N/A	35.5	35.6	11.7	N/A
Mackay – CC ₂	21.5	19.2	1.0	N/A	36.8	37.6	10.2	N/A
Mackay – CF ₁	10.0	10.6	0.6	-17.0	21.7	34.1	14.1	28.0
Mackay – CF ₂	18.7	26.7	2.4	N/A	27.6	38.1	14.8	N/A
Mackay – OPF ₁	14.2	5.4	-4.5	-15.9	25.3	26.2	14.8	33.3
Mackay – OPF ₂	21.0	2.4	-15.1	-21.0	24.6	29.5	19.1	26.0
Storm Cay – CC ₁	20.7	19.7	-0.4	N/A	32.7	33.7	10.8	N/A
Storm Cay – CC ₂	27.1	22.9	-0.2	N/A	36.0	36.4	10.7	N/A
Storm Cay – CF ₁	11.5	14.8	1.4	-16.3	23.2	35.1	16.1	28.4
Storm Cay – CF ₂	23.6	31.6	2.3	N/A	31.4	39.4	14.4	N/A
Storm Cay – OPF ₁	20.1	12.0	-4.5	-24.3	29.5	28.6	16.9	35.2
Storm Cay – OPF ₂	22.0	5.0	-16.0	-21.1	25.0	27.9	20.8	27.5

Table 4. Median relative errors (MREs) and median absolute relative errors (MAREs) for natural mortality, M , and the power of the relationship between commercial fishing effort and fishing mortality, δ (expressed as a percentage) for the base case trial and the base case estimator.

Cluster	Natural mortality		Catchability power	
	MRE	MARE	MRE	MARE
Lizard	-0.2	4.6	-44.9	44.9
Townsville	-0.9	5.0	-37.2	37.2
Mackay	-0.9	4.7	-37.5	37.5
Storm Cay	-0.8	4.6	-37.1	37.1

The biases evident in Table 3 for the estimator, even when it is confronted with the “ideal” case, may seem surprising. However, this is a consequence of the fact that the population dynamics model underlying the estimator, while similar to that underlying the operating model, actually differs from that model in several ways. For example, the estimator assumes that recruitment is knife-edged at age 5 whereas the operating model incorporates a selectivity pattern that is length-specific (Fig. A.1). Another notable difference between the estimator and the operating model is that the estimator assumes constant recruitment whereas the operating model allows recruitment to be stochastic, and, even in expectation, recruitment is not the same each month. The impact of this model misspecification was confirmed using deterministic (i.e., zero observation error, very high samples for age-structure) simulations.

The MAREs for biomass are generally lower for the “Closed Fished” (CF) and “Open Hard Fished” (OPF) reefs than for the “Closed Control” (CC) reefs. The MAREs for depletion are lower for the “Closed Control” reefs. This is not surprising because, given the zero catches for these reefs, the operating model predicts that the population on these reefs does not change over time. Although the actual population size does change over time because of variation in recruitment and natural mortality, the extent of change is small relative to changes on pulsed reefs so the assumption of no change is reasonably adequate. The MARE for the estimate of F_{97} for reef CF₁ is lower for the reefs on which pulsing is assumed to have been successful. It should be noted that comparisons of MREs and MAREs among reefs is not totally valid because the sample sizes for the estimation of the average age of the catch differs among reefs.

To reduce the volume of statistics for the sensitivity tests, the results have been summarized further by condensing them into eight statistics:

1. The average MRE and MARE for B_{96} over all 24 reefs.
2. The average MRE and MARE for B_{04} over all 24 reefs.
3. The average MRE and MARE for B_{04}/B_{96} over all 24 reefs.
4. The average MRE and MARE for F_{97} over the four CF₁ reefs.

The values of the eight summary statistics should be interpreted with caution to some extent because inclusion of the Lizard cluster (where the pulsing in 1997 is assumed to have failed and which is assumed not to have been impacted by the environmental perturbations in 1997) in their calculation will tend to make the results slightly more pessimistic (i.e., more biased and less precise) than if only the more homogeneously responding southern three clusters had been included. Also, inclusion of the results for the “Closed Control” reefs will tend to increase the MREs and MAREs for biomass and reduce them for depletion. However, the summarized results substantially ease the process of comparing among different estimator and operating model variants. The qualitative conclusions of the analyses are insensitive to omitting the results for the Lizard cluster and those for the “Closed Control” reefs.

Performance of Different Estimator Variants

Table 5 lists the values for the eight summary statistics for the base case estimator and three variants thereof (see Table C.2 for details). The performance of the estimator deteriorates markedly if the data from the research line fishing surveys are ignored and (particularly) if the “Open Hard Fished” reefs are assumed to be unfished at the start of the experiment (i.e., it is assumed that previous fishing had little impact on the abundance on all reefs and the number of estimable parameters per cluster is reduced by two). Ignoring the observation error deviations (see Appendix C) leads to less biased results and slightly lower MAREs for B_{04}/B_{96} and F_{97} . However, these gains are at the expense of much larger MAREs for B_{96} and B_{04} . Making allowance for the observation error deviations therefore reduces the overall variability of the estimates although at the expense of some additional bias. On balance therefore, the base case estimator is to be preferred of the four variants included in Table 5.

Sensitivity Tests

Table 6(a) lists the values of the eight summary statistics for the base case scenario as well as for three alternative experimental/sampling regimes:

1. The experiment (manipulations and data collection) stops at the end of 1998 (abbreviation “Stop experiment now”).
2. The proposed manipulations for 1999 are cancelled, but data collection continues as planned (abbreviation “No future manipulations”).

Table 5. Summary statistics for the base case trial for different variants of the estimator.

Specifications	Median relative error				Median absolute relative error			
	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}
Base case	17.3	13.9	-2.5	-15.0	29.3	33.5	14.2	29.7
Assume all virgin	166.9	108.5	-11.8	-38.4	170.3	113.5	22.5	46.9
No environmental error	13.1	14.1	0.3	3.6	34.1	38.5	13.4	28.5
No catch survey data	13.5	10.2	-3.0	8.4	33.2	39.9	15.2	37.4

3. The proposed manipulations for 1999 are cancelled and it is assumed that the 1997 manipulations never took place (abbreviation “No manipulations”).

Comparison of the base case results with those for the “Stop experiment now” regime allows an evaluation of the combined benefits of the future manipulations and the future collection of data. The difference between the results for the “Stop experiment now” regime and the “No future manipulations” regime reflects the benefits of future monitoring of experimental reefs without future manipulations. Comparison of the base case results with those for the “No future manipulations” regime indicates the likely benefits of further manipulations over simply monitoring the experimental reefs. The third regime (“No manipulations”) has been considered to assess the value of the manipulations generally. Results are shown in Table 6(a) for the base case scenario and an ideal scenario in which catchability was not affected by the environmental perturbations during 1997.

The benefits of continuing to collect data even if the planned manipulations for 1999 are cancelled are substantial (contrast the MAREs for the “No further manipulations” regime with those for the “Stop experiment now” regime). The additional benefits of the manipulations in 1999 are notable though not nearly as large as the basic benefits of continuing the data collection program. The benefits of the first set of manipulations can be assessed by comparing the results for “No manipulations” with those for “No further manipulations.” This comparison indicates that the benefits of the first manipulation were substantial even though those of the second manipulation are likely to be less so.

Table 6(b) shows results for variants of the base case trial in which it is assumed that:

1. There will be no increase in fishing mortality at the open reefs that are to be “pulsed” in 1999 (abbreviation “No open”).

Table 6. Summary statistics for the sensitivity tests. The results for the “other sensitivity tests” apply to the scenario in which catchability was affected by the environmental perturbations. “N/A” denotes that the estimator cannot determine the quantity concerned.

(a) Manipulation of experimental regimes

Specifications	Ideal scenario				Catchability impacted			
	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}
Median relative errors								
Base case	16.3	12.3	-3.6	-14.3	17.3	13.9	-2.5	-15.0
Stop experiment now	-23.3	N/A	N/A	16.3	-13.8	N/A	N/A	4.2
No further								
manipulations	14.4	10.0	-3.3	-16.7	11.1	8.0	-2.8	-15.5
No manipulations	23.5	18.3	-3.5	N/A	19.5	15.1	-3.0	N/A
Median absolute relative errors								
Base case	28.7	31.9	14.1	29.3	29.3	33.5	14.2	29.7
Stop experiment now	48.5	N/A	N/A	39.5	50.5	N/A	N/A	41.4
No further								
manipulations	36.5	38.8	13.7	34.2	35.5	38.2	13.7	34.0
No manipulations	51.6	50.5	13.4	N/A	49.3	49.0	13.3	N/A

(b) Other sensitivity tests

Specifications	Median relative error				Median absolute relative error			
	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}	B_{96}	B_{04}	B_{04}/B_{96}	F_{97}
Base case	17.3	13.9	-2.5	-15.0	29.3	33.5	14.2	29.7
No open	16.8	14.9	-2.2	-15.4	30.3	34.7	14.2	30.7
No lizard	17.4	14.8	-2.6	-15.6	31.7	35.6	14.1	31.1
No open/Lizard	17.5	14.7	-2.3	-15.5	32.8	36.3	14.1	31.8
$\sigma_r = 0.4$	15.8	12.2	-3.0	-15.6	25.7	27.4	10.2	25.1
$\sigma_q = 0.32$	18.7	15.7	-2.5	-15.6	32.1	36.2	14.6	32.8
$\sigma^F = 0.16$	18.1	14.6	-3.1	-14.8	29.4	33.0	14.4	29.7
$H_1 = 0.50$	46.6	43.7	-1.3	-25.6	54.5	55.6	16.8	42.7
$H_2 = 9$	16.8	14.6	-2.3	-17.7	30.8	34.5	14.1	32.9
$F_{\text{back}} = 0.085$	16.3	16.0	-1.0	-15.4	41.9	47.7	13.4	47.6

2. There will be no increase in fishing mortality on the reefs (CF_2 and OPF_2) in the Lizard cluster that are to be “pulsed” in 1999 (abbreviation “No Lizard”).
3. There will be no increase in fishing mortality on the open reefs (OPF_2) that are to be “pulsed” in 1999 for all clusters or for the closed reef (CF_2) in the Lizard cluster that is to be “pulsed” in 1999 (abbreviation “No open/Lizard”).

Not surprisingly, the MAREs increase as the number of successful manipulations is reduced. The results for the “No open/Lizard” trial are intermediate between those for the base case trial and those for the “No further manipulations” trial. This indicates that there is additional information to be gained from pulsing additional “closed” reefs alone, but that more information will be gained if the OPF_2 reefs in all clusters, and both the CF_2 and OPF_2 reefs at the Lizard cluster can be pulsed successfully as well.

Table 6(b) also lists MREs and MAREs for the base case trial and six sensitivity tests that involve changing the values of some of the parameters of the operating model. Decreasing the extent of variation in recruitment, σ_r , from 0.6 to 0.4 leads to improved performance. This is not surprising because the reduction in recruitment variability reduces the extent to which the assumption made by the estimator that the population dynamics are deterministic is violated. Decreasing the precision of the abundance indices from $\sigma_q = 0.2$ to 0.32 or reducing the impact of the manipulations ($H_2 = 9$) leads, as expected, to larger MAREs. Reducing the variation in fishing mortality, σ^f from 0.25 to 0.16 has almost no impact on performance.

Assuming that the “closed reefs” are actually subject to a fairly high level of fishing ($H_1 = 0.5$) leads to estimates of biomass with substantial positive bias. This is to be expected, however, because the “closed” reefs are no longer unfished, as is assumed by the method used to estimate M , and leads to positively biased estimates of M . It is well known (e.g., Lapointe et al. 1989, Punt 1994) that there is a strongly positive correlation between estimates of M and those of biomass so the positive bias in M leads to a positive bias in the estimates of biomass. Decreasing the background level of fishing mortality from 0.17 to 0.085 ($F_{back} = 0.085$) also leads to markedly increased MAREs. This is because the reduction in “contrast” associated with a lower level of overall fishing mortality substantially increases the variances of the estimates of all the quantities.

Discussion

It is hard to assess what constitutes “satisfactory performance” for an estimator in terms of its ability to estimate key parameters, and what improvement in performance should be considered to be “significant,” or at least sufficient to warrant additional expenditure. This is because the estimates will be used to parameterise a simulation model whose objective is to evalu-

ate management actions so the estimates relate only indirectly to the management of the fishery. In fact, it is especially difficult in this case, because the management objectives for the coral trout fishery are only generally and not specifically defined. However, it is clear that under almost any criterion, the benefits of the first round of manipulations in 1997 were "significant" as are the benefits of continuing the data collection program. Indeed, the large biases and MAREs for the "Stop experiment now" regime indicate that any estimates of biomass based on data collected only up to the end of 1998 would need to be interpreted with extreme caution because they would be very imprecise. The results suggest that there is likely to be marked further reductions in the uncertainty of the estimates with further manipulations. However, it is apparent that the benefits from a second set of manipulations will be less than those from the first set. The smaller reduction in MAREs from the second set of manipulations compared to that of the first is primarily a reflection of diminishing return for effort.

The MAREs for the base case trial are not notably different from those calculated by Punt (1997) for estimators based on ad hoc tuned virtual population analysis (VPA), but are somewhat higher than those calculated by Patterson and Kirkwood (1995) for ADAPT and ad hoc tuned VPA estimators. This suggests that even though the estimator considered in this paper is relatively simple, its performance is consistent with what would be considered normal in fisheries.

As is the case for all evaluations of performance based on Monte Carlo simulation, this one is subject to the criticism that some values for the parameters of the operating model may be in error and/or that some of the structural assumptions of the operating model are unrealistic. Although this criticism has been addressed to some extent through tests of sensitivity (Table 6), the qualitative conclusions of the paper depend on the trials conducted being sufficiently broad to cover what is likely to be the case in the real world. It is clear from Table 6(b) that performance is most sensitive to choices for the parameters related to fishing mortality. Unfortunately, these parameters are the most difficult to specify. This is because the only information about them relates to fishing effort and the results in Tables 3 and 4 show that it is almost impossible to determine the relationship between changes in fishing effort and those in fishing mortality.

Adaptive management approaches have been advocated as a means to learn about management of human interactions with natural systems (e.g., Walters 1986, McAllister and Peterman 1992). However, few actual examples exist (Sainsbury 1991, Sainsbury et al. 1997 are notable exceptions). Reasons for this are documented elsewhere (e.g., McAllister and Peterman 1992, Gunderson et al. 1995, Walters 1997, Lee 1999). However, prime among them are cost, the lengthy duration of the experimental manipulations, and the associated monitoring program, maintaining institutional commitment, and the difficulty associated with convincing decision makers to change the status of spatial management zones. These problems have been

encountered for the ELF Experiment, but the ability to provide a quantitative evaluation of likely benefits provides a strong (and defensible) rationale for investing in this type of experimental management. In addition, the ability to implement the experiment has involved considerable consultation with stakeholders (e.g., fishers, management agencies, conservation groups) and complex institutional arrangements to implement the changes in the management status of the reefs. Clearly, anyone wishing to implement an experiment of this nature cannot ignore these important but often complicated issues. However, we suggest that the combined approach of simulation modeling, stakeholder consultation, and experimental management remains the most promising approach to improve our understanding and management of complex natural systems.

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Appendix A. The Operating Model

Basic Population Dynamics

The resource dynamics are modeled using the equations:

$$N_{y+1,a}^{i,j,k} = \begin{cases} N_{y+1,a}^{i,j,k} & a = 0, 1 \\ N_{y,a-1}^{i,j,k} e^{-Z_{y,a-1}^{i,j,k}} & a = 2, \dots, x-1 \\ N_{y,x-1}^{i,j,k} e^{-Z_{y,x-1}^{i,j,k}} + N_{y,x}^{i,j,k} e^{-Z_{y,x}^{i,j,k}} & a = x \end{cases} \quad (\text{A.1})$$

where $N_{y,a}^{i,j,k}$ is the number of fish of age a in group k on reef i of cluster j at the start of year y ,

$Z_{y,a}^{i,j,k}$ is the total mortality on fish of age a in group k on reef i of cluster j during year y :

$$Z_{y,a}^{i,j,k} = \sum_{m=1}^{12} Z_{y,m,a}^{i,j,k} = \sum_{m=1}^{12} (M_{y,a} / 12 + R_{L_{k,a}+(m-0.5)/12} S_{L_{k,a}+(m-0.5)/12} F_{y,m}^{i,j}) \quad (\text{A.2})$$

$M_{y,a}$ is the rate of natural mortality on fish of age a during year y -generated using the equation:

$$M_{y,a} = M_a (1 + \varepsilon_{y,a}^M) \quad \varepsilon_{y,a}^M \sim N[0; (\sigma^M)^2] \quad (\text{A.3})$$

M_a is the expected rate of natural mortality on animals of age a (see Table A.1),

σ^M is the parameter that determines the extent of variation in natural mortality,

S_L is the selectivity of the gear on fish of length L (see Fig. A.1),

R_L is the fraction of animals of length L that die following capture (see Fig. A.1),

$F_{y,m}^{i,j}$ is the fully selected ($S = 1$) fishing mortality on fish from reef i of cluster j during month m of year y ,

$L_{k,a}$ is the length of a fish of age a in group k ; and

x is the maximum age considered (taken to be a plus group).

The above formulation implies that natural mortality is perfectly correlated among reefs. In an ideal world, all undersized animals should be released alive following capture so that R_L should be a knife-edged function at the minimum size (36 cm fork length). However, some undersized animals will die following release and some undersized coral trout will be marketed illegally.

Larvae

All fish are born as females. The number of larvae on reef i of cluster j at the start of year y (Births are assumed to occur at the start of the year, following Ferriera and Russ [1994] and Russ et al. [1996]) is determined from a contribution from spawning on reef i of cluster j and from a contribution from all other reefs:

$$N_{y,0}^{i,j,k} = K^k (ss L_y^{i,j} + c_j BL) e^{\varepsilon_y^{i,j} - \sigma_r^2/2} \quad (\text{A.4a})$$

$$\varepsilon_y^{i,j} = \tau_1^r z_y + \sqrt{(\tau_2^r)^2 - (\tau_1^r)^2} z_y^j + \sqrt{1 - (\tau_2^r)^2} z_y^{i,j} \quad (\text{A.4b})$$

where

$L_y^{i,j}$ is the number of larvae produced from spawning on reef i of cluster j during year y :

$$L_y^{i,j} = \tilde{f} E_y^{i,j} / (1 + \tilde{f} E_y^{i,j} / \tilde{k}) \quad (\text{A.5})$$

$E_y^{i,j}$ is size of the reproductive component of the population on reef i of cluster j at the start of year y , taken here to be the biomass of mature females:

$$E_y^{i,j} = \sum_{a=1}^x \sum_k f_{L_{k,a}} w_{L_{k,a}} N_{y,a}^{i,j,k} (1 - P_{L_{k,a}}) \quad (\text{A.6})$$

\tilde{f} is the maximum rate of larval survival to settlement in the absence of density-dependent mortality of larvae, multiplied by the average number of eggs per kg body weight,

\tilde{k} is the larval “carrying capacity,”

ss is the proportion of larvae which settle on the same reef as they were spawned,

K^k is the fraction of larvae which fall into group k ,

w_L is the mass of a fish of length L :

$$w_L = a^s (L)^{b^s} \quad (\text{A.7})$$

f_L is the fraction of animals of length L which are mature (see Fig. A.2),

P_L is the probability that a fish of length L is male (see Fig. A.2),

a_s, b_s are the parameters of the relationship between length and mass,

BL is the overall mean background supply of larvae from all other reefs,

c_j is the scaling factor for cluster j to account for variation in background larval supply among clusters (Mapstone et al. 1996b):

$$c_j = \frac{2[p-1+(j-1)(n-1)]}{(p-1)(n+1)} \quad (\text{A.8})$$

n determines the extent of scaling across the GBR,

$z_y, z_y^j, z_y^{i,j}$ are iid random deviates from $N(0; \sigma_r^2)$,

σ_r^2 is the overall interannual variation in larval abundance,

τ_1^r is the correlation in larval abundance among reefs in different clusters; and

τ_2^r is the correlation in larval abundance among reefs in the same cluster.

The values selected for τ_1^r and τ_2^r can be used to represent a variety of assumptions about the variation in larval abundance among reefs. For example, $\tau_1^r = 0$; $\tau_2^r = 1$ corresponds to the assumption that the variation in larval abundance from the expected value is perfectly correlated within clusters but uncorrelated among clusters. The value of the parameter BL is selected so that the average number of adults (animals aged 4 years and older) over all 24 experimental reefs in an unexploited state equals a pre-specified value, \bar{A} .

The value of the parameter \tilde{f} is selected to be consistent with the approach used by Mapstone et al. (1996b), i.e.:

$$\tilde{f} = \sum_{a=4}^x \sum_{k'} \tilde{N}_{a'}^{k'} / \sum_{a=1}^x \sum_k f_{L_{k,a}} w_{L_{k,a}} \tilde{N}_a^k (1 - P_{L_{k,a}})$$

where \tilde{N}_a^k is the age-structure of the population in the absence of exploitation.

Recruitment to Reefs

The number of 1-year-olds in group k on reef i of cluster j at the start of year y is given by:

$$N_{y+1,1}^{i,j,k} = N_{y,0}^{i,j,k} e^{-(M_{y,0} + M_y')} \quad (\text{A.9a})$$

$$e^{-M_y'} = [1 + \sum_k (N_{y,0}^{i,j,k} e^{-M_{y,0}} + \sum_{a=2}^J N_{y+1,a}^{i,j,k}) / (r^{i,j,k'})]^{-1} \quad (\text{A.9b})$$

where k' is the juvenile "carrying capacity,"

J is the maximum age of a "juvenile,"

$r^{i,j}$ is the scaling factor for reef i of cluster j :

$$r^{i,j} = \frac{2[q_j - 1 + (i - 1)(m_j - 1)]}{(q_j - 1)(m_j + 1)} \quad (\text{A.10})$$

m_j determines the extent of scaling across cluster j .

Growth

The growth of an individual is assumed to be governed by the von Bertalanffy growth equation:

$$L_{k,a} = L_{\infty}^k (1 - e^{-\kappa^k(a-t_0^k)}) \quad (\text{A.11})$$

Variation in growth among individuals is modeled by assuming that the parameter κ is lognormally distributed within the population while L_{∞} and t_0 are the same for all individuals. Table A.2 lists the values assumed for the parameters which determine length-at-age and mass-at-length. To simplify the calculations, the population is divided into 10 groups and it is assumed the value of κ is the same for all of the animals in a group.

Catches

The catch (in mass) of fish from reef i of cluster j during month m of year y , $C_{y,m}^{i,j}$, is computed using the equation:

$$C_{y,m}^{i,j} = \sum_{a=0}^x \sum_k \frac{W_{L_{k,a}+(m-0.5)/12} R_{L_{k,a}+(m-0.5)/12} S_{L_{k,a}+(m-0.5)/12} F_{y,m}^{i,j}}{Z_{y,m,a}^{i,j,k}} N_{y,a}^{i,j,k} e^{-\sum_{m'=1}^{m-1} Z_{y,m',a}^{i,j,k}} (1 - e^{-Z_{y,m,a}^{i,j,k}}) \quad (\text{A.12})$$

Fishing Mortality

The expected fully selected fishing mortality on an experimental reef is assumed to be determined by whether it is closed, open, or is being pulsed:

$$E(F_{y,m}^{i,j}) = \begin{cases} H_1 F_{back} / 12 & \text{if the reef is closed during month } m \text{ of year } y \\ F_{back} / 12 & \text{if the reef is open during month } m \text{ of year } y \\ H_2 F_{back} / 12 & \text{if the reef is pulsed during month } m \text{ of year } y \end{cases} \quad (\text{A.13})$$

where F_{back} is the background level of fishing mortality (annual),

Table A.1. Age-specific values for natural mortality.

Age	M_a (yr ⁻¹)
0	0.4
1	0.35
2	0.3
3	0.25
4+	0.2

H_1 is the fraction of the background level of fishing mortality expected on a closed reef (ideally $H_1 = 0$, but, in reality, $H_1 > 0$); and H_2 is the extent to which fishing mortality increases when a reef is being pulsed.

When a reef is pulsed, it is assumed that this only impacts the fishing mortality in the two months immediately after the opening (April and May for the simulations of this paper). This assumption is based on observations of effort at pulsed reefs (B.M. Mapstone, Pers. obs.).

The actual fully selected fishing mortality is normally distributed about its expected value:

$$F_{y,m}^{i,j} = E(F_{y,m}^{i,j})(1 + \varepsilon_y^{F,i,j}) \quad \varepsilon_y^{F,i,j} \sim N[0; (\sigma^F)^2] \quad (\text{A.14})$$

where σ^F reflects the extent of variability in fishing mortality (both interannually and between reefs).

The assumption of no autocorrelation or seasonal pattern in fishing mortality has been made based on an examination of effort data for the open reefs (A.E. Punt, unpubl. data).

Parameterization of the Operating Model

The base-case values assumed for the biological parameters of the operating model are listed in Table A.3. The rationale for most of the choices in Table A.3 is given by Mapstone et al. (1996b). The choice of 0.6 for σ_r was made because 0.6 is typical of the recruitment variation for marine teleosts (Beddington and Cooke 1983). The values assumed for the level of background fishing (F_{back}) and the amount by which fishing mortality is expected to change due to pulsing (H_2) are largely guesses as there are no quantitative estimates of fishing mortality for coral trout on the GBR. Therefore, sensitivity tests examine the implications of different (less optimistic from the point of view of estimation ability) values for these two quantities.

Table A.2. Values assumed for the parameters of the biological model related to growth (G.R. Russ, pers. comm.).

Parameter	Value
L_{∞} (cm)	60.67
κ (yr ⁻¹)	0.35
CV (κ)	0.2
t_0 (yr)	-1.82
$\ell n(b_1)$	-11.03
b_2	2.97

Table A.3. Values of the parameters of the population dynamics model.

Parameter	Value
Maximum age - χ	25 yr
Average number of adults per reef - \bar{A}	10 ^a
Background larval abundance - BL	See text
Larval “carrying capacity” - \tilde{k}	100 ^a
Larval retention probability - ss	0.05 ^a
Larval survival rate - \tilde{f}	See text
Cluster scaling parameter - n	3 ^a
Maximum age of a “juvenile” - J	χ ^a
Juvenile “carrying capacity” - k'	1,000 ^a
Reef scaling parameter - m_j	3 ^a
Background fishing mortality - F_{back}	0.17 ^a yr ⁻¹
Variation in fishing mortality - σ^F	0.25 ^a
Impact of a closure - H_1	0 ^a
Impact of a reef pulse - H_2	13 ^b
Variation in natural mortality - σ^M	0.05 ^a
Variation in larval abundance - σ_r	0.6
Correlation in larval abundance	
Between clusters - τ_1^r	0.3
Between reefs within a cluster - τ_2^r	0.6

^a Based on the base-case choices by Mapstone et al. (1996b).

^b Chosen so that the impact of pulsing is the same as in Mapstone et al. (1996b), who did not explicitly include month in their model.

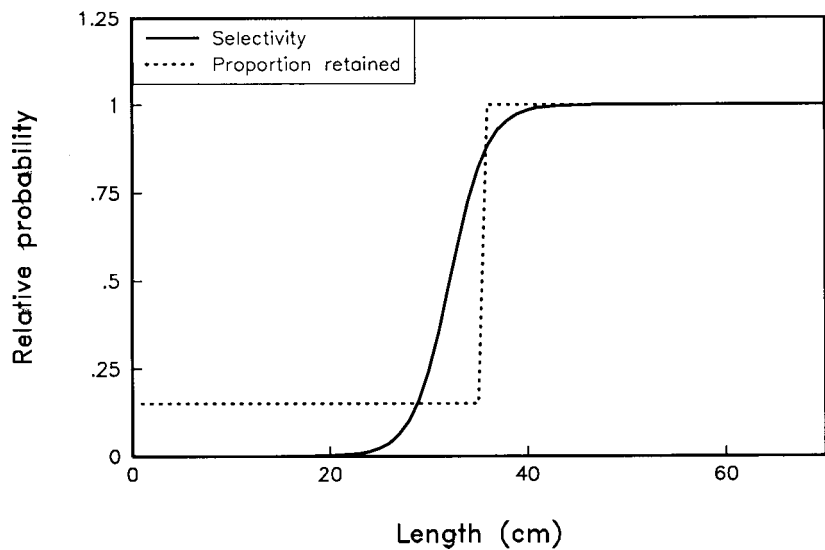


Figure A.1. Selectivity and the fraction retained as a function of length (B. Fulton, CSIRO Marine Research, pers. comm.).

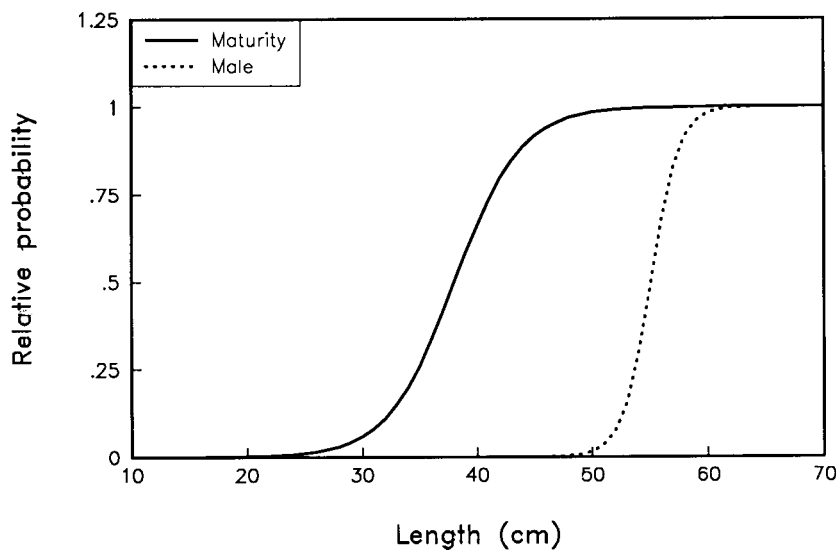


Figure A.2. Maturity and probability of being male against length.

Appendix B. Generation of the Artificial Data Sets

The data collected from the experimental reefs includes catches (by mass), effort, indices of relative abundance from visual line-transect and research line fishing surveys, and estimates of the age-composition of the catch from research line fishing surveys. “Independent” information about the constant of proportionality (the catchability coefficient) for the visual line-transect surveys is assumed to be available from inferences from the relative sizes of the reefs. It is assumed that this is represented by unbiased relative measures of the constant of proportionality for the visual surveys that are lognormally distributed with a coefficient of variation of 40%.

The catches are assumed to be unbiased estimates of actual removals:

$$\hat{C}_{y,m}^{i,j} = C_{y,m}^{i,j} e^{\eta_{y,m}^{i,j} - \sigma_\eta^2/2} \quad (\text{B.1})$$

where $\hat{C}_{y,m}^{i,j}$ is the observed catch (in mass) during month m of year y for reef i of cluster j ; and $\eta_{y,m}^{i,j}$ is a factor to account for stochastic variation in reporting of catches [$\eta_{y,m}^{i,j} \sim N(0; \sigma_\eta^2)$].

The impact of dumping of dead fish and illegal landing of undersized animals is included in the model by restricting the summation in equation A.12 to animals that are larger than the minimum size of 36 cm (fork length) when applying equation B.1. For the sensitivity tests that involve fishing on nominally closed reefs (i.e., $H_1 > 0$), it is assumed that the reported catch is zero.

The effort data for reef i of cluster j during month m of year y , $\tilde{E}_{y,m}^{i,j}$, is assumed to be related to the fully selected fishing mortality for reef i of cluster j during month m of year y , $F_{y,m}^{i,j}$ according to the equation:

$$\tilde{E}_{y,m}^{i,j} = \tilde{q}(F_{y,m}^{i,j})^\delta e^{\varsigma_{y,m}^{i,j} - \sigma_\varsigma^2/2} \quad (\text{B.2})$$

where \tilde{q} is the catchability coefficient, δ is the nonlinearity factor; and $\varsigma_{y,m}^{i,j}$ is a factor to account for random variation in catchability [$\varsigma_{y,m}^{i,j} \sim N(0; \sigma_\varsigma^2)$].

The visual surveys provide an index of total (selected) population density in numbers. Indices of selected biomass and selected numbers are obtained from research line fishing surveys. The following is the generic algorithm for generating indices of relative abundance.

$$I_{y,m}^{i,j,v} = q^v (E_{y,m}^{i,j})^{\gamma^v} e^{\phi_{y,m}^{i,j,v} - \sigma_q^2/2} \quad (\text{B.3a})$$

$$\phi_y^{i,j,\nu} = \tau_1^q z_{y,m} + \sqrt{(\tau_2^q)^2 - (\tau_1^q)^2} z_{y,m}^j + \sqrt{(\tau_3^q)^2 - (\tau_2^q)^2} z_{y,m}^{i,j} + \sqrt{1 - (\tau_3^q)^2} z_y^{i,j,\nu} \quad (\text{B.3b})$$

where $I_{y,m}^{i,j,\nu}$ is the index of type ν ($\nu = 1$ for the visual surveys and $\nu = 2$ for research line fishing surveys) for month m of year y from reef i of cluster j ,

q^ν is the (average) catchability coefficient for index type ν (assumed to be 1 without loss of generality),

γ^ν reflects the extent of nonlinearity in the relationship between the index and the quantity being measured for index type ν ,

$E_{y,m}^{i,j}$ is the expected value of the index (for $\gamma^\nu = 1$) during month m of year y from reef i of cluster j ,

σ_q^2 is the overall interannual variation in catchability,

τ_1^q is the correlation in catchability among reefs in different clusters,

τ_2^q is the correlation in catchability among reefs in the same cluster,

τ_3^q is the correlation in catchability among different indices on the same reef; and

$z_{y,m}$, $z_{y,m}^j$, $z_{y,m}^{i,j}$, and $z_y^{i,j,\nu}$ are iid random deviates from $N(0; \sigma_q^2)$.

The expected value of an index depends on the type of survey:

$$E_{y,m}^{i,j} = \sum_{a=0}^x \sum_k w_{L_{k,a+(m-0.5)/12}} S_{L_{k,a+(m-0.5)/12}}^\nu N_{y,a}^{i,j,k} e^{-\sum_{m'=1}^{m-1} z_{y,m',a}^{i,j,k}} e^{-z_{y,m,a}^{i,j,k}/2} \quad (\text{B.4a})$$

for indices of selected biomass; and

$$E_{y,m}^{i,j} = \sum_{a=0}^x \sum_k S_{L_{k,a+(m-0.5)/12}}^\nu N_{y,a}^{i,j,k} e^{-\sum_{m'=1}^{m-1} z_{y,m',a}^{i,j,k}} e^{-z_{y,m,a}^{i,j,k}/2} \quad (\text{B.4b})$$

for indices of selected numbers.

The random variates for the two indices based on research line fishing surveys are the same to reflect the fact that the two indices are based on the same data. The selectivity function for the research line fishing surveys is taken to be the same as that for commercial fishing while all animals larger than 20 cm are assumed to be equally vulnerable to being seen during the visual surveys (i.e., the uniform selectivity assumption). The results from the visual and research line fishing surveys are generated for both legal and sublegal animals (above and below 36 cm fork length).

The age-composition information is assumed to be a multinomially distributed sample from the catch; i.e., a sample where the probability of selecting an animal of age a is given by:

$$C_{y,m,a}^{i,j} / \sum_{a'=0}^x C_{y,m,a'}^{i,j} \quad (\text{B.5})$$

Table B.1. Values of the parameters related to the collection of data from the experimental reefs.

Parameter	Value
Variation in catch reporting - σ_η	0.2
Overall variation in catchability - σ_q	
Visual surveys	0.2
Research line fishing surveys	0.2
Correlation in catchability	
Between clusters - τ_1^q	0.0
Between reefs within a cluster - τ_2^q	0.3
Between fishing types within a reef - τ_3^q	0.5
Nonlinearity factor (visual) - γ^1	1
Nonlinearity factor (research line fishing) - γ^2	1.33
Variation in catchability (effort) - σ_ζ	0.2
Nonlinearity factor (effort) - δ	0.5

The catch-at-age is based on the assumption that the catch for scientific purposes reflects a small fraction of the deaths in the population so that $C_{y,m,a}^{i,j}$ can be assumed to be proportional to:

$$\sum_k S_{L_{k,a+(m-0.5)/12}} N_{y,m,a}^{i,j,k} e^{-\sum_{m'=1}^{m-1} Z_{y,m',a}^{i,j,k}} e^{-Z_{y,m,a}^{i,j,k}/2} / \sum_{a'=0}^x C_{y,m,a'}^{i,j} \tag{B.6}$$

For the purposes of this study, it is assumed that ageing is exact. Equation B.6 ignores the factor to account for deaths following release/illegal marketing, R_t , because all of the animals captured during the research line fishing surveys are aged.

Table B.1 lists the base-case values for the parameters related to the generation of data. The values were chosen based on analyses of existing data (e.g., Mapstone et al. 1996b) or set equal to educated guess (e.g., the extent of correlation in catchability). The impact of the environmental perturbations is modeled by reducing catchability by a factor x from April to October 1997 where $x = 0.4 e^{\zeta - \sigma_g^2/2}$ and $\zeta \sim N(0; \sigma_g^2)$ where $\sigma_g = 0.2$. It is also assumed that the impact of these perturbations was restricted to the three southernmost clusters (i.e., Townsville, Mackay, and Storm Cay).

Appendix C: The Delay-Difference Estimator

The delay-difference models of Deriso (1980) and Schnute (1985) incorporate age-structure effects (subject to certain assumptions) and treat each component of production and mortality separately. Each parameter of this model has a specific biological interpretation. It is thus less subject to the criticism of simplicity often leveled at lumped biomass models, but nevertheless does not require a large amount of data for estimation purposes (only a time series of relative abundance indices, given independent availability of values for certain biological parameters). However, if desired, it can be tailored to make use of a wide variety of sources of data. For a monthly time-step, the population dynamics equation for the Deriso-Schnute model is given by:

$$B_{m+1} = B_m(1 + \rho)\lambda_m - \rho\lambda_m\lambda_{m-1}B_{m-1} + R_{m+1}w_r \quad (\text{C.1a})$$

$$N_{m+1} = N_m\lambda_m + R_{m+1} \quad (\text{C.1b})$$

$$\bar{a}_{m+1} = [(\bar{a}_m + 1/12)N_m\lambda_m + rR_{m+1}] / N_{m+1} \quad (\text{C.1c})$$

where B_m is the (exploitable) biomass at the start of month m ,
 N_m is the number of (exploitable) animals at the start of month m ,
 \bar{a}_m is the mean age of recruited animals at the start of month m ,
 ρ is the Brody growth coefficient,
 λ_m is the survival rate during month m :

$$\lambda_m = e^{-M/12}(1 - C_m / B_m) \quad (\text{C.2})$$

M is the instantaneous rate of natural mortality (assumed to be independent of age for ages above the age-at-recruitment),
 C_m is the catch during month m ,
 R_{m+1} is the number of recruits entering the fishery at the start of month $m+1$ (assumed to be independent of time, i.e., $R_m = R$); and
 w_r is the mass of a recruit (age r).

The derivations for equations C.1a and C.1b are given by Deriso (1980), Schnute (1985), and Walters (1986). Equation C.1c follows directly from equation C.1b, noting that animals are assumed to recruit to the fishery at age r .

The data included in the likelihood function are: (a) the indices of (adult) abundance from the visual and research line fishing surveys; and (b) the time series of the mean age of recruited (age $\geq r$) animals by month. The abundance indices based on the visual and research line fishing surveys

are assumed to be lognormally distributed about the model estimates. The model also assumes that systematic variation in the values for the indices among reefs is a consequence of factors common to all reefs which influence survey catchability, rather than “process error” effects such as systematic variation among reefs in natural mortality or larval settlement. The negative of the logarithm of the likelihood function (excluding constants independent of the model parameters) for the abundance index information is therefore given by:

$$L_1 = \sum_i \sum_v \sum_m \left\{ \ell n \sigma_q + \frac{1}{2\sigma_q^2} \left(\ell n I_m^{i,v} - \ell n \hat{I}_m^{i,v} + \varepsilon_y \right)^2 \right\} \quad (C.3)$$

where

- $I_m^{i,v}$ is the observed index for index-type v (visual or research line fishing surveys) and reef i during month m ,
- $\hat{I}_m^{i,v}$ is the model-estimate of the index for index-type v and reef i during month m :

$$\hat{I}_m^{i,v} = q^{i,v} [(B_m + B_{m+1}) / 2]^{\gamma^v} \quad (C.4)$$

- $q^{i,v}$ is the survey catchability coefficient for reef i and index-type v ,
- ε_y accounts for sources of observation error which vary systematically among reefs (assumed to depend on year rather than on month),
- γ^v is a factor to account for nonlinearity in the relationship between research survey catch rate and abundance ($\gamma = 1$ for the index based on the visual surveys); and
- σ_q is the standard deviation of the logarithms of the random fluctuations in survey catchability.

The information on the mean age of the catch is assumed to be a relative index of the model-estimate of mean age of the catch (see equation C.1c). The negative of the logarithm of the likelihood function (excluding constants independent of the model parameters) for the mean age data is therefore given by:

$$L_2 = \sum_i \sum_m \left\{ \ell n \ddot{\sigma}_m^{i,obs} + \frac{(\bar{a}_m^{i,obs} - \tilde{q}^i \bar{a}_m^i)^2}{2(\ddot{\sigma}_m^{i,obs})^2} \right\} \quad (C.5)$$

where $\bar{a}_m^{i,obs}$ is the observed mean age of recruited (age $\geq r$ years) animals on reef i during month m ,

$\ddot{\sigma}_m^{i,obs}$ is the standard deviation of $\bar{a}_m^{i,obs}$, defined using the equation:

$$\ddot{\sigma}_m^{i,obs} = \sqrt{\frac{1}{n_m^i(n_m^i-1)} \sum_{a \geq r} n_{a,m}^i (a - \bar{a}_m^{i,obs})^2}$$

n_m^i is the number of animals sampled from reef i during month m and aged to be age r or greater

$n_{a,m}^i$ is the number of animals sampled from reef i during month m and aged to be age a ($n_m^i = \sum_{a \geq r} n_{a,m}^i$); and

\tilde{q}^i is the constant of proportionality between the observed and model-predicted mean ages.

Term L_2 assumes that the mean age information is a *relative* index of the mean age of the population (i.e., $\tilde{q}^i \neq 1$). This is because there are structural differences between the operating model and the estimator; fixing $\tilde{q}^i = 1$ would lead to biased estimates. Equation C.5 is based on the assumption that mean age of the catch is normally distributed. This assumption differs from the conventional assumption made when conducting statistical catch-at-age analysis that the proportion of the catch in a given age class is multinomially distributed (e.g., Fournier and Archibald 1982) because the delay difference model does not keep explicit track of the number of animals in each age class.

The negative of the logarithm of the likelihood function also includes constraints on the year-specific deviations in catchability and on the values for the catchability coefficients for the visual surveys:

$$L_3 = \sum_y \left\{ \ell n \sigma_r + \frac{\varepsilon_y^2}{2\sigma_r^2} \right\} \quad (C.6)$$

$$L_4 = \sum_i \left\{ \ell n \tilde{\sigma}_q + \frac{[\ell n q_i^{obs} - \ell n (z q^{i,1})]^2}{2\tilde{\sigma}_q^2} \right\} \quad (C.7)$$

where z is the mean of the catchability coefficients for the visual surveys,

σ_r is the variance of the ε_y 's,

q_i^{obs} is a relative measure of the catchability coefficient for the visual survey index for reef i (the area of the reefs—see Appendix B); and

$\tilde{\sigma}_q$ is the standard error of the logarithm of q_i^{obs} .

It is assumed that the value of ρ is known and equal to $e^{-0.15/12}$ and those of σ_q and $\tilde{\sigma}_q$ are known and equal to 0.2 and 0.4 respectively. The value of M is determined by regressing the logarithm of the frequency of occurrence of each age in the catch on age. The data for all closed reefs in a cluster are pooled to estimate M . The age-at-recruitment (r) is taken to be 5 years. For the reefs that are “closed” at the start of the experiment, the

Table C.1. The free parameters of the model. The number of parameters refers to a fit to the information for a cluster of six reefs.

Symbol	Description	Number of parameters
R	Recruitment	6
B_1	Ratio of initial to virgin biomass	2
σ_r	Extent of systematic variation in catchability	1
γ	Nonlinearity factor	1
q	Survey catchability coefficients	12
z	Mean survey catchability (visual surveys)	1
ϵ_v	Observation error deviations	each year
\tilde{q}	Constant of proportionality-age data	6

population is assumed to be in equilibrium while for the reefs that are “open” at the start of the experiment, the equilibrium biomass is multiplied by a reef-specific factor B_1 . The model is fitted to the data for each of the clusters separately. The free parameters of the model are listed in Table C.1.

The commercial catch and effort data are not included in the estimation procedure; only the commercial catches are used for estimation of biomass. This is because estimators that use the commercial catch rate data lead to poorer performance than the estimator outlined above. The estimates of commercial catchability, q , and extent of nonlinearity in the relationship between fishing mortality and fishing effort, δ , are determined by regressing the effort data on the estimates of fishing mortality determined by applying the estimator described above.

The estimator described above has a fairly large number of parameters (see Table C.1). Therefore to assess whether it is perhaps over-parameterized, a number of special cases of the estimator (see Table C.2) are considered. These special cases involve reducing the number of parameters by assuming that all reefs are unexploited at the start of the experiment, setting the observation error deviations (ϵ_v) to zero, and ignoring the catch survey data.

Table C.2. The variants of the estimator. The column “number of parameters” indicates the reduction in the number of estimable parameters compared to the base case for an analysis of a cluster of six reefs.

Abbreviation	Description	Number of parameters
Base case		0
Assume all virgin	The ratio of initial to virgin biomass is assumed to be 1 for all reefs.	2
No environmental error	The observation error deviations are assumed to be 0.	Each year + 1
No catch survey data	The data from the catch surveys are ignored; the observation error deviations are assumed to be 0.	Each year + 8

Spatial Modeling of Atlantic Yellowfin Tuna Population Dynamics: Application of a Habitat-Based Advection-Diffusion-Reaction Model to the Study of Local Overfishing

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Abstract

This paper presents a spatial multigear population dynamics model forced by the environment for Atlantic Ocean yellowfin tuna. The model simulates the population's distribution as a function of environmental variables and observed fishing effort. It is age-structured to account for age-dependent population processes and catchability. It is based on an advection-diffusion-reaction equation in which the advective term is proportional to the gradient of a habitat suitability index derived from temperature, salinity, and tuna forage data. Functional relationships between movement parameters, catchability, and environmental variables are based on nonlinear relationships estimated with generalized additive models (GAM) to characterize, on the one hand, yellowfin environmental preferences and, on the other hand, their catchability to different gears. Analytically formalized, GAM's relationships characterizing environmental preferences enable the habitat index to be calculated at each point in time

and space. Also formulated analytically, the relationships characterizing catchability to different gears enable the calculation of predicted catches, which are compared to observed catches to estimate the model parameters. In this paper, the problem of local overfishing of adult tuna in the Gulf of Guinea is addressed through different simulations and discussed.

Introduction

Yellowfin tuna (*Thunnus albacares*) is a cosmopolitan species whose distribution covers tropical and subtropical waters of the three oceans. In the Atlantic Ocean, three main fleets fish for this important pelagic resource. The purse-seine fleet (mainly French and Spanish vessels in the eastern Atlantic and Venezuelan vessels in the western side of the ocean) catches all yellowfin sizes in surface waters. The bait-boat fleet catches mainly young fishes associated with other tropical tunas (skipjack, *Katsuwonus pelamis*; and bigeye, *Thunnus obesus*) in coastal waters; and the longline fleet catches older yellowfin and bigeye in open sea waters. During recent years, total yellowfin catches in the Atlantic Ocean were approximately 150,000 t and reached a 175,000 t maximum in 1991 (ICCAT 1997).

Because tuna populations exhibit particular characteristics (i.e., the presence of a cryptic fraction of the biomass in the population dynamics [Fonteneau and Soubrier 1996], massive movements and migrations linked to the environment [Cayré et al. 1988a,b], very heterogeneous fisheries spread over ocean scale distribution areas, etc.), spatial models are needed to realistically represent their dynamics (Sibert et al. 1999). Among exploited species in the Atlantic Ocean, yellowfin tuna is an interesting candidate for application of an advection-diffusion-reaction model forced by the environment. Indeed, yellowfin exhibits important movements at different scales, which make spatial distribution a central problem for management and conservation (Fonteneau 1998, Maury 1998).

Yellowfin movements seem to be directly linked to a highly variable environment (Mendelssohn and Roy 1986; Cayré et al. 1988a,b; Fonteneau and Marcille 1988; Mendelssohn 1991; Marsac 1992): tunas continuously look for micronectonic aggregates for feeding and their three-dimensional distribution is limited by physiology to well defined dynamic environmental ranges.

In this context, environmental characteristics are probably the major driving force for yellowfin population movements (Cayré 1990). Consequently, environmental forcing on yellowfin distribution, movements, and catchability must be explicitly incorporated in any realistic high resolution spatial model. GAM analysis of the relationships linking yellowfin density to the ocean environment distinguished four main scales of variability in the Atlantic yellowfin population movements (Maury 1998). At each scale there is a corresponding movement type, which is associated with the variability of a given environmental factor (Maury 1998, Maury et al. 2001). Such scale-dependent relationships are used here to analytically formulate

a heuristic age-dependent habitat model for yellowfin. This model is used to force an advection-diffusion-reaction equation, which represents the space-time population dynamics. Using this model, different ecological assumptions can be explored. In this paper, we particularly focus on local overfishing of yellowfin populations.

Spatial Modeling of the Population Dynamics of Yellowfin Tuna

The model developed here includes three coupled components: environment, population, and fishing effort. The population dynamics component is modeled with an advection-diffusion-reaction model. Such models have a long history in ecology (Skellam 1951, Okubo 1980, Holmes et al. 1994) but their use in fishery science has grown only recently (MacCall 1990, Bertignac et al. 1998, Sibert et al. 1999). To be realistic in our case, they must reflect the heterogeneous distribution and movement of the tuna population linked to environmental heterogeneity. To model this linkage, we transform the environmental multivariate heterogeneity into the variability of a single functional parameter, which characterizes the habitat suitability and depends on physiological stage of the fish. For this purpose, population functional responses to the environment need to be determined. In addition, it is necessary to estimate catchability and its variations with the ocean environment and the fishery configuration. Then, given modeled fish density, observed fishing effort, and modeled catchability, expected catches can be calculated and compared with observed catches to estimate the model parameters (Fig. 1).

Model Formulation

Advection-Diffusion-Reaction of the Population

An advection-diffusion-reaction equation is used to model yellowfin population dynamics, spatial distribution, and movements. In such a model, fish movement has two components: a random one, a diffusion term which characterizes "dispersive" movements; and a directed one, an advection term which describes movement directed along the habitat suitability gradient. Both components are included in a partial differential equation (PDE) continuous in time and space (Okubo 1980, Bertignac et al. 1998, Sibert et al. 1999). The equation used in the present work includes a density-dependent diffusion term to model possible density-dependent habitat suitability (DDHS) (MacCall 1990, Maury 1998, Maury and Gascuel 1999):

$$\frac{\partial N}{\partial t} = \frac{\partial \left((D + k\gamma N^\gamma) \frac{\partial N}{\partial x} \right)}{\partial x} + \frac{\partial \left((D + k\gamma N^\gamma) \frac{\partial N}{\partial y} \right)}{\partial y} + \frac{\partial \left(\frac{\partial b}{\partial x} N \right)}{\partial x} + \frac{\partial \left(\frac{\partial b}{\partial y} N \right)}{\partial y} - ZN \quad (1)$$

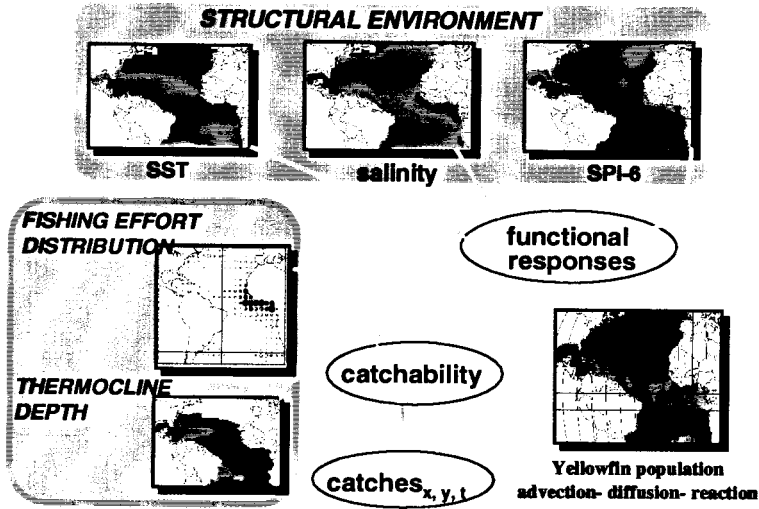


Figure 1. Schematic diagram of the model. Population movements are forced by the sea surface temperature (SST), the water salinity, and a forage index (SPI-6). The catchability is calculated locally as a function of local fishing effort density and thermocline depth (see text).

With $N = N_{x,y,t}$ representing the cohort density at point (x, y) at time and age t and $D = D_{x,y,t}$ the diffusivity coefficient; k and g are constants characterizing the shape of the density-dependence habitat selection relationship (the more the fish density increases, the more the habitat suitability decreases); $b = b_{x,y,t}$ is the local habitat suitability (biotic affinity); and $Z = Z_{x,y,t}$ the local mortality rate including the natural and the local fishing mortality rate.

For simplicity, we do not allow the diffusion D and the natural mortality coefficient M to vary with the habitat suitability. On the other hand, the advection term is proportional to the habitat suitability (b) spatial gradient. Therefore, the modeled fish population moves with respect to the local “suitability” gradient, and swims toward better environmental suitability. Equation 1 is solved numerically using an “alternating-direction implicit method” (Press et al. 1994) on a $1^\circ \times 1^\circ$ square from 30° south to 50° north. A daily time step and closed reflective boundaries are used (Neumann conditions: $\frac{\partial N}{\partial x} = 0$ at boundaries) to model an impassable frontier such as a shore.

Functional Responses to the Environment and Calculation of the Biotic Affinity, b

Habitat suitability depends on various biotic and abiotic factors. At the same time, functional responses linking the biotic affinity b to measured environmental factors are likely to be nonlinear functions (dome-shaped

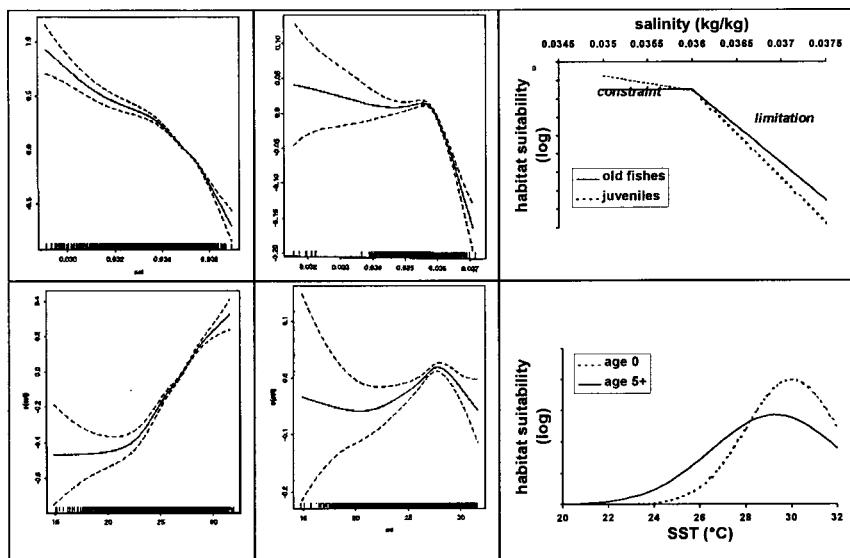


Figure 2. Observed GAM relationships between the log of the biotic affinity and the salinity (first row) and the SST (second row) for young yellowfin (age 1) on the left and for adult fishes (age 5+) in the middle (redrawn from Maury et al. 2001). On the right, the modeled relationships (arbitrary units): for salinity (first row), an age-dependant threshold relationship is used and for SST (second row), an age-dependent gaussian relationship is retained.

functions, thresholds, etc.). Maury et al. 2001 conducted a multivariate GAM analysis of the relationships linking yellowfin density to the environment. Generalized additive models (GAM) are nonparametric statistical methods which allow one to determine nonlinear relationships between variables (Hastie and Tibshirani 1990). Among numerous factors, they found that the sea surface temperature (SST), the salinity (*salt*), and a tuna forage index (secondary production index *SPI-6*, calculated by transporting the satellite-derived primary production with ocean currents [Maury 1998]) explain the major part of the Atlantic yellowfin tuna distribution variability at four different spatiotemporal scales, from a local scale ($1^{\circ} \times 1^{\circ} \times 15$ days) to the scale of the whole distribution area. All the oceanographic data used (SST, salinity, thermocline depth, oceanographic currents used to derive *SPI* from satellite-derived primary production) are simulated data from the OGCM OPA7.1 (Delecluse et al. 1993).

In the present work, the parametric formulation of relationships linking the habitat suitability to the environment is derived from GAM relationships obtained by Maury (1998). Four relationships are used to characterize environmental forcing. Each varies with the age of the fish:

- A threshold relationship for salinity which combines two different linear relationships (a constraint for low salinity and a limitation for high levels) (Fig. 2).
- A gaussian relationship between the log of the habitat suitability and the temperature (Fig. 2).
- A linear relationship between the log of the biotic affinity and the tuna forage indices SPI_6 .

The generalized additive models we used to assess the shape of the relationships between yellowfin abundance and environmental factors are additive representations of the relationships between environmental factors and habitat suitability. The definition of biotic affinity suggests a transformation to a multiplicative model, which is more in accordance with the ecological niche theory where a niche is viewed as a hyper-volume with n environmental dimensions:

$$\begin{cases} \log(-b_{age} + 1) = \left[\frac{\alpha_{age}}{\sigma_{age}} e^{\left(\frac{sst - \beta_{age}}{2\sigma_{age}} \right)^2} \right] - \gamma_{age} salt - \kappa salt + \lambda_{age} SPI_6 \\ \gamma_{age} = 0 \text{ if } age > 3 \\ \kappa = 0 \text{ if } salt < 0.036 \text{ kg kg}^{-1} \end{cases}$$

$$\Leftrightarrow \begin{cases} b_{age} = - \frac{e^{\left[\frac{\alpha_{age}}{\sigma_{age}} e^{\left(\frac{sst - \beta_{age}}{2\sigma_{age}} \right)^2} \right] e^{\lambda_{age} SPI_6}}}{e^{\gamma_{age} salt} e^{\kappa salt}} + 1 \\ \gamma_{age} = 0 \text{ if } age > 3 \\ \kappa = 0 \text{ if } salt < 0.036 \text{ kg kg}^{-1} \end{cases} \quad (2)$$

Five of the six parameters used to model the biotic affinity are age-dependent (α_{age} , β_{age} , σ_{age} , γ_{age} , λ_{age}) while κ is the same for all ages.

Fish Diffusion

The diffusivity coefficient D is related to the mean distance that a fish moves during a time step. This distance varies with the swimming speed of the fish, which depends on their size (Sharp and Dizon 1978). In the model, a power law with an exponent θ characterizes the potential nonlinearity of this relationship (Aleyev 1977):

$$D = \delta l^\theta \quad (3)$$

The two stanzas growth model of Gascuel et al. (1992) is used to convert age into size to calculate diffusion as a function of age (Fig. 3).

Natural Mortality

The yellowfin natural mortality rate used for stock assessment by the ICCAT (International Commission for the Conservation of Atlantic Tunas) scientific committee is arbitrarily fixed at 0.8 year^{-1} for age 0 to 1 fish and at 0.6 year^{-1} for older fish. The use of two mortality rates accounts for the fact that juvenile mortality is likely to be higher than adult mortality. In the present study, an age-dependent natural mortality curve is used. The use of a second order polynomial function characterizes a high mortality rate for young fish, a lower mortality rate for adults, and slight increase for the oldest fish due to senescence (Fig. 4).

Recruitment

Our advection-diffusion-reaction model only deals with the recruited life history stages. It does not explicitly represent the recruitment process, which provides the initial state to the dynamics of each cohort. The spatial distribution of recruitment is obtained with a simple algorithm. For each of the seven cohorts modeled, the recruitment levels are calculated by a monthly VPA. Recruitment in the model is uniformly distributed in the tropical areas where salinity on the first of January is lower than an arbitrarily fixed threshold equal to 0.03 kg kg^{-1} . Those low salinity regions, thought to be nursery areas, are mainly located from the Gulf of Guinea to Guinea shores and seaward of the Amazon River mouth (Fig. 5).

The population obtained is considered to be prerecruited. To get a "close to equilibrium" state, the prerecruits are redistributed without mortality for five time steps by using equation 1 with environmental conditions corresponding to the first of January of the year being modeled and age-0 functional relationships to environmental conditions. The resulting distribution of age 0 fish is used to initialize simulations.

Parameterization of Purse-Seiner Catchability

The GAM analysis of commercial CPUE conducted by Maury et al. 2001 provides a model of catchability to purse-seiners for the period 1980-1991. The fishing data used in the present study comes from the ICCAT database

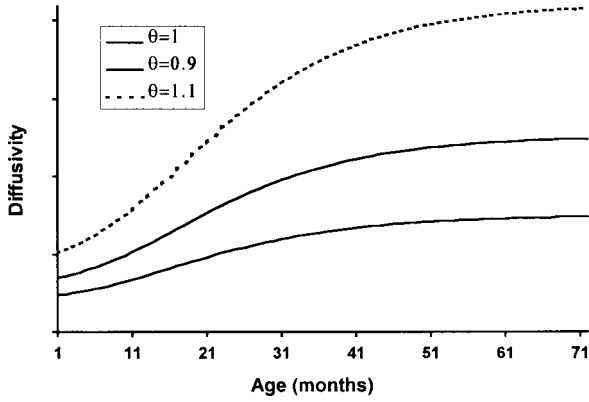


Figure 3. Yellowfin diffusivity modeled as a function of their age for different q parameters (arbitrary units).

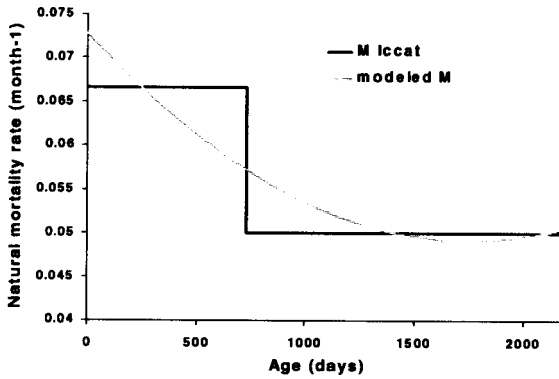


Figure 4. Monthly natural mortality rate as a function of yellowfin age (days). Black line, the natural mortality coefficient used by ICCAT. Grey line, the natural mortality used in the present work.

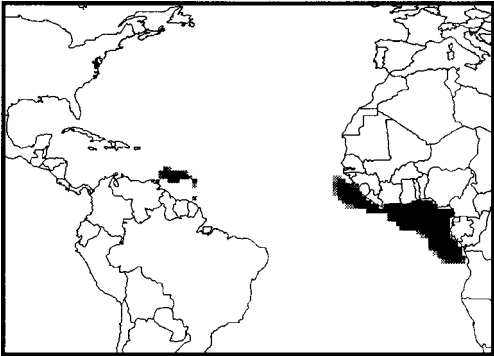


Figure 5. Model nursery zones where recruitment calculated by VPA is distributed (see text). Case of 1 January 1980.

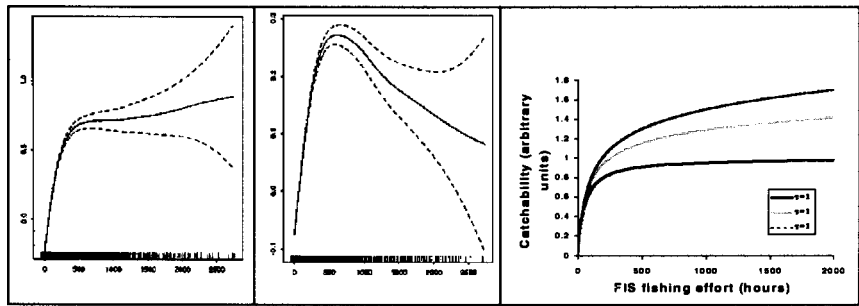


Figure 6. GAM relationships between the log of the 1980-1991 mean catchability and the fishing effort for young yellowfin (age 1) in the left panel and for adult fishes (age 5+) in the middle panel (redrawn from Maury et al. 2001). In the right, the parametric model used to represent the relationship between yellowfin catchability to purse-seiners and fishing effort.

which centralizes statistical data for all tuna fisheries in the whole Atlantic Ocean. In the present study, only catches by age and effort for the FIS (France, Ivory Coast, and Senegal) purse-seiners during the period 1980-1993 were used. Catchability is related to the local fishing effort and to the depth of the thermocline (approximated by the 20°C isotherm depth). To characterize the increase in catchability when local fishing effort increases and the approach to an asymptote (Maury 1998, Maury et al. 2001), we use a simple nonlinear function (Fig. 6). The increasing part of the curve corresponds to the increase of purse seiner's catchability when the fishing effort increases (cooperation and spying between vessels). The decreasing part of the curve observed for adult fishes is interpreted as a local overfishing (Maury and Gascuel 2001) and is not included in the model catchability ($\tau \geq 1$ in equation 4).

The effect of thermocline depth on catchability is considered to be linear (the deeper the thermocline, the lower the catchability) and it varies with yellowfin age. Therefore, the catchability model is expressed as follows:

$$\ln(q+1) = \frac{\mu_{age} f}{(1+\omega f)^\tau} - \rho_{age} Z20 \Leftrightarrow q_{age} = \frac{e^{\frac{\mu_{age} f}{(1+\omega f)^\tau}}}{e^{\rho_{age} Z20}} - 1 \quad (4)$$

Where q is the catchability; f is the fishing effort; $Z20$ is the thermocline depth; μ_{age} is the parameter characterizing the increase of catchability with effort; ω , a parameter characterizing the saturation of such effect; τ , a shape parameter (Fig. 6) and ρ_{age} , the weight of the linear thermocline effect on catchability.

Parameter Estimation and Model Validation

Model Tuning and Fitting to FIS (France, Ivory Coast, and Senegal) Purse-Seiner CPUEs

When the six modeled age classes for yellowfin (from age 0 to 5+) are taken into account, the whole model (functional responses + population dynamics + catchability) has 47 parameters (α_{age} , β_{age} , σ_{age} , γ_{age} , κ , λ_{age} , D , θ , τ , μ_{age} , ω , ρ_{age}) (Table 1). Even with the high number of CPUE observations available for this study (35,725 observations at 1 degree per 15 days resolution), the identification of such a nonlinear numerical model is a difficult task. Thus, as a first step, we chose to tune the model parameters “by hand” and to estimate only the catchability parameters $\mu_{age\ 0\ and\ 1}$ and $\mu_{age\ 2,\ 3,\ 4\ and\ 5+}$ numerically at each step. The fit of these six parameters provides statistical criteria characterizing the fit of the model to observed data.

Assuming a lognormal distribution for CPUE, a simple least square fit to $\ln(CPUE+1)$ is used to estimate catchability parameters and to guide tuning of the other parameters. Assuming that the observed $\ln(CPUE_k+1)$

Table 1. Parameter values estimated by calibrating the model.

Preferences		Catchability		Diffusion	
α_{0-1-2}	2.0	μ_{0-1}	10.0^{-6}	δ	$72 \text{ nm}^2 \text{ days}^{-1} \text{ cm}^{-1}$
α_{3-4-5+}	5.2	$\mu_{2-3-4-5+}$	3.10^{-6}	θ	1.05
β_{0-1-2}	30°C	$\omega_{0-1-2-3-4-5+}$	0.02		
β_{3-4-5+}	29.7°C	$\tau_{0-1-2-3-4-5+}$	1.0		
σ_{0-1-2}	2.0	$\rho_{0-1-2-3-4-5+}$	0.1		
σ_3	2.6				
σ_{4-5+}	2.8				
γ_0	6.0				
γ_1	4.0				
γ_2	0.5				
γ_{3-4-5+}	0				
κ	50.0				
$\lambda_{0-1-2-3-4-5+}$	0.1				

($k=1 \dots n$ observations) are a realization of the random vector $[\ln(\text{CPUE}+1)]_k$, the statistical model is written as follows:

$$\left[\ln(\text{CPUE}_{i,j,t} + 1) \right]_k = f \left(\mathbf{x}_{i,j,t,k}, \theta \right) + \varepsilon_{i,j,t,k} \quad k = 1 \dots n$$

f being a deterministic function of the variables \mathbf{x} and the parameters θ and $\varepsilon_{i,j,t,k}$ are the errors which are assumed to be independent for each observation.

Since the observed $\ln(\text{CPUE}+1)$ series is highly heteroscedastic (its variance is linked with the $\ln(\text{CPUE}+1)$'s value), we use a weighted least square criterion (*SCE*) which gives to each observation an importance proportional to the inverse of the fortnightly variance σ_{qz}^2 :

$$SCE = \sum_{i=1}^n \frac{\left[\ln(\text{CPUE}_i + 1) - \ln(\hat{\text{CPUE}}_i + 1) \right]^2}{\sigma_{qz}^2}$$

The least square estimator corresponds to the maximum likelihood estimate of q if measurement errors are independent and normally distributed (Bard 1974). If the model is correct, weighted reduced residuals

$$e_k = \frac{f(x_k, \hat{\theta}) - [\ln(\text{CPUE}_k + 1)]_{obs.}}{\hat{\sigma}_{qz}} \text{ should behave as independent random vari-}$$

ables $N(0,1)$. Assuming independent errors, the focus is now on the normality of residuals and their homoscedasticity. A simple graphical examination of the residuals (Fig. 7) shows that, apart from diagonal structures characterizing positive distributions, residuals form a horizontal band centered around zero.

However, normality of residuals is clearly not observed and their distribution is very asymmetric. Consequently, the simple minimum least square criteria we used is not consistent with the maximum likelihood estimator of the model given the data.

Model Validation and Consistency of the Outputs

The nonlinear features of our model make parameter estimation a complex task. Indeed, different parameter sets may give very close values to the objective function. Thus, even with many observations, simple tuning is problematic and results have to be evaluated for their ecological plausibility. On the other hand, it is important to use independent information to validate the model. For this, data from the longline fishery were used for validation. The longline fishery characteristics (selectivity, spatial distribution, catchability trends, etc.) are very different from the purse seine fishery data used to fit the model. The global consistency of the model outputs is analyzed by comparing the predicted monthly distribution of adult (age 5+) yellowfin (Fig. 8C) with the mean spatial distribution of longliner catches calculated by averaging the monthly longliners catches over the period 1956-1993 (Fig. 8A). Because longliners mainly catch fish aged 4-5 years and older, such a comparison is only applicable to characterize the model's ability to represent the spatial distribution and movements of the adult population.

Even with such a rough validation method (we compare mean catch distribution with the model predictions of the fish population spatial distribution for a given year), the model results seem to be very consistent and represent fairly well the large-scale spatial distribution and movements of the adult yellowfin population (age 4-5+). Results concerning young fishes (age 0-1) seem consistent also with scientific knowledge concerning spatial distribution and movements of juvenile yellowfin (Bard and Hervé 1994). The distribution of 2-3 year-old yellowfin is more questionable and requires further investigation concerning the parameterization of seasonal catchability (for details, see Maury 1998).

Simulations Analysis: Local Overfishing of Yellowfin

Strong local fishing pressure is likely to induce a significant local decrease of both resource biomass and fishing yields. That is what we call "local overfishing" (Maury and Gascuel 2001). In general, local overfishing is well documented for tuna fisheries (Fonteneau and Soubrier 1996, Fonteneau



Figure 7. Reduced residuals versus estimated values of the response variable .

et al. 1997). Concerning the Atlantic yellowfin tuna, a spatial VPA analysis indicated that very high local mortality rates could be exerted on reproductively active adult fish in the eastern Atlantic ocean ($F = 0.8$ per quarter during the first quarter of the year) (Maury 1998). Such high mortality rates are likely to induce important local depletions of adult fish. The comparison of two simulations of the spatial distribution of age 5+ fish clearly demonstrates the effect of local overfishing. The first simulation accounts for the observed FIS purse-seiner catches (Fig. 8B). The second simulates a virgin population without fishing pressure (Fig. 8C). For age 0-3 fish, fish density is very high compared to the realized catches and the effects of local overfishing do not appear in simulations. For older fish, important local biomass depletions appear in the simulated population when observed FIS purse-seiner catches are taken into account (Fig. 8B). At different periods during the year, one can observe a “wound” and “healing” pattern as produced with theoretical simulations by Maury and Gascuel 2001. The pattern is less clear for age 4 fish than for age 5+ fish. The highest depletions of fish occur in February, March, and April, off the Gulf of Guinea. In May, the adult population “heals” before it experiences significant “wounds” again after July in the Gulf of Guinea. At that time, fish are sufficiently concentrated off Senegal to remain numerous despite the significant catches. From July to the end of the year, there are almost no 5+ fish in the Gulf of Guinea. Such depletion of old fish in the Gulf of Guinea could explain the low longline catches observed in the area from August to November (Fig. 8A).

Only the FIS purse-seiner catches (more than 40% of the total yellowfin catches) are included in the simulations presented here. If all the other fishing fleets are taken into account (and particularly the Spanish purse-seiner fleet with a catch level of the same order of magnitude as FIS), local overfishing of old fish would have been much more significant, perhaps too significant to be considered plausible. Consequently, four alternative hypotheses must be studied in future work:

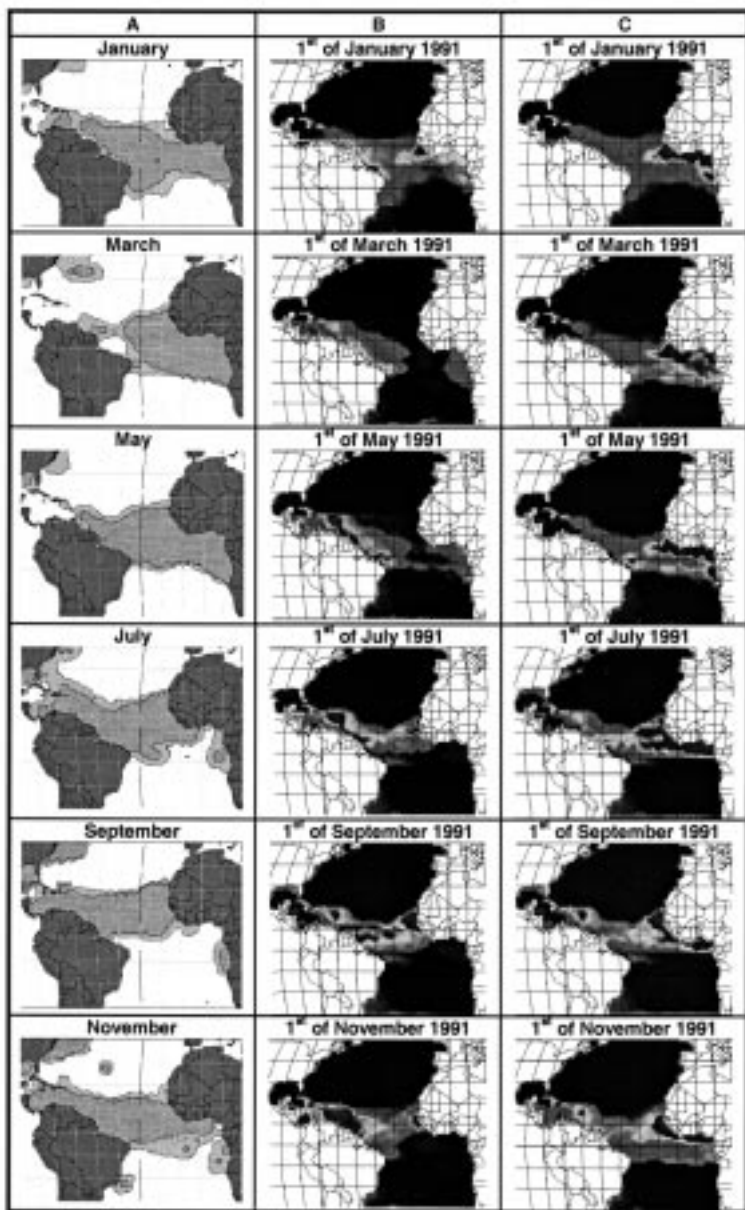


Figure 8. On the left (A), spatial distribution of cumulative longliner catches over the 1956-1993 period. Middle (B) and right (C) columns, simulations of age 5+ yellowfin distribution in 1991. Two simulations are compared: one taking into account observed FIS purse-seiner catches (in the middle, B) and another without (on the right, C).

- Local overfishing of old fish is actually extremely strong.
- Our model does not sufficiently concentrate the population of old fish in the Guinea Gulf to explain the very high catches which are observed.
- The yellowfin population “viscosity” is too high in the model and is responsible for an insufficiently strong “healing” of old fish.
- The total number of fish derived from VPA recruitment is not sufficient to explain the high local catches. If this is the case, VPA may underestimate total fish abundance, for instance, by ignoring a potentially important cryptic biomass.

At this point, we are unable to distinguish which of these possibilities is most likely. Nevertheless, **our work suggests a potential for strong seasonal local overfishing of old yellowfin, even if the “wound” and “healing” phenomenon is exaggerated by our advection-diffusion simulation.** Such strong local overfishing may have significant impacts on the utility of CPUE as an abundance index (Maury and Gascuel 2001). Moreover, an important reduction in local biomass could have a long-term impact on the yellowfin population genetic structure. For example, strong local fishing pressure on the main reproductive grounds could select artificially for fish reproducing in marginal areas such as Cabo Verde (Santa Rita Vieira 1991).

To address this question, improvement of our ecological knowledge concerning yellowfin tunas is needed. By allowing theoretical ecological assumptions to be studied, our model could help make advances in this direction.

Conclusions

The advection-diffusion-reaction model of the Atlantic yellowfin tuna gives satisfactory results. Fish population distribution and movements seem to be well characterized, at least at the large scale for ages 0-1 and ages 4-5+. The model is devoted to spatialized assessment, in particular to a better understanding of the interaction between population dynamics and the dynamics of fishing fleets. In addition, since it is spatially explicit, our modeling study allows the exploration of ecological hypotheses concerning yellowfin movements and behavior given the environment. In this paper, local overfishing of yellowfin is addressed through different simulations. It appears that the phenomenon is extremely marked in the model for old fish in the eastern Atlantic. Other simulations have been performed which study the homing of adults to the Gulf of Guinea reproductive grounds and analyze the impact of the 1983-1984 environmental anomaly on fish spatial distribution and catches (Maury 1998).

The model presented here is still preliminary. Nevertheless, some conclusions can already be drawn. Despite many limitations, commercial fisheries data are often the only means of accurately estimating tuna distribution on a large scale. For this reason, it is necessary to identify technical and environmental factors involved in local catchability. From this perspective, the Atlantic Ocean has the advantage of being a small basin exploited by rather homogeneous fleets distributed over wide areas covering various biotopes. Nonlinear analyses which take into account the antagonistic features of environmental influences on tuna distribution are needed. GAM models would be very useful for such nonlinear analysis. Different improvements of the model are currently under way:

- Integration of a diffusivity coefficient varying with environment favorability (Mullen 1989, Bertignac et al. 1998).
- Further study of the salinity effect into the model; it seems to be too strong in some regions and too weak in others.
- The secondary production index used here (*SPI-6* index) is a mean index which is currently being improved by developing a new “tuna forage” modeling effort in collaboration with scientists from the LODyC (Laboratoire d’Océanographie Dynamique et de Climatologie, Paris VI). This model is based on a coupled bio-geochemical model as described by Lehodey et al. (1998).
- The model must consider catches from all fishing fleets in the Atlantic Ocean and not only from FIS purse-seiners.

Finally, the model tuning presented here is extremely rough. A rigorous estimation of all parameters (including recruitment) with a likelihood approach should be attempted. Such a parameter estimation procedure could simultaneously incorporate data from both fishery and tagging.

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Integrated Tagging and Catch-at-Age Analysis (ITCAAN): Model Development and Simulation Testing

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Abstract

I present an integrated tagging and catch-at-age analysis (ITCAAN) that combines and extends recent developments in simulation tagging models and migratory catch-at-age analysis. The underlying concept of ITCAAN is that both tagged and untagged populations are modeled simultaneously using the same population dynamics assumptions, which allows for the estimation of shared parameters and the incorporation of auxiliary data. In the example I present, the unknown parameters are estimated using maximum likelihood with distributional constraints on annual recruitment anomalies. Model predicted age-specific tag recoveries and catch-at-age data are fitted to observed values. Tests using artificial data sets are carried out to investigate the robustness of ITCAAN to different population characteristics of three interacting subpopulations. The results show that the integrated approach is a promising method to incorporate tagging data into fisheries stock assessment. There is little bias or variance in estimates of total population average productivity; however, variance is much larger for estimates of individual subpopulation average productivity. Estimates of current stock status are unbiased and have relatively low variance. The addition of catch-at-age data in combination with the estimation of annual recruitment anomalies reduces variance in the estimates of subpopulation average productivity and in both total and subpopulation current stock status. In comparison, traditional methods that ignore movement and use Petersen estimates of biomass, produce highly biased estimates of subpopulation average productivity and subpopulation current stock status.

Introduction

Tagging studies are a common, and often the only, way to assess stock size, natural mortality, and fishing mortality, in exploited fish populations. This information can be used to form management advice. Often management wants to be more sophisticated and includes these estimates in a population dynamics model to predict the outcome of alternative management strategies (Hilborn and Walters 1992). This is usually implemented using a two-step process, where the tagging data are analyzed to estimate the stock biomass (or exploitation rate) and then a population dynamics model is fitted to the biomass estimate (e.g., Maunder and Starr 2000). This two-step procedure has a number of deficiencies, and they are listed below.

1. Information is lost in the process of estimating the biomass. There may be additional information contained in the raw tagging data (i.e., age-structure) that is useful for estimating the parameters of the population dynamics model (i.e., selectivity) and this information is lost when only the estimated biomass (or exploitation rate) is used in the fitting procedure of the population dynamics model.
2. Inconsistencies in assumptions. The two analyses may use different parameter values or different model structures. These differences often occur because the analyses are done independently by different researchers or at different times.
3. Difficulty in determining error structure. The error structure that should be used to incorporate the biomass (or exploitation rate) estimate into the fitting procedure may be more difficult to determine than the error structure for the raw tagging data.
4. Difficulty in including uncertainty. The representation of correlation between parameters from the first analysis into the second analysis requires the use of joint prior distributions in the second analysis, which are harder to represent than the marginal distributions that are commonly used.
5. Reduced diagnostic ability. A major technique used to evaluate the fit of a model to the data is to view the residuals (difference between the observed data and the values predicted by the model). If only the biomass estimate is used in the fitting procedure, the analyst is unable to determine if a lack of fit is due to the biomass estimation procedure or the population dynamics model fitting procedure.

An integrated approach that combines the population dynamics model with the tagging analysis can overcome some, if not all, of the disadvantages listed above. The main idea behind the integrated approach is to combine analyses, that are usually carried out separately, allowing parameters and information to be shared. Recent studies have integrated tagging

data into population dynamics models in fairly simplistic ways. Richards (1991) developed an integrated model to assess a Canadian lingcod stock. The term composite model was used to describe the integrated model. Essentially the same equations were used to model the tagged and total populations and the effect of sharing parameters between the two models was investigated. The model used was very simple, with no age or spatial structure. The integrated modeling approach can easily be extended to the more complex general catch-at-age models (e.g., Methot 1990) or, more importantly, to migratory catch-at-age analysis (Quinn II et al. 1990). Catch-at-age data are insufficient to adequately estimate the parameters of a catch-at-age model (Deriso et al. 1985); however, Gove (1997) found that combining a Petersen type tagging likelihood with the catch-at-age likelihood enabled the parameters to be estimated. Gove (1997) also showed how a multinomial likelihood for telemetry data could be combined with the catch-at-age likelihood. Haist (1998) presented a sex- and depth-structured catch-at-age analysis for sablefish that integrated depth-structured tagging data, but neither explicitly modeled movement nor fit to age or size-structured tagging data. Punt and Butterworth (1995) and Porch et al. (1995) used an integrated migratory VPA fitted to area-structured tagging data to assess the North Atlantic bluefin tuna, but neither of these models used age or size-structured tagging data. Maunder (1998) developed an integrated tagging and catch-at-age analysis (ITCAAN) that explicitly includes movement and fits to both age-structured tagging data and catch-at-age data. The ITCAAN model was applied to a snapper population off the northeast coast of New Zealand. Hampton and Fournier (1999) developed a model for yellowfin tuna based on MULTIFAN-CL (Fournier et al. 1998) that uses an age-structured model fitted to catch-at-length data and length-structured tagging data.

Recently, in the fisheries tagging literature, there has been the development of more complex methods to estimate movement rates from tagging data (Hilborn 1990, Sibert et al. 1999). The tagged population is modeled using a simulation technique to calculate the tagged population size in any strata at any time. The recovery sampling is then modeled to predict the number and distribution of recoveries, which are compared with observed recoveries, and an optimization routine is used to estimate the parameters of the model. These types of models have very similar structure to the population dynamics models used in stock assessment and therefore can easily be combined with population dynamics models as described in the previous paragraph.

I present an integrated tagging and population dynamics model (ITPDM) that combines the recently developed simulation tagging model (Hilborn 1990) and a population dynamics model into one analysis which explicitly models movement. Both tagged and total populations are modeled sharing the same dynamics and parameter values. When tagging data and catch-at-age data are incorporated into the model, I term the technique an integrated tagging and catch-at-age analysis (ITCAAN). Using simulated data, I

test the performance of the ITPDM and investigate the benefit of including catch-at-age data (ITCAAN).

Method

In this section I present a simple estimation model that I use to investigate the performance of the ITPDM and ITCAAN models. The total population is modeled forward in time from a virgin state using a simple age-structured model. Each tag group (tagged individuals that have the same area of release and time of release) is modeled from the time of release as a separate population using the same age-structured model. The numbers of recoveries-at-age predicted in each subpopulation are compared to the observed recoveries using maximum likelihood. Other data observed from the fishery (e.g., catch-at-age data) can also be compared with the model's predictions using maximum likelihood. The sum of the negative logarithm of these likelihoods is used to estimate the parameters of the model using a minimization routine.

A difference equation model is used that assumes catches are taken in a discrete event at the start of the year before natural mortality, but after movement. Movement is simplified by assuming that it occurs as a discrete event at the start of the year and the population is closed. Movement and natural mortality are independent of time and age. Vulnerability at age, weight at age, and fecundity at age are independent of time and subpopulation. Random mixing between the tagged and untagged populations is assumed. There is no tag loss, tag induced mortality, nor nonreporting of tags.

Model Description

Movement is assumed to occur at the start of the year and is modeled following a Markov process.

$$N'_{y,a,l} = \sum_x P_{x \rightarrow l} N_{y,a,x}$$

$N_{y,a,x}$ is the number of individuals in year y of age a in subpopulation x at the start of the year.

$N'_{y,a,l}$ is the number of individuals in year y of age a in subpopulation l after movement and before fishing.

$P_{x \rightarrow l}$ is the probability that an individual in subpopulation x moves to subpopulation l .

Constraints are added to the movement parameters to keep them in the appropriate range

$$0 \leq P_{x \rightarrow l} \leq 1$$

and an additional constraint that the movement parameters sum to one is used to reduce the number of estimated parameters.

$$P_{x \rightarrow l} = 1 - \sum_{l \neq x} P_{x \rightarrow l}$$

$$\sum_l P_{x \rightarrow l} = 1$$

Recruitment follows the Beverton-Holt stock-recruitment relationship formulated with a steepness parameter, h , which is the proportion of the virgin recruitment that is realized at a spawning biomass level that is 20% of the virgin spawning biomass (Francis 1992). Annual recruitment is log-normally distributed and is implemented using the log-normal bias correction to allow virgin recruitment to be equal to the mean recruitment in an unfished population. If the recruitment anomalies are not estimated, σ_r is set to zero canceling out the bias correction factor.

$$N_{y+1,l} = \frac{S_{y,l}}{\alpha_l + \beta_l S_{y,l}} \exp(\epsilon_{y,l} - 0.5\sigma_r^2)$$

$$\alpha_l = \frac{S_{0,l}(1-h)}{4hR_{0,l}}$$

$$\beta_l = \frac{5h-1}{4hR_{0,l}}$$

$$S_{y,l} = \sum_a N'_{y,a,l} f_a$$

$S_{y,l}$ is the spawning biomass in year y and subpopulation l .

$S_{0,l}$ is the virgin spawning biomass in subpopulation l .

$R_{0,l}$ is the virgin recruitment in subpopulation l .

h is the steepness of the Beverton-Holt stock recruitment relationship.

f_a is the fecundity of an individual aged a .

$\epsilon_{y,l}$ is the recruitment anomaly in year y for subpopulation l . $\epsilon \sim N(0, \sigma_r)$

σ_r is the standard deviation of the logarithm of the annual recruitment anomalies.

A is the maximum age.

Fishing and natural mortality are modeled using a difference equation that assumes catch is taken at the start of the year after movement, but before natural mortality.

$$N_{y+1,a+1,l} = (N'_{y,a,l} - C_{y,a,l})e^{(-M)}$$

M is the instantaneous natural mortality rate.

The final age-class (A) is used as a plus group to accumulate all older individuals.

$$N_{y+1,A,l} = (N'_{y,A-1,l} - C_{y,A-1,l})e^{(-M)} + (N'_{y,A,l} - C_{y,A,l})e^{(-M)}$$

Catch at age is calculated using the separability assumption, which separates the fishing mortality into year and age-specific components.

$$C_{y,a,l} = N'_{y,a,l} u_{y,l} v_a$$

$C_{y,a,l}$ is the total number of individuals caught in year y of age a in subpopulation l .

$u_{y,l}$ is the annual exploitation rate in year y and subpopulation l .

v_a is the relative vulnerability at age a .

The exploitation rate in year y is calculated as the catch divided by the exploitable biomass, $B_{y,l}$.

$$u_{y,l} = \frac{Y_{y,l}}{B_{y,l}}$$

$$B_{y,l} = \sum_a N'_{y,a,l} v_a w_a$$

$v_a = 0$ for $a < a_{vul}$

$v_a = 1$ for $a \geq a_{vul}$

$$w_a = \delta \left(L_{\infty} \left\{ 1 - \exp[-K(a - t_0)] \right\} \right)^\phi$$

a_{vul} is the age when individuals become vulnerable to the gear.

$Y_{y,l}$ is the total weight of the catch in year y for subpopulation l .

$B_{y,l}$ is the exploitable biomass at the start of year y in subpopulation l , after movement.

w_a is the weight of an age a individual.

- δ is the length-weight scalar parameter.
 ϕ is the length-weight exponent parameter.
 K is the von Bertalanffy growth equation parameter.
 L_{∞} is the von Bertalanffy growth equation parameter.
 t_0 is the von Bertalanffy growth equation parameter.

The tagged population, T , is modeled assuming the same dynamics and parameters as the untagged population, with the only difference being that recruitment to the tagged population occurs through releases and can therefore occur at any age. Each set of releases (a release group), k , that can be uniquely identified in the recoveries is modeled as a separate population. The releases are assumed to occur after movement, fishing, and natural mortality.

$$T'^k_{y,a,l} = \sum_x p_{x \rightarrow l} T^k_{y,a,x}$$

$$T^k_{y+1,a+1,l} = (T'^k_{y,a,l} - \hat{r}^k_{y,a,l})e^{(-M)} + R^k_{y,a,l}$$

$$\hat{r}^k_{y,a,l} = T'^k_{y,a,l} u_{y,l} v_a$$

$\hat{r}^k_{y,a,l}$ is the predicted number of recoveries from release group k in year y of age a in subpopulation l .

$T^k_{y,a,l}$ is the number of tagged individuals from release group k at the start of year y that are age a and in subpopulation l .

$T'^k_{y,a,l}$ is the number of tagged individuals from release group k in year y of age a in subpopulation l after movement, but prior to fishing and natural mortality.

$R^k_{y,a,l}$ is the number releases from release group k in year y of age a in subpopulation l .

It should be noted that $T'^k_{y,a,l}$ will be zero when y is less than or equal to the time that individuals from release group k are released and $R^k_{y,a,l}$ will only have a nonzero value for one time period, the time at release.

Initial Conditions

At the start of the modeling time period, the population is assumed to be in deterministic equilibrium with regard to natural mortality and movement. The initial population is generated by modeling each cohort over the number of years corresponding to its age in the initial population using only movement and natural mortality (i.e., $u = 0$). The abundance of the plus group is approximated by summing up the individuals that would be alive in cohorts from the maximum age to age 200 (assuming attributes of an individual that is of the maximum age).

Likelihoods

Maximum likelihood has become the standard technique for parameter estimation in the fisheries literature (Polacheck et al. 1993, Hilborn and Mangel 1997). The multinomial likelihood function is appropriate when there are more than two types of outcomes, and is the most commonly used likelihood for tagging data (e.g., Kleiber and Hampton 1994). If each release group-age combination is viewed as a trial, the multinomial likelihood can be used to model which recovery strata the tagged individual is recovered in or whether it is recovered at all. The constants can be left out of the likelihood because they do not add any information for estimating parameters, performing likelihood ratio tests, or calculating Bayes posteriors. The likelihood function is given below.

$L(\text{tagging data} \mid \text{parameters}) =$

$$\prod_{a',k} \left[\left(1 - \sum_{t,l} p_{y'+t,a'+t,l}^k \right)^{\left(R_{a'}^k - \sum_{t,l} r_{y'+t,a'+t,l}^k \right)} \prod_{t,l} p_{y'+t,a'+t,l}^k r_{y'+t,a'+t,l}^k \right]$$

$$p_{y'+t,a'+t,l}^k = \frac{\hat{r}_{y'+t,a'+t,l}^k}{R_{a'}^k}$$

k is the release group, where a release group is defined as all tags released at the same time and in the same subpopulation.

$R_{a'}^k$ is the total number of individuals released at age a' from release group k .

$r_{y,a,l}^k$ is the number of observed recoveries from release group k in year y of age a in subpopulation l .

a' is the age at release.

y' is the year of release.

t is the time after release in years.

l is the subpopulation of recapture.

Catch-at-age data are commonly included in the objective function using a multinomial likelihood (e.g., Methot 1990).

$$L(\text{catch-at-age data} \mid \text{parameters}) = \prod_l \prod_y \prod_a p'_{y,a,l} c_{y,a,l}^{\text{Sample}}$$

$$p'_{y,a,l} = \frac{N_{y,a,l} v_a}{\sum_a N_{y,a,l} v_a}$$

$C_{y,a}^{Sample}$ is the number of individuals in the catch at age sample from year y that are of age a and in subpopulation l .

It is convenient to use the negative logarithm of the likelihood because likelihoods may be very small numbers and most optimization routines are minimizers (Hilborn and Mangel 1997). The negative log likelihood from other release groups or independent auxiliary information can be added to the total negative log likelihood. If we assume that the catch-at-age data is independent from the tagging data (i.e., no tagged individuals were included in the catch-at-age data) then we can simply add the negative log likelihood from the catch-at-age data to the total negative log likelihood.

When the annual recruitment parameters are estimated, a penalty based on the log-normal distribution is added to the negative log-likelihood function to reduce the amount that recruitment can vary from the underlying stock-recruitment relationship. This is essentially a prior distribution on the annual recruitment variation and makes the analysis Bayesian in nature. The mode of the joint posterior distribution is used to represent point estimates and is based on Bard's (1974) maximum of the posterior distribution estimates, which were used by Fournier et al. (1998). The term added to the total negative log-likelihood (ignoring constants) is:

$$-\ln P(\text{recruitment anomalies} \mid \text{prior}) = \sum_{y,l} \frac{\varepsilon_{y,l}^2}{2\sigma_r^2}$$

where the value of σ_r can be used to weight the penalty on the recruitment variation.

The parameters of the model were estimated using an iterative minimization routine to minimize the total negative log-likelihood. The auto differentiation method supplied with AD Model Builder (© Otter Consulting) was used in the following analyses.

Simulated Data Sets

As is the case with any new assessment method, it is important to test the effectiveness of the ITPDM and ITCAAN models before applying them to real populations. Simulation of artificial data is one way of testing assessment methods (Hilborn and Mangel 1997). However, it should be noted that simulation analysis is limited and applying stock assessments to real data can highlight deficiencies that are not detected in simulation analysis. Simulation of artificial data relies on constructing a mathematical representation of the population to simulate its dynamics. This mathematical representation is termed the operating model and can be used to produce observational data that is used in the estimation methods. The observational data includes error and the results of the estimation procedures

using this data can then be compared to the true dynamics represented by the operating model. As with many other studies (e.g., de la Mare 1986), I use the model being tested to also generate the artificial data.

The ITPDM was used to simulate three interconnected subpopulations forward in time for a total of 20 years starting from an unexploited population and using a fixed exploitation history (Table 1). In the 10th year, a single tag release was carried out in all subpopulations (releases are given in Table 2) and the dynamics were simulated for another 10 years. The simulated observational data that was generated includes age-specific tag recoveries and catch-at-age data for the last 10 years. Error in the simulated data was introduced as process error in recruitment and as process errors in the natural mortality, movement, and exploitation rates of the tagged population.

Log-normal variation with a σ_r of 0.6 ($\sigma_r \approx$ coefficient of variation) was incorporated into annual recruitment and recruitments used to generate the initial age-structure of the population. The plus group was assumed to have no variation because fluctuations are averaged out over many cohorts. The initial conditions were generated, as described for the estimation procedure, by simulating each cohort from the age at recruitment to the age in the initial population using only movement and natural mortality.

$$R_{y,l} = \frac{S_{y,l}}{\alpha_l + \beta_l S_{y,l}} \exp(\varepsilon_{y,l}^r - 0.5\sigma_r^2)$$

$$\varepsilon_{y,l}^r \sim N(0, \sigma_r^2)$$

To allow for random differences between the exploitation rate on tagged individuals and the exploitation rate on the total population, log-normal variation with a σ_u of 0.3 was incorporated into the exploitation rate on the tagged individuals affecting both the dynamics of the tagged population and the observed recoveries. This implementation for the variation in exploitation rate assumes that individuals tagged in the same subpopulation and of the same age have the same exploitation rate, which is consistent with species that school by age. To keep the recoveries as integers, the binomial distribution was used to randomly determine the number of recoveries from a given exploitation rate and size of the tagged population. This is similar to the individual based approach used by Hampton (1991). The use of the binomial distribution adds a small additional error to the recovery data.

$$r_{y,a,l}^k \sim \text{Binomial}[n = T_{y,a,l}, p = u_{y,l} v_a \exp(\varepsilon_{y,a,l}^u - 0.5\sigma_u^2)]$$

Table 1. Annual exploitation rates.

Year	Exploitation rate
1	0.05
2	0.05
3	0.05
4	0.05
5	0.1
6	0.1
7	0.1
8	0.1
9	0.2
10	0.2
11	0.3
12	0.3
13	0.1
14	0.1
15	0.1
16	0.1
17	0.1
18	0.1
19	0.1
20	0.1

Table 2. Releases by age used in each subpopulation.

Age	Releases
4	1,000
5	740
6	548
7	406
8	301
9	223
10	165
11	122
12	90
13	67
14	49
15	36
16	27
17	20
18	14
19	11
20	8
21	6
22	4
23	3
24	2
25	1
26	1
27	1

$$\varepsilon_{y,a,l}^{\mu} \sim N(0, \sigma_{\mu}^2)$$

To keep the tag recoveries as integers, the number of individuals in the tagged population dying from natural mortality and the number of individuals in the tagged population moving were modeled as binomial and multinomial events, respectively.

$$T_{y+1,a+1,l}^k = \text{Binomial}(n = T_{y,a,l}^k - r_{y,a,l}^k, p = e^{-M})$$

$$X_{y,a,x \rightarrow \cdot}^k = \text{Multinomial}(n = T_{y,a,x}^k, p = p_{x \rightarrow \cdot})$$

$$T_{y,a,l}^k = \sum_x X_{y,a,x \rightarrow l}^k$$

The observed catch-at-age ($C_{y,a}^{\text{Sample}}$) data were generated using a multinomial distribution with a sample size of 500.

$$C_{y,a,l}^{\text{Sample}} \sim \text{Multinomial} \left(n = 500, p = \frac{N_{y,a,l} v}{\sum_a N_{y,a,l} v_a} \right)$$

The artificial data sets were used to investigate the robustness of the ITPDM and ITCAAN models to different characteristics of the population's structure. The population characteristics investigated are outlined below and summarized in Table 3. The exploitation history is given in Table 1, a 10% movement rate is used between all populations for the scenarios with equal movement, and movement rates for the scenarios with unequal movement are given in Table 4B.

- Test 1. Three subpopulations with equal recruitments, the same exploitation histories, and equal movement.
- Test 2. Three subpopulations with *different recruitments*, the same exploitation histories, and equal movement.
- Test 3. Three subpopulations with equal recruitments, the same exploitation histories, and *unequal movement*.
- Test 4. Three subpopulations with equal recruitments *different exploitation* histories, and equal movement.

Table 3. Population characteristics tested in the simulation analysis.

Test	Subpopulation virgin recruitment			Subpopulation exploitation			Movement
	1	2	3	1	2	3	
1	1,000	1,000	1,000	1	1	1	Equal
2	500	1,000	1,500	1	1	1	Equal
3	1,000	1,000	1,000	1	1	1	Unequal
4	1,000	1,000	1,000	0.5	1	2	Equal
5	500	1,000	1,500	0.5	1	2	Unequal

Table 4. Movement rates between subpopulations when movement is (A) equal and (B) unequal.

From	To		
	1	2	3
A: Equal			
1	0.8	0.1	0.1
2	0.1	0.8	0.1
3	0.1	0.1	0.8
B: Unequal			
1	1	0	0
2	0	0.9	0.1
3	0.1	0.2	0.7

Test 5. Three subpopulations with *different recruitments, different exploitation histories, and unequal movement*.

For each of the different population characteristics, 500 artificial data sets were generated and two models were tested by comparing the model estimates to the underlying “real” data. These two models are outlined in the following list.

ITPDM. Integrated tagging and population dynamics model. This model was fitted to the age- and subpopulation-specific tag recovery data while estimating the virgin recruitment and movement parameters.

ITCAAN. Integrated tagging and catch-at-age analysis. This model is similar to ITPDM, except it investigates the benefit of including catch-at-

age data in the likelihood function and estimating the annual recruitment anomalies.

Stock assessments attempt to estimate two main characteristics of a fishery: the status of the stock and the productivity of the stock. These two characteristics can be described by two quantities. The first is the current biomass as a fraction of the initial biomass (B_{cur}/B_1), which indicates the status of the stock in terms of the depletion level. The second is virgin recruitment (R_0), which scales the average productivity of the stock. Estimates of these two values were compared to the true values for the total combined population and for individual subpopulations.

Results

The results are presented graphically as box plots of the relative error in the virgin recruitment (R_0), the initial biomass (B_1), and the depletion level (B_{cur}/B_1) (Figs. 1-7). Relative error is defined as the estimate minus the true value divided by the true value.

$$\text{relative error} = \frac{(\hat{x} - x)}{x}$$

The box represents the quartiles and the whiskers extend to the furthest point excluding outliers (no more than one and a half times the inter-quartile range from the quartile). Each figure includes a cluster of box plots for each of the tests described above. I first describe the results from the ITPDM, then I describe the improvements in the results obtained by adding catch-at-age data (ITCAAN), and finally I discuss the estimates of the movement parameters.

Virgin Recruitment (R_0)

The estimates of R_0 for each subpopulation from the ITPDM are unbiased, but have high variation (Fig. 1). The estimates of total combined R_0 have much lower relative variation. The high variation of the subpopulation R_0 s is caused by interaction between the populations and a confounding between movement and subpopulation R_0 . Variation in subpopulation R_0 and movement cancel each other out in the calculation of initial biomass (B_1) reducing the variation in the estimates of the initial biomass (Fig. 2).

When the three interacting subpopulations have different levels of virgin recruitment (test 2) the relative variation in the estimates decreases as virgin recruitment increases. When movement rates differ between the subpopulations (test 3), subpopulation one has the lowest variation because it has the least interaction with the other subpopulations.

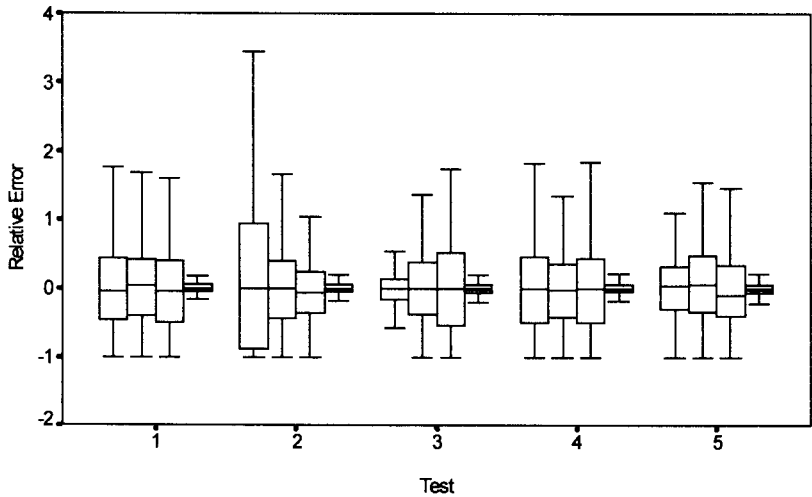


Figure 1. Relative error in the estimation of virgin recruitment, R_0 for ITPDM. The first three box plots in each cluster represent estimates for each subpopulation. The last box plot in each cluster represents the total R_0 , which is the sum of the subpopulation R_0 s.

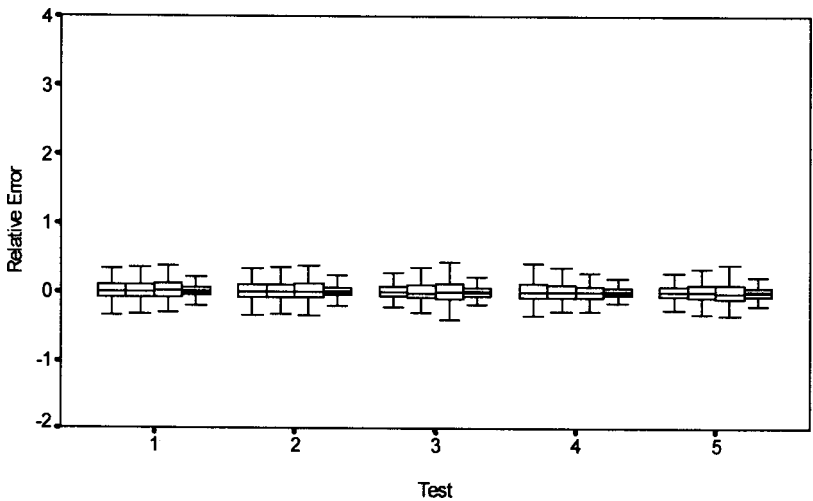


Figure 2. Relative error in the estimation of initial biomass, B_1 for ITPDM. The first three box plots in each cluster represent estimates for each subpopulation. The last box plot in each cluster represents the total B_1 , which is the sum of the subpopulation B_1 s.

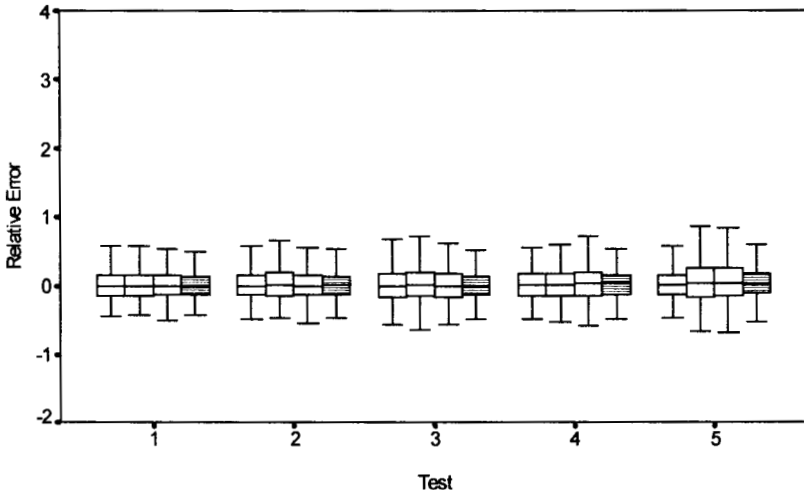


Figure 3. Relative error in the estimation of current stock status, B_{cur}/B_1 for ITPDM. The first three box plots in each cluster represent estimates for each subpopulation. The last box plot in each cluster represents the total B_{cur}/B_1 , which is the sum of the subpopulation B_{cur}/B_1 s.

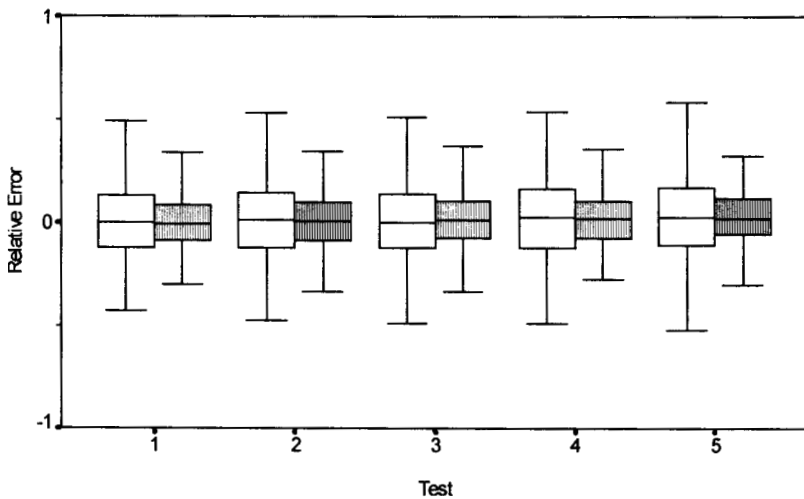


Figure 4. Relative error in the estimation of total combined current stock status, B_{cur}/B_1 , with (ITCAAN) and without (ITPDM) catch-at-age data. The first box plot in each cluster represent estimates without catch-at-age data and the second box plot represents estimates with catch-at-age data.

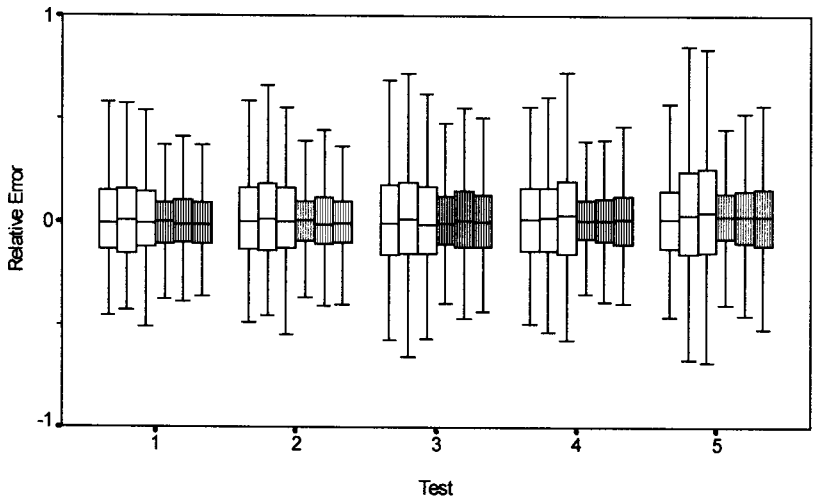


Figure 5. Relative error in the estimation of individual subpopulation current stock status, B_{cur}/B_1 , with (ITCAAN) and without (ITPDM) catch-at-age data. The first three box plots in each cluster represent estimates for each subpopulation without catch-at-age data. The last three box plots in each cluster represent estimates for subpopulations with catch-at-age data.

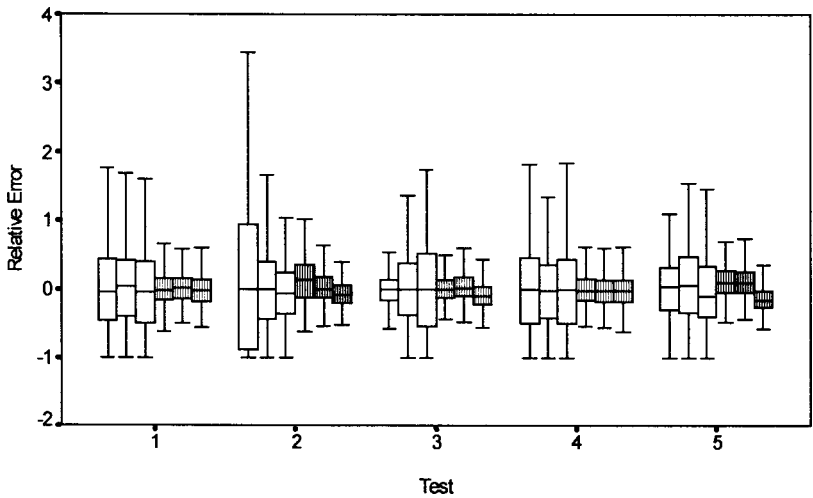


Figure 6. Relative error in the estimation of individual subpopulation virgin recruitment, R_0 , with (ITCAAN) and without (ITPDM) catch-at-age data. The first three box plots in each cluster represent estimates for each subpopulation without catch-at-age data. The last three box plots in each cluster represent estimates for each subpopulation with catch-at-age data.

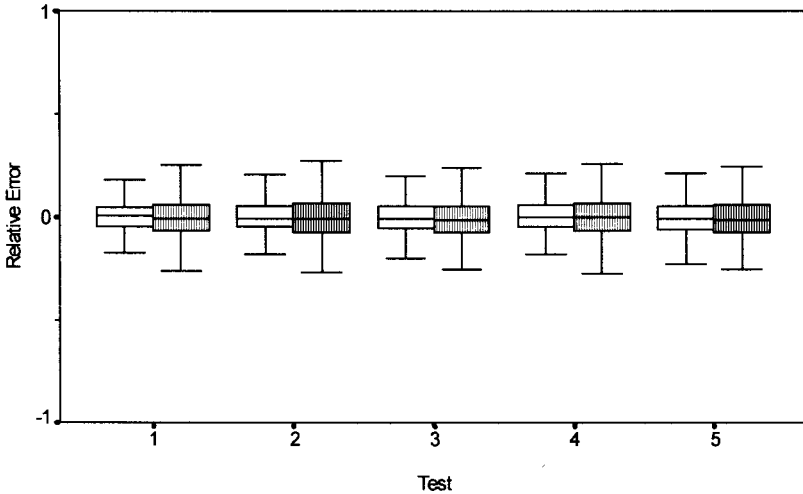


Figure 7. Relative error in the estimation of total combined virgin recruitment, R_0 , with (ITCAAN) and without (ITPDM) catch-at-age data. The first box plot in each cluster represents estimates without catch-at-age data and the last box plot represents estimates with catch-at-age data.

Current Biomass as a Proportion of Virgin Biomass (B_{cur}/B_0)

There is no bias in the estimates of B_{cur}/B_1 from ITPDM (Fig. 3). Relative variation in the estimates of subpopulation B_{cur}/B_1 is much smaller than for the estimates of R_0 (Fig. 1), but slightly higher than the relative variation in estimates of B_1 (Fig. 2). Variation in the estimates of total combined B_{cur}/B_1 are only slightly smaller than those for individual subpopulations estimates.

Catch-at-Age Data

The addition of catch-at-age data (ITCAAN) reduces the variation in the estimates of total combined (Fig. 4) and subpopulation (Fig. 5) B_{cur}/B_1 . This reduction in variation is expected because of the addition of information on recruitment strength. The ITCAAN model also greatly reduces the variation in the estimates of subpopulation R_0 (Fig. 6) at the expense of slightly increasing the variation in the estimates of the total combined R_0 (Fig. 7).

Movement

Estimates of movement parameters from ITPDM had no bias and small variation (90% of the artificial data sets gave an error approximately between -20% and 20%). The addition of catch-at-age data (ITCAAN) produced

a slight bias of around 1%-2%, but reduced the variation (90% of the artificial data sets gave a error approximately between -15% and 15%).

Discussion

Testing the integrated tagging and population dynamics model (ITPDM) against artificial data sets indicates that the integrated approach is a promising method to incorporate tagging data into fisheries stock assessments. The parameter estimates (movement and virgin recruitment) and current stock status were not highly biased. There was very little variation in the estimates of productivity (virgin recruitment) for the total population, but greater relative variation in estimates of productivity for individual subpopulations. The addition of catch-at-age data and estimation of annual recruitment anomalies in the ITCAAN model greatly reduces the variation in estimates of virgin recruitment for individual subpopulations. Relative variation in the estimates of individual subpopulation current stock status (B_{cur}/B_1) is small compared to the relative variation in estimates of productivity and this variation can be further reduced by including catch-at-age data and estimating recruitment anomalies.

Individual estimates of virgin recruitment for each subpopulation are very sensitive to small changes in the movement rates. This sensitivity is due to the compounding of the movement effect on the equilibrium unexploited population size. The estimates of the sum of virgin recruitment over all subpopulations and the estimates of individual subpopulation initial population size are less variable, indicating a confounding between movement and individual subpopulation virgin recruitment. The addition of catch-at-age data and estimation of annual recruitment anomalies in the ITCAAN model appears to remove the confounding. This is a promising characteristic and it may be possible that the ITCAAN model, which provides information on selectivity from the age-specific tagging data and information on recruitment from the catch-at-age data, can also remove the confounding between estimates of recruitment and selectivity that has been seen in some assessment models (e.g., Annala and Sullivan 1997).

Estimates of current stock status (B_{cur}/B_1) are only moderately variable despite annual variation in recruitment. This leaves little room for catch-at-age data to reduce the variance. Increased recruitment variability or higher dependence of the population size on recruitment will increase the variability in the estimation of current stock status. In these cases, the inclusion of catch-at-age data will be more important for reducing variance in estimates of current stock status. In this study, recruitment was assumed to be independent between subpopulations; however, real populations may show correlation in annual recruitment strength between subpopulations, which may increase variation in estimates of current stock status.

I have also used the simulated data to investigate the performance of fitting the population dynamics model to biomass estimates from a Petersen analysis (Petersen 1896, see Maunder 1998). This method produced biased estimates of subpopulation productivity and subpopulation current stock status. In addition, the variation for estimates of individual R_0 were much smaller in the Petersen analysis than for the ITPDM and could therefore give a false sense of security if bias is not taken into consideration. The biased estimates were caused by interactions between the subpopulations and the lack of movement in the population dynamics model. Stratified-Petersen estimates (Schwarz and Taylor 1998) could be used to incorporate movement, but the integrated approach would be a more flexible framework.

The results suggest that a tagging study with a single release period and multiple recovery periods may be adequate to assess a recently exploited fishery that is based on interacting subpopulations. All that is needed, in addition to the total catch data and the standard biological parameters, is tagging data recorded by age and subpopulation. The method can be compared to cohort analysis (Pope 1972) with the addition that the population size and age-structure of the tagged population are known at the time of tagging. For this reason, the Integrated Tagging and Population Dynamics Model should be superior to a simple VPA that uses only catch-at-age data. As indicated by the results presented in this study, the ITCAAN model, which also includes catch-at-age data, should perform even better. Any comparisons should consider sample size limitations based on the costs of the tagging study. Additional biases caused by the inherent problems in tagging studies (reporting rates, tag mixing, tag shedding, tagging mortality, etc.) and problems with aging released and recovered fish also need to be considered.

A main assumption of the multinomial likelihood function is that the fate of each tagged animal is independent of other tagged animals. Kleiber and Hampton (1994) suggest that the multinomial likelihood may be inappropriate because tags are not independent due to the schooling behavior of fish. To overcome this schooling effect, a number of studies start recording recoveries after a given time to allow mixing of tags (e.g., Kleiber and Fonteneau 1991). In the analyses presented here, errors introduced into the tag recovery data assumed that fish school by age. The results indicate that there will be no bias in point estimates caused by schooling if there is random fishing on these schools, but it is likely that schooling increases the variance of parameter estimates.

The model used to generate the artificial data was based on the ITCAAN estimation model. Therefore, it should not be surprising that the ITCAAN estimation model performed well. The performance of the estimation model will be dependent on what parameters are estimated and how much variability (process and observation error) is included in the simulation model. Despite the deficiencies of simulation testing, some important results have been highlighted and are discussed above. Simulation testing using more

complex models to generate the simulated data and applications to real data (see Maunder [1998] for an application) are needed to further investigate the ITCAAN approach.

Despite the advantages of the ITPDM approach, three major disadvantages must be noted. First, as the data become more detailed, the approach requires more complex models to represent the observed data. Secondly, because each tag group is modeled as a separate population, the computational time is great. Finally, the method relies on knowing the age of all the released individuals, which can usually only be done by converting the length at release into age using an age-length key. An age-structured (Fournier et al. 1998) or length-structured (Maunder 1999) catch-at-length model integrated with the tagging analysis may be more appropriate when aging is difficult.

It is important to understand that the framework described here is not a single model, but a modeling approach that can be applied in many more situations than the simple ITPD or the ITCAAN models described above. Modifications can be made to the structure of the model, the parameters that are estimated, or the data and the objective functions that are used. Alternative model structures could include age specific or seasonal movement (Maunder 1998), multiple gears (Fournier et al. 1998, Maunder and Starr 2000), advection-diffusion movement (Sibert et al. 1999), or continuous fishing and natural mortality (Fournier et al. 1998, Haist 1998). The use of the ITCAAN model shows that it is easy to incorporate additional data into the likelihood function, and data that is commonly included in fishery stock assessments can be added to the analysis: for example, relative abundance indices based on standardized catch per unit of effort, recruitment indices (Maunder and Starr 2000), or catch-at-length data (Fournier et al. 1998). Other likelihood functions can be used for the tagging data; for example, the Poisson (i.e., Kleiber and Hampton 1994, Sibert et al. 1999) or Fournier et al.'s (1998) robust likelihoods modified for tagging data. There is also the possibility to estimate additional parameters (i.e., natural mortality, gear selectivity, stock recruitment steepness, tag loss, tag mortality, and tag reporting rates) or start from an exploited population size (Maunder and Starr 2000). Other data that are usually analyzed separately could be incorporated into the ITPDM in a similar fashion to the tagging data (integration into the population dynamics model of standardized CPUE analysis [Maunder 2001], trawl survey data, environmental variables [Maunder and Starr 2000], growth estimation [Maunder 1999], etc.).

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Toward an Environmental Analysis System to Forecast Spawning Probability in the Gulf of California Sardine

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Abstract

The fisheries for small pelagic fish are subject to large fluctuations in landings and hence are difficult to manage. The necessity of including environmental variability and its effects in monitoring and evaluation of

these fisheries is well recognized. Comparative approaches used in modern fisheries science have identified temperature and wind-driven oceanographic features as the main physical mechanisms through which environmental variability affects changes in populations. In particular it appears that these oceanographic features play a key role in determining reproductive success. In this paper we attempt to link these physical and biological processes by designing functions that relate temperature and upwelling to spawning activity and explore the feasibility of integrating these functions into an information system for the Gulf of California sardine fishery. Specifically, we have derived double logistic functions relating spawning probability to sea surface temperature and an upwelling index and these functions are then used to compute a spawning probability time-series. These functions may also provide estimates of annual landings. The second part of this paper explores the design of a geographical information system in which data on winds, satellite-derived temperatures, and pigment concentrations would be stored and used to calculate modeled individual-associated spawning probability leading to forecasts of spawning probability. If successful, this system could be applied to other regional resources.

Introduction

The fishery for small pelagics in the Gulf of California is both the largest fishery in Mexico (representing up to 40% of total catch for some years), and also one of the most problematic to manage. As happens in many small pelagic fisheries around the globe, large fluctuations in catch result in severe economic and social problems. In the Gulf of California, the collapse of the 1990-1993 fishery resulted in the loss of more than 3,000 direct jobs and about half of the fleet capacity and processing plants (Cisneros-Mata et al. 1995). Substantial evidence from this and other regions of the world indicates that large fluctuations in catch are not explained solely by the effects of fishing (Holmgren-Urba and Baumgartner 1993, Cisneros-Mata et al. 1995, Nevárez-Martínez et al. 1999), and this evidence emphasizes the necessity of including environmental effects into management schemes. One approach used by fishery scientists is to look at critical periods in the population's life history cycle (for example, spawning) and attempt to identify key environmental stresses for that biological process. The mechanisms by which the environment affects the biology are then investigated, and functions and models relating physical to biological processes are introduced into environmental analysis systems to forecast conditions.

Comparative research programs in fishery science have already led to advances in this approach. For example, the Climate and Eastern Ocean Systems Project (CEOS; Bakun et al. 1998) has provided key clues to understanding the mechanisms linking physical forcing agents to biological populations (e.g., Parrish et al. 1983, Roy et al. 1992, Bakun 1993). Regarding

small pelagics, perhaps the best known example of such advances in the study of small pelagics was the observation by Cury and Roy (1989) of a level of wind stress that provides optimal environmental conditions for reproduction. More recently Bakun (1996) has proposed a fundamental triad consisting of enrichment, concentration, and retention.

Despite improved understanding of the linkages between physics and biology, there has been limited success in designing quantitative, predictive functions and models of recruitment and catch. This report describes preliminary results of efforts to build such an environmental monitoring and analysis systems for the small pelagic fisheries.

Gulf of California Sardine as a Case Study

Due to a unique combination of factors the Gulf of California sardine fishery offers much promise as a site for analysis of spatial processes and new management approaches. The Gulf of California is a suitably sized basin for mesoscale physical modeling: it is often cloud-free, which makes it ideal for monitoring by satellite imagery; and it has been sufficiently studied to offer a good amount of environmental data. There have been, for example, many basic studies of sardine biology (Nevárez-Martínez 1990, Cisneros-Mata et al. 1995, Lluch-Belda et al. 1995), and there is currently much effort to identify population responses to environmental variability (Hammann 1991, Hammann et al. 1998, Nevárez-Martínez et al. 1999). Furthermore, despite being relatively young (considered stable only since 1982-1983), there have been large and rapid changes in the fishery during the last 15 years: (1) a dramatic collapse between 1989-1990 and 1992-1993 when landings decreased from nearly 300,000 t to less than 7,000 in four years; (2) a rapid recovery leading to increased landings up to 200,000 t by 1996-1997; and (3) a recent drop to 64,000 t, apparently related to the 1997-1998 El Niño Southern Oscillation (ENSO). The rapid recovery during the present season, as indicated by partial catch trends and other indirect evidence, suggests that 1997 ENSO primarily affected fish distribution (M.O. Nevárez-Martínez, National Fisheries Institute [INP], Mexico, pers. comm.). While these rapid variations in catch have resulted in substantial problems for fishermen and managers, they do provide an excellent case study to explore forecasting and early detection capabilities of dramatic fluctuations in biomass.

Methods

Functions

To explore the feasibility of expressing the productivity of the Gulf of California's small pelagic fishery in terms of easily measured environmental variables, the proportion of positive stations (stations where sardine eggs and/or larvae were found) was used as a proxy for spawning success. The data set that we used came from 24 cruises conducted between 1971

and 1987 and covered the central Gulf of California (data provided by M.O. Nevárez-Martínez, INP, Mexico). We examined the time series of eggs and larvae within the context of the coincident time series for temperature (SST), extracted from the Reynolds SST database (Reynolds and Smith 1994), and a monthly upwelling index (UI) for the central Gulf of California (Lluch-Cota 2000).

Because relationships between physical and biological variables are commonly nonlinear (dome-shaped) and not symmetric, the function that we have applied to our analysis of spawning probability was a function recently proposed by Lluch-Cota et al. (1999). In this function spawning probability (SP) is expressed as the product of two logistic equations, each a function of a single environmental parameter (the independent variable):

$$SP = [1 / (1 + ae^{b \times Ph})][1 / (1 + ce^{d \times Ph})]$$

Where SP is the spawning probability; Ph is the value of the physical (independent) variable; a , b , c , d are constants; and b and d will be of opposite sign. According to this formulation spawning success responds to two mutually exclusive inverse processes that are each determined by the value of the independent variable. If b is positive and d is negative, the first term on the righthand side of the equation describes nonlinear increases in spawning success with increases in the value of the physical variable, and the second factor describes nonlinear decreases in spawning success with increases in the value of the physical variable. Because the response variable is given as a probability, the maximum possible value of individual curves (commonly called K) takes the value 1.

In our analysis we apply two such formulations. One function represents spawning success as a function of the value of the upwelling index at a selected time, and the other function represents spawning success as a function of temperature at a selected time. The function relating spawning probability to the upwelling conforms to the concept of the optimal environmental window. The rationale for an optimal window for the upwelling is based upon Bakun's hypothesis of fishery production. At low rates of upwelling spawning probability is limited by enrichment. Increases in upwelling winds will increase nutrient supplies to surface waters and increase the availability of food to spawners. On the other hand, low rates of upwelling will be accompanied by low rates of Ekman transport and eggs and larvae will tend to be retained in the region where spawning occurs. These conditions may promote spawning by adults. Increases in upwelling winds will lead to increased Ekman flow and eggs and larvae will be more rapidly transported offshore from the region of spawning. These conditions may suppress spawning by adults.

In previous studies, Lluch-Cota et al. (1999) proposed a theoretical model for the physical settings of a triad system in the Gulf of California, where enrichment processes (strong tidal mixing and coastal upwelling driven by northwesterly winds) provide nutrient-rich waters that are carried by sur-

face currents and Ekman transport into an area of high water column stability, food concentration, and larval retention. We used monthly UI values as a proxy for the triad elements, in this case the limiting factors considered by the double logistic model are that weaker winds result in low upwelling related enrichment and weak circulation (gyres), while stronger winds result in extremely high dynamics and poor retention and concentration conditions (Fig. 1).

In the case of temperature the rationale is more straightforward since temperature directly affects growth rates and other specific metabolic activities, and optimum values have already been observed by other authors (Hammann et al. 1998, Lluch-Cota and Lluch-Belda 2000).

In previous studies, the probability of finding sardine eggs at different SST was estimated from the percentage of positive stations and the corresponding in-field temperature values. By fitting a 5-term polynomial model, Hammann et al. (1998) inferred a temperature-dependent spawning habitat for sardine in the Gulf of California. Lluch-Cota and Lluch Belda (2000) tested the feasibility of using a mesoscale, near-real-time, temperature data source (Reynolds SST) instead of sampling-derived temperature data. For this study we fitted the double logistic model relating spawning probability to SST (Fig. 1) which resulted in a similar shape to that of Hammann et al. (1998) and Lluch-Cota and Lluch-Belda (2000).

Clearly, interactions between the different environmental stress sources are to be expected. As a preliminary exploration, we computed the spawning probability time series by applying the functions to the original environmental data, and then empirically compared it to the catch series. After testing for time lags, we combined the two individual double logistic models (SST and UI) into a response surface (Fig. 1) where probability of spawning success is expressed as the product of the two double logistic curves (temperature and upwelling related spawning success) and the maximum possible probability takes again the value 1.

Environmental Analysis System Design

The second part of this paper deals with the design of an environmental monitoring system. In doing so, we considered three main components: input data coming from near real-time monitoring of environmental variables; distribution in time and space of key environmental proxies derived from the original input data (temperature, enrichment, concentration, and retention); and a geographical information system that will integrate this information, thereby giving a proxy of reproductive habitat.

Because satellite color and thermal imagery offers detailed spatial and temporal information on the concentration of chlorophyll and sea surface temperature, we feel that the processes of enrichment and temperature are more easily monitored than are the two remaining parameters of the triad, concentration and retention. The consistently clear skies above the Gulf of California ensure the acquisition of a relatively continuous time series. On the other hand, retention and concentration are very hard to quantify, and

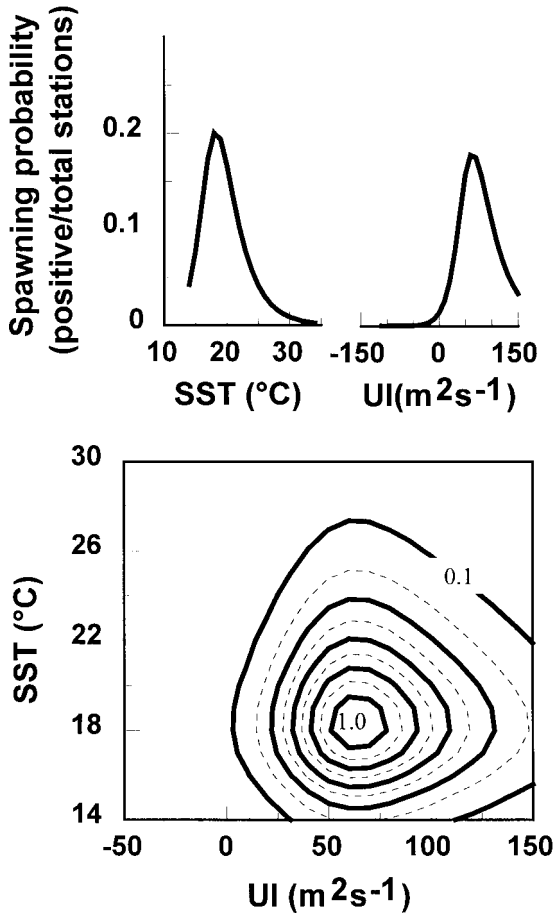


Figure 1. Double logistic models relating spawning probability to SST and UI, and response surface representing the product.

neither a time series nor a monitoring system for these variables exists. One means of estimating these parameters of circulation is to model flow fields by application of dynamic numerical models. Outputs from the circulation model can then supply inputs to a Lagrangian model which will provide direct estimates of parameters that characterize concentration and retention.

Specifically, concentration can be estimated by running the Lagrangian model after seeding the computational grid with particles and registering their distribution after a certain time interval. After running the experiment several times, average results should provide a characterization of concentration at convergence zones. Similarly, retention can be estimated by measuring the time it takes for each of the seeded particles to leave from a predetermined area.

We have been working with the *S*-coordinate Rutgers University Model (SCRUM; Song and Haidvogel 1994) implemented for the Gulf of California by one of the coauthors of this paper (A.P.S.) using a 40×200 horizontal grid and vertical resolution level of 20. The simulation contains realistic bathymetry, and open boundary at the gulf entrance, and is forced with a monthly resolution by a wind field computed from COADs observations and tropical Kelvin waves at the south end of the gulf. This model could be improved by including tidal-driven diffusion, variable density values, and ocean-atmosphere heat exchange.

The advantages using this type of model are the explicit representation of vertical velocities and transports, the capability of increasing the vertical and horizontal resolution in selected areas, and the high spatial resolution. The open boundary at the entrance of the gulf allows us to examine the influence of the Kelvin waves. An additional advantage that we feel is unique and most important to successful prediction in the gulf is forcing the model with near-real wind measurements rather than a constant, equally distributed, discrete wind field. We plan to explore the possibility of obtaining such information from radar measurements.

Results and Discussion

Figure 2 shows times series of catch records and the spawning probability time series calculated from temperature and upwelling index (averaged over the November to May reproductive season). The upper panel shows that during the entire series the spawning probability calculated from the upwelling index precedes the catch with variable time lags but with the best fit (linear cross correlation) at a time lag of 1 year. No time lag is observed between temperature-dependent spawning probability and catch, and the temperature-dependent spawning probability time series shows very poor sensitivity except for extreme events (1997-1998 ENSO). We are aware that this finding is puzzling and we do not have a full explanation; however, there is evidence indicating that temperature affects spawning by controlling the size and location of the spawning ground (Lluch-Belda et

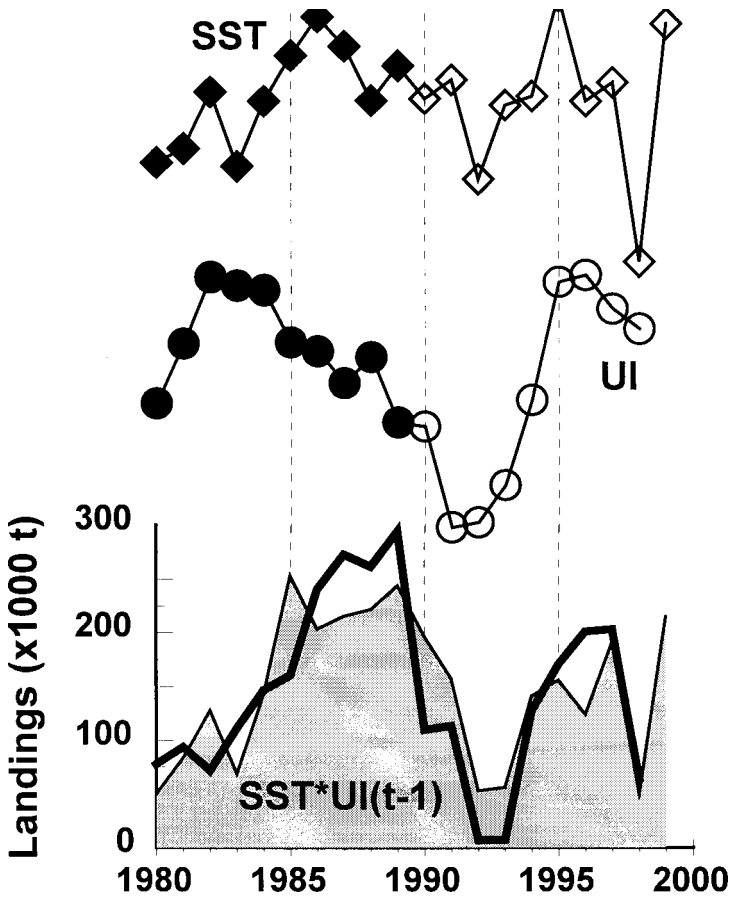


Figure 2. Time series of spawning probability estimated from the SST (diamonds) and UI (circles) functions, and from the combined functions (shade; product of the SST and UI functions, with UI related series lagged 1 year), as compared to annual landings (heavy line). Open diamonds and circles represent years for which no data were used to fit the functions.

al. 1986, Hammann et al. 1998), and by controlling the southward movement of adults before the spawning season. We believe that our observation is better explained in terms of the effects of temperature on the distribution of adults. It is likely that ongoing research on the relationship between adult distribution and environmental conditions (M.O. Nevárez-Martínez, INP, Mexico, pers. comm.) will provide further clues to this puzzle.

The lower panel in Fig. 2 shows the spawning probability series derived by combining UI and SST related spawning probability, and observed catch. Clearly, the effects on spawning are better described by the upwelling proxy, while the SST series might only provide information relating to changes in spawner distributions during extreme SST events. The correspondence between the combined spawning probability time-series and observed catch is highly encouraging, especially for the periods of collapse (1990-1993), recovery (1993-1997), and the 1997-1998 sharp catch decrease. The last point (1999) in the spawning probability curve was estimated using only temperature records, and this calculation predicts a recovery in the catch level that has been confirmed by coincidence with field observations and preliminary catch records (M.O. Nevárez-Martínez, INP, Mexico, pers. comm.). In our analysis, values for the spawning probability are dimensionless, consisting of probability values between 0 and 1. Development of a forecasting model to predict catch levels could be built by simple linear regression; however, we believe that this further step should be taken once other sources of data (i.e., fishing effort, adult information, age structure, fish availability, etc.) are incorporated into the analysis.

A fact worth recalling is that the SST and UI functions were derived using cruise data (independent from the catch series) collected before 1989; thus, the variability calculated by our function between that year and 1998, when the strongest and most rapid fluctuations took place, was completely predictive and independent of the database.

Figure 3 shows an example of the possible indices to be used at designing the information system. Proxies of relevant environmental processes were computed as spatial distribution of enrichment as predicted from the average monthly pigment concentration, concentration as predicted from calculations with the Lagrangian model of transport of particles initially uniformly distributed across the central Gulf of California after 1 month of wind-driven circulation, and retention as determined by calculation with the model of particle escape velocity 15 days after initialization during the months of May and August. The circle at each figure represents the region where major egg distribution is to be expected, according to previous descriptions.

In this example, enrichment, concentration, and retention all occur within the selected area during May, usually the last month of the spawning season. During August, high enrichment is not clearly taking place inside the circle, except for a small region at the western coast. While retention is always present, concentration of particles takes place only at the eastern

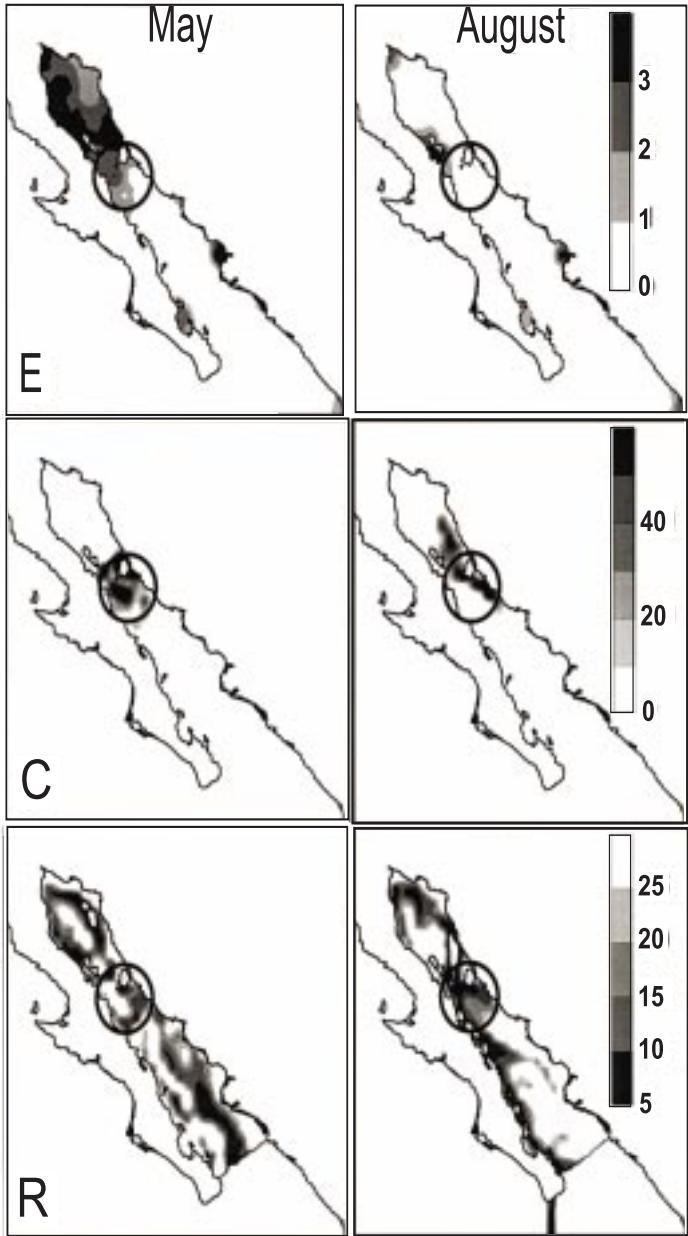


Figure 3. Example of spatial distributions of enrichment (E; monthly pigment concentration), concentration (C), and retention (R) proxies for average May and August modeled circulation. The circle represents the area where sardine eggs are more frequently found.

coast, where there is no enrichment. These indices could be dynamically estimated using a wind matrix of measured values.

One promising approach to integrate these key environmental variables is to compute the spawning probability of individual fish distributed within the central Gulf of California. Such integration of information from field data, models, and satellite imagery can be achieved by application of a geographic information system, and we believe that a software package called EASy (Environmental Analysis System) offers much promise (Tsontos and Kiefer 1998). EASy is an advanced GIS, designed (1) to import and assimilate diverse types of information (textual, tabular, graphical, and imagery); (2) to analyze this information by application of custom algorithms and models; and (3) to display the products as maps, plots, and tables. The software, which has been developed in part by one of the coauthors of this paper (D.K.) provides an integrated graphical and computational framework in which diverse types of information can be placed within a common four-dimensional context: time, latitude, longitude, and altitude or depth. The system can be operated in several modes, using the menu bar: (a) simulation of a time series, (b) real-time processing of data from sensors or remote computer sites, (c) creating and running motion pictures of a time series, and (d) browsing maps and images independently of time. Our examination indicates that EASy provides sufficient functionality and ease of use to build the monitoring and analysis system that we envision.

Despite encouraging advances in designing the functions and the information system, further work is required to estimate spawning probability functions for each of the selected environmental proxies. The calculation of spawning probability will likely require inputs in addition to the upwelling index and temperature. The inputs may also require greater spatial and temporal resolution. For example, our upwelling index is simply the transformed wind signal from a single local weather station and our temperature series is a gross proxy for the entire central Gulf of California. It is also likely that predictions will improve by including information on vertical profiles of properties such as temperature and chlorophyll concentration which can be measured from moorings and ships. Geographical information systems such as EASy easily handles such information as well as the time-dependent, three-dimensional information that is provided by circulation models.

We believe research must be conducted to test and improve the forecasting capabilities of this system. More survey data on egg and larval distributions, recruitment and biomass estimates, and longer time series will come in the future. Finally, it is clear to us that at this stage only one part of the population dynamics is considered (reproduction), and that additional modules dealing with aspects such as adult distribution and accessibility, fishing mortality, and growth should be incorporated in the future. If successfully implemented, this system can be adapted to aid the

monitoring and analysis of small pelagic fisheries in other coastal regions of the world.

Acknowledgments

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Ocean Current Patterns and Aspects of Life History of Some Northwestern Pacific Scorpaenids

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Abstract

The life histories of the most commercially important northwestern Pacific scorpaenids (shortraker rockfish, *Sebastes borealis*; shortspine thornyhead, *Sebastolobus alascanus*; and broadbanded thornyhead, *Sebastolobus macrochir*) and the role of ocean current patterns in transporting pelagic larvae and/or juveniles throughout their range are poorly understood.

Ocean current observations along with biological data on spawning locations, size compositions, and information from captured benthic juveniles from sampling conducted from 1993 to 1999 in the western North Pacific Ocean waters off the northern Kuril Islands, southeastern Kamchatka, and the western Bering Sea were analyzed and compared with published data. From these comparisons, some characteristics of their life histories are considered.

Adult shortraker rockfish are most abundant in waters of eastern Kamchatka, the western Bering Sea, the Gulf of Alaska, and the coastal waters of Washington, Oregon, and British Columbia. Juveniles in significant numbers occur only off the Kuril and Aleutian islands, and in the eastern Bering Sea. Comparison of current data in the subarctic Pacific region suggests that shortraker rockfish complete lengthy migrations. Pelagic larvae and juveniles born off the British Columbia, Oregon, and Washington coasts and in the Gulf of Alaska are transported by currents mostly to the Aleutian Islands. Pelagic larvae and juveniles originating off eastern Kamchatka and to a lesser extent Paramushir Island, are primarily carried by currents to the Kuril Islands. From the western Bering Sea and the Commander Islands, pelagic larvae and juveniles are carried mainly to the northern Aleutians and into the eastern Bering Sea. Settlement of juveniles occurs at a length of approximately 10 cm. Reverse migrations to

reproductive areas peak at lengths over 35 cm. Some juveniles may not perform lengthy reverse migrations but instead form temporary dependent populations by lingering in areas with quasi-stationary anticyclonic eddies.

The main spawning areas of thornyheads and capture sites of their benthic juveniles occur off southeastern Kamchatka, Paramushir Island, and around an underwater plateau southeast of Onkotan Island coinciding with quasi-stationary anticyclonic eddies. Settlement of shortspine thornyhead occurs by a length of about 25 mm while broadbanded thornyheads settle to the sea bottom at a length of approximately 70 mm. After settlement, juvenile broadbanded thornyhead migrate into shallower waters while, conversely, shortspine thornyhead migrate deeper.

Introduction

Shortraker rockfish (*Sebastes borealis*), shortspine thornyhead (*Sebastolobus alascanus*), and broadbanded thornyhead (*Sebastolobus macrochir*) represent an important component of the outer shelf and continental slope fish fauna in temperate and subarctic regions and are common in the North Pacific Ocean. These species are especially prized because their red color and delicious meat make them valuable on the Asian market.

The shortraker rockfish is endemic to the North Pacific Ocean. It is distributed from Japan (39°50'N) and southern California (40°46'N) to the Bering Sea including the Pacific waters off the Kuril and Aleutian islands, the east coast of Kamchatka, the Gulf of Alaska, British Columbia, Oregon, and Washington. This species is considered commercially important off eastern Kamchatka, off the northern Kuril Islands, in the Aleutian Islands region, and in the Bering Sea and Gulf of Alaska.

In the northwestern Pacific, the genus *Sebastolobus* is represented by two species: broadbanded thornyhead (*S. macrochir*), and shortspine thornyhead (*S. alascanus*). The first species is distributed from the Pacific coast of Japan (Sagami Bay) to the central Bering Sea and Aleutian Islands including the continental slope of the Sea of Okhotsk. The other species is distributed more widely, along both American and Asian coasts, from California and northeastern Hokkaido in the south to the central Bering Sea in the north including the southeastern Sea of Okhotsk. Both species are commercially important targets of bottom trawl and gillnet fisheries in the North Pacific (Low 1991, Koya et al. 1995).

All three species have pelagic larvae and juveniles (Moser 1974, Matarese et al. 1989). Their life history is poorly studied and the role of ocean currents in carrying larvae and/or juveniles throughout their geographical range remains unclear. Information important for rational management of the species such as stock structure and the degree of mixing among populations is still missing. Questions such as whether these species perform lengthy migrations or whether discrete populations exist are unanswered. Some recent publications dealing with genetic and parasitologic studies of

rockfishes (Moles et al. 1998, Hawkins et al. 1998) attempted to answer the above questions. In this paper we analyze the spatial distribution and the relative abundance of shortraker rockfish and two species of thornyheads. We provide information on the location of their benthic juveniles, and consider regional changes in size composition of these species. A hypothesis regarding the role of North Pacific current patterns in the life histories of shortraker rockfish and thornyheads is presented.

Material and Methods

Data were analyzed from research cruises conducted from 1995 to 1997 by Japanese trawlers in the western Bering Sea (*Kayo Maru* No. 28 and *Tenyu Maru* No. 57) and from cruises conducted from 1993 to 1999 in waters off the northern Kuril Islands and southeastern Kamchatka (*Tora Maru* No. 58, *Tomi Maru* No. 82, *Tomi Maru* No. 53, and *Hokuyu* No. 88). Data were obtained from more than 1,300 bottom trawl hauls conducted during research surveys and commercial fishing operations. Fishing was conducted 24 hours a day at 75-850 m depths using a 5.0-7.0 m (vertical opening) by 25.0-30.0 m (horizontal opening) bottom trawl constructed from 60 mm (stretched mesh) polyethylene netting. The trawl was outfitted with a steel rubber ball roller gear footrope extending from the forward wings to the mouth of the trawl.

During bottom trawl surveys, the entire catch was weighed and enumerated. During commercial fishing operations, representative samples were obtained from each trawl haul, sorted by species and then counted and weighed. The results were then extrapolated to the total catch.

The total fish length (TL) was measured for each of the three species considered, from the tip of the snout to the end of the center of the caudal fin. To analyze regional geographic variations of shortraker rockfish size composition in the northwestern Pacific, we combined length frequency data within 1° latitudinal sections. To analyze seasonal and interannual changes of shortraker rockfish size composition in the northwestern Pacific, we combined the length frequency data within six areas (central Kuril Islands, north Kuril Islands, southeastern Kamchatka, Olyutorskiy Gulf, and Shirshov Ridge, 171°-177°E, 177°E-180°). During the period of investigation, more than 66,000 specimens of shortraker rockfish, 26,000 specimens of shortspine thornyhead, and 114,000 specimens of broadbanded thornyhead were measured. Data from bottom trawl surveys published by NMFS (Bakkala et al. 1992, Harrison 1993, Ronholt et al. 1994, Martin 1997) were used to derive an analysis of shortraker rockfish size composition in the northeastern Pacific Ocean.

The minimum length of benthic juveniles in bottom trawl hauls was 86 mm for shortraker rockfish, 84 mm for shortspine thornyhead, and 103 mm for broadbanded thornyhead. Broadbanded thornyhead with lengths under 130 mm, and specimens of the other two species with lengths under 150 mm were chosen for an analysis of the spatial distribution of benthic juveniles. Benthic juveniles of both thornyhead species are readily

distinguished each from other by their body form, head spines, and thorns. Larvae and pelagic juveniles of shortraker rockfish have not been described until now. Benthic *Sebastes borealis* juveniles are readily identified by distinctive characteristics. Moreover, there are only two abundant rockfish species in the area considered (Pacific ocean perch [*S. alutus*] and shortraker rockfish), which are easily distinguished from each other by body form, coloration, and size of the symphyseal knob on the tip of the lower jaw. Juvenile shortraker rockfish are also distinguished by their body color from juvenile rougheye rockfish (*S. aleutianus*), which is rare in the northwestern Pacific.

Results

Shortraker Rockfish

The analysis of shortraker rockfish size composition data from the northwestern Pacific showed that from the Kuril Islands to the western Bering Sea the mean lengths, modal classes, and abundance of large-size fishes in bottom trawl catches increased, and that the number of juveniles, in contrast, decreased (Fig. 1). The length frequencies of shortraker rockfish in various parts of the northwestern Pacific over a several-year period are presented in Table 1. Shortraker rockfish size composition is characterized also by considerable seasonal variation (Table 2). In the central Kuril Islands area, seasonal and interannual changes in the size composition of shortraker rockfish are low, while in other areas they are rather large.

The map of the multiannual spatial distribution in April-June (Fig. 2) shows that shortraker rockfish are most abundant in the postspawning period within only two areas (CPUE over 500 kg per hour): off southeastern Kamchatka and south of the strait between Paramushir and Onkotan islands. In the same time period, shortraker rockfish juveniles are only abundant (Fig. 3) in the second of the above areas. These juveniles occupied a more narrow depth range in comparison with adults (Table 3). Thus, most adults (64.46 % relative abundance) are distributed within 351-500 m depths while most juveniles (79.08%) inhabit the depth range between 401 and 550 m. From April to June, smaller shortraker rockfish are taken in the southern part of the investigated area and within localized areas off southeastern Kamchatka to the north of 51°N (Fig. 4). Within the same time frame, larger specimens with a mean length over 60 cm are caught off Paramushir Island and southeastern Kamchatka to the north of 52°N, suggesting these areas as potential spawning grounds.

Thornyheads

Records of pelagic egg balloons (Pearcy 1962, Fukataki 1963) and the dynamics of gonad maturation of thornyheads (Koya et al. 1995, Koya and Matsubara 1995) showed that mating and spawning occur from February to April. Our observations off the northern Kuril Islands and southeastern

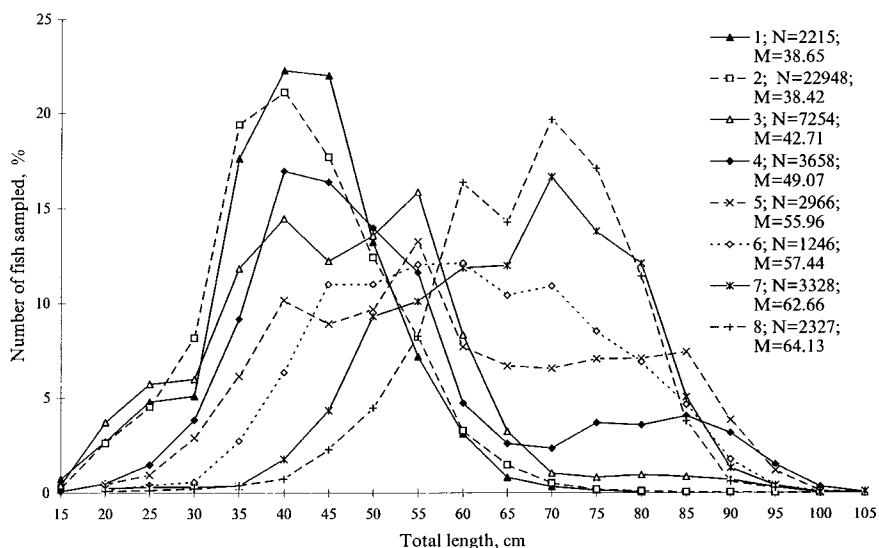


Figure 1. Length frequencies of shorttraker rockfish in various areas of the north-western Pacific Ocean. N = number of fish sampled, M = mean length, 1 = 47-48°N, 2 = 48-49°N, 3 = 49-50°N, 4 = 50-51°N, 5 = 51-52°N, 6 = 59-60°N, 7 = 60-61°N, 8 = 61-62°N.

Kamchatka are limited to the period from April to December, therefore information on spawning of thornyheads is derived from indirect data. In April, all mature fishes of both thornyhead species are in postspawning condition. The maps of mean multiannual distribution of thornyheads during April-June, i.e., just after spawning, may allow assessment of their spawning distributions. Catch rates for broadbanded thornyhead of over 50 kg per hour (Fig. 5) were observed along much of the slope with the largest catches (over 500 kg per hour trawling) occurring southeast of Onekotan Island, indicating that spawning may occur continuously within the entire investigated area, but more strongly in the southern part.

This hypothesis is confirmed by the pattern of distribution of broadbanded thornyhead benthic juveniles (Fig. 6), which are also caught more frequently in the above area. Conversely, shortspine thornyhead in postspawning condition are most abundant off Paramushir Island and south-eastern Kamchatka (Fig. 7), where mean CPUEs were over 100 kg per hour of trawling. Benthic juveniles were also more frequently observed in the same areas (Fig. 8).

Size composition of broadbanded thornyhead in the Kuril-Kamchatka region is characterized by a high degree of heterogeneity (Fig. 9). The largest fish occurred in three areas: the underwater plateau in the southern

Table 1. Interannual changes in length composition (percent total fish sampled) of shorttraker rockfish, *Sebastes borealis*, in various areas of the northwestern Pacific.

Area	Years	Total length (TL), cm																								N	M
		10-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101+							
Central Kuril Islands	1992	—	—	0.8	9.2	9.2	17.1	18.3	15.8	15.9	5.4	9.5	4.1	1.7	0.4	0.6	0.7	0.3	—	—	—	—	—	—	954	36.75	
	1993	0.1	1.5	2.5	6.2	18.2	19.6	20.0	14.7	10.8	3.4	1.2	3.4	1.2	0.4	0.3	0.3	0.4	0.3	0.1	+	+	—	—	8,524	40.49	
	1994	0.3	1.9	4.1	7.5	17.6	19.7	16.3	14.1	11.4	4.4	1.4	4.4	1.4	0.4	0.3	0.2	0.1	0.1	0.1	—	—	—	—	6,725	39.93	
	1995	0.5	3.7	5.7	8.1	19.2	20.3	14.7	10.7	7.9	4.8	2.5	1.0	0.3	0.2	0.3	0.2	0.2	0.1	0.1	+	+	—	—	10,427	38.50	
	1996	0.5	5.4	7.6	7.2	13.0	17.6	14.6	12.9	11.1	5.6	2.6	0.8	0.3	0.4	0.1	0.3	0.4	0.1	0.3	+	+	—	+	4,502	39.29	
	1997	0.2	4.3	9.2	6.8	9.0	14.7	13.6	18.6	12.5	6.8	2.0	0.9	0.5	0.6	0.2	—	0.1	0.1	—	—	—	—	—	1,415	40.72	
Northern Kuril Islands	1998	0.6	7.3	10.0	7.3	9.6	14.6	13.1	14.1	12.1	7.3	2.4	0.5	0.3	0.3	0.3	0.2	0.1	+	—	—	—	—	—	6,812	39.28	
	1999	0.2	3.9	8.0	9.2	10.1	12.0	14.9	17.1	12.1	7.5	2.9	0.9	0.4	0.3	0.3	0.1	0.1	+	—	—	—	—	—	4,427	40.22	
	1993	—	—	—	0.5	2.6	2.6	3.1	6.8	9.4	3.1	3.7	8.9	15.2	16.8	13.1	3.7	1.1	—	—	—	—	—	—	191	68.63	
	1994	—	—	1.0	—	—	5.1	9.1	11.1	18.2	25.3	14.1	6.1	2.0	5.0	2.0	—	—	—	—	—	—	—	—	99	50.20	
	1995	0.3	0.3	2.3	4.4	12.7	14.5	15.9	19.1	15.7	8.1	2.6	1.2	2.6	0.3	—	—	—	—	—	—	—	—	—	345	43.97	
	1996	—	1.7	2.3	4.0	11.3	18.5	20.7	14.6	14.6	6.3	3.3	1.0	1.0	0.3	0.3	—	—	—	—	—	—	—	—	302	43.05	
South-eastern Kamchatka	1998	—	—	1.1	4.6	10.2	13.6	19.3	10.2	20.5	9.1	5.7	3.4	1.1	1.1	—	—	—	—	—	—	—	—	—	88	45.80	
	1993	—	0.4	0.8	2.3	4.7	5.1	6.4	6.2	9.5	6.6	5.7	5.3	8.2	11.3	15.1	8.4	3.6	0.4	—	—	—	—	—	2,475	63.49	
	1994	0.1	0.5	1.4	4.5	8.9	16.4	14.3	13.1	11.8	4.9	4.3	4.1	4.6	4.3	3.9	2.4	0.6	0.1	+	—	—	—	+	3,428	49.48	
	1995	—	0.3	1.6	2.5	5.0	19.7	22.2	16.3	12.8	6.9	3.8	5.6	2.8	0.6	—	—	—	—	—	—	—	—	—	320	45.40	
	1996	—	—	1.3	1.3	3.8	15.2	11.4	8.9	36.7	11.4	6.3	2.5	1.3	—	—	—	—	—	—	—	—	—	—	79	48.24	
	1995	—	—	—	—	2.5	7.9	10.7	11.5	13.0	13.6	9.9	11.6	5.4	7.3	5.0	1.1	0.3	0.1	—	—	—	—	—	756	57.01	
Western Bering Sea 168°-171°E	1996	0.1	0.6	0.7	2.4	3.9	5.5	10.6	12.8	12.5	9.7	11.1	8.1	10.5	6.7	3.5	1.0	0.4	—	—	—	—	—	—	1,683	55.62	
	1997	+	—	0.9	1.6	2.1	4.2	7.4	8.7	7.3	8.9	9.1	11.3	13.8	12.6	7.8	2.9	1.0	0.4	+	—	—	—	+	3,773	56.97	
	1995	—	0.2	0.1	—	0.2	0.7	2.8	6.8	8.9	15.1	12.9	19.7	15.2	11.8	4.4	0.9	0.3	—	—	—	—	—	—	0.1	3,339	63.86
	1996	—	0.2	0.4	1.0	1.9	4.0	9.3	16.5	18.5	11.9	9.3	8.3	7.8	6.4	3.7	0.8	0.1	—	—	—	—	—	—	1,646	56.04	
	1997	—	0.5	0.9	1.8	3.0	6.9	9.8	12.4	12.3	11.2	11.2	11.3	9.4	5.8	2.2	0.8	0.4	0.2	—	—	—	—	—	1,271	55.67	
	1995	—	0.1	0.7	0.9	1.3	1.7	4.8	10.3	9.5	14.1	11.4	14.8	14.8	11.5	3.1	0.6	0.1	0.1	—	—	—	—	—	702	61.12	
Western Bering Sea 177°E-180°	1997	2.9	1.5	—	—	—	—	—	4.3	14.5	24.6	14.5	7.3	15.9	10.1	1.5	1.4	1.4	—	—	—	—	—	—	69	56.43	
	1998	—	0.1	0.7	0.9	1.3	1.7	4.8	10.3	9.5	14.1	11.4	14.8	14.8	11.5	3.1	0.6	0.1	0.1	—	—	—	—	—	240	53.85	

N = number of fish measured, M = mean length (cm), + = <0.1.

Table 2. Seasonal changes in length composition (percent total fish sampled) of shorttraker rockfish, *Sebastes borealis*, in various areas of the northwestern Pacific.

Area	Season	Total length (TL), cm																			N	M
		10-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105		
Central Kuril Islands	Spring	0.2	2.8	6.2	5.9	12.7	16.3	18.2	14.0	13.1	5.7	3.2	0.8	0.4	0.3	0.1	0.1	+	—	—	4,345	40.89
	Summer	0.4	4.6	6.8	8.4	15.7	18.0	15.1	13.3	9.8	5.0	1.6	0.5	0.3	0.2	0.1	0.1	+	+	—	21,984	38.59
	Autumn	0.3	2.9	5.6	7.6	16.3	18.5	16.5	13.4	10.2	5.0	2.2	0.7	0.2	0.2	0.2	0.1	+	+	—	15,414	39.51
	Winter	0.7	4.8	5.7	5.2	10.6	16.6	18.2	18.4	11.2	5.4	1.7	0.3	0.3	—	0.8	—	—	—	0.1	724	40.48
Northern Kuril Islands	Spring	0.2	0.2	2.0	2.2	10.6	12.6	11.7	14.2	24.3	11.1	4.6	1.2	1.5	1.8	1.2	0.5	0.3	—	—	605	47.32
	Summer	0.1	0.6	1.2	2.4	7.8	11.0	10.9	11.8	10.7	7.7	3.2	2.7	4.7	5.7	8.3	7.2	3.4	0.7	0.1	1,650	55.93
	Autumn	—	0.2	0.9	3.0	7.0	10.7	14.5	20.2	20.0	11.3	4.5	1.8	2.5	2.3	—	0.9	0.2	—	—	441	48.06
	Winter	—	—	4.5	3.0	1.5	7.5	4.5	13.4	9.0	4.5	9.0	4.5	10.5	7.5	14.9	6.0	—	—	—	67	59.74
South-eastern Kamchatka	Spring	—	1.2	—	—	3.5	15.3	10.6	11.8	34.1	11.8	7.1	2.4	2.3	—	—	—	—	—	—	85	49.02
	Summer	—	0.2	0.6	1.4	3.3	7.1	9.9	9.0	14.1	7.3	5.3	4.5	7.9	9.7	12.7	4.5	2.4	0.2	—	1,572	59.89
	Autumn	0.1	0.6	1.4	4.5	8.8	14.6	12.9	11.5	10.3	5.1	4.5	4.1	4.2	5.2	5.9	4.6	1.4	0.2	+	4,371	51.89
	Winter	—	0.3	0.4	0.4	—	1.1	1.1	1.8	2.8	5.0	6.4	13.8	21.2	18.7	17.8	5.7	3.9	—	—	283	72.04
Western Bering Sea 168°-171°E	Spring	—	0.3	0.1	0.6	3.1	6.7	9.3	11.3	15.3	14.1	12.4	8.9	8.7	5.8	2.5	0.7	0.1	0.1	+	711	56.12
	Summer	0.1	0.6	0.9	1.4	2.4	5.4	8.2	9.6	10.7	9.7	12.6	13.3	12.2	8.0	3.5	1.2	0.3	+	+	3,947	58.27
	Autumn	—	0.8	1.8	2.8	5.6	9.1	11.4	9.4	9.0	10.1	9.6	11.8	9.3	6.1	2.2	0.6	0.4	+	+	2,300	53.98
	Winter	—	—	—	—	3.5	4.7	7.7	6.5	10.0	12.9	10.0	13.5	12.9	8.2	8.2	1.2	0.6	+	+	170	61.02
Western Bering Sea 171°-177°E	Spring	—	0.7	0.5	0.5	0.2	2.9	8.1	14.9	15.6	10.7	9.2	10.7	9.5	10.4	4.8	0.9	0.4	+	+	578	58.76
	Summer	—	0.3	0.3	0.6	1.2	2.6	6.0	10.2	12.2	13.1	11.5	14.5	13.6	8.8	4.1	0.7	0.2	+	0.1	3,937	60.32
	Autumn	0.1	0.1	0.2	0.4	1.3	3.0	5.1	10.6	11.0	16.1	12.5	16.0	10.	9.1	3.0	1.1	0.3	0.1	+	2,069	60.09
	Winter	—	—	—	—	1.7	6.7	15.0	6.7	8.3	10.0	3.3	10.0	13.3	15.0	6.7	3.3	—	—	—	60	60.85
Western Bering Sea 177°E-180°	Spring	—	—	6.3	3.1	6.3	3.1	21.9	37.5	3.1	3.1	9.4	6.2	—	—	—	—	—	—	—	32	45.41
	Summer	—	0.2	0.5	0.8	0.6	1.4	4.6	10.3	10.3	13.5	11.0	15.1	15.2	12.5	3.0	0.6	0.2	0.2	—	630	61.80
	Autumn	0.6	0.3	—	—	0.8	2.8	7.2	17.5	16.9	22.7	14.4	10.0	4.2	0.8	1.7	0.3	—	—	—	361	55.17
	Winter	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

N = number of fish measured, M = mean length (cm), + = <0.1.

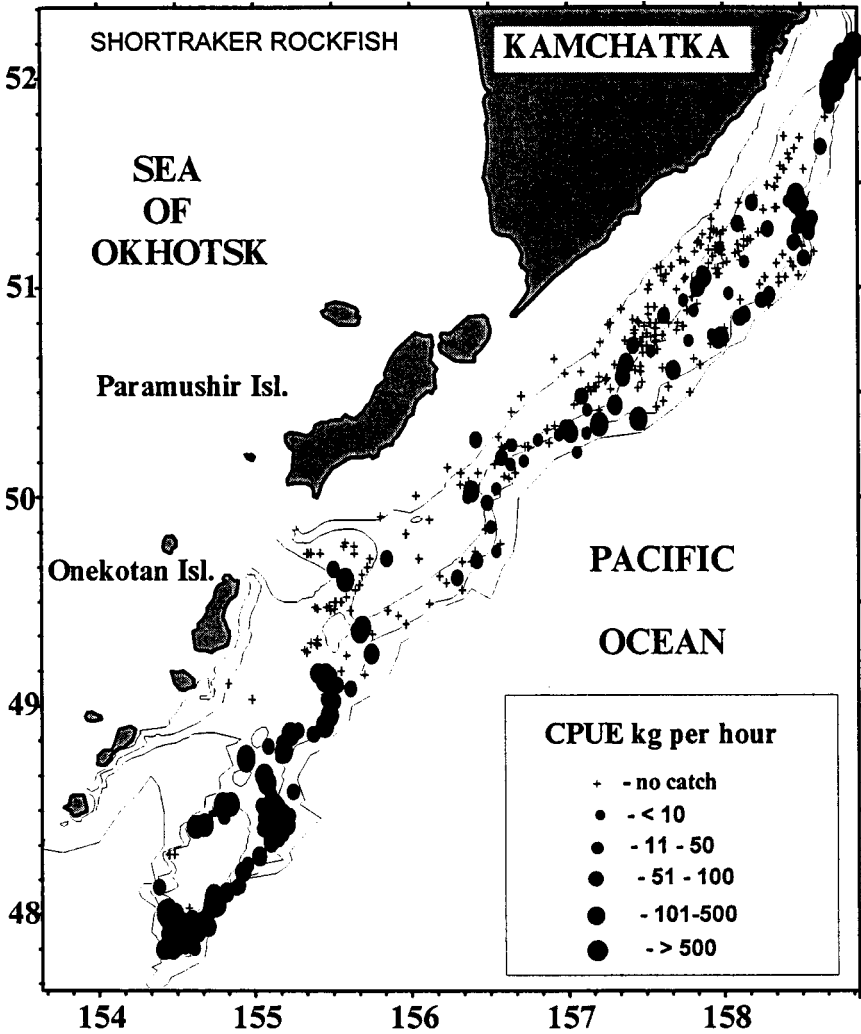


Figure 2. Distribution and relative abundance of shorttraker rockfish categorized by CPUE (kg per hour of trawling) in April-June, 1993-1999 off the northern Kuril Islands and southeastern Kamchatka.

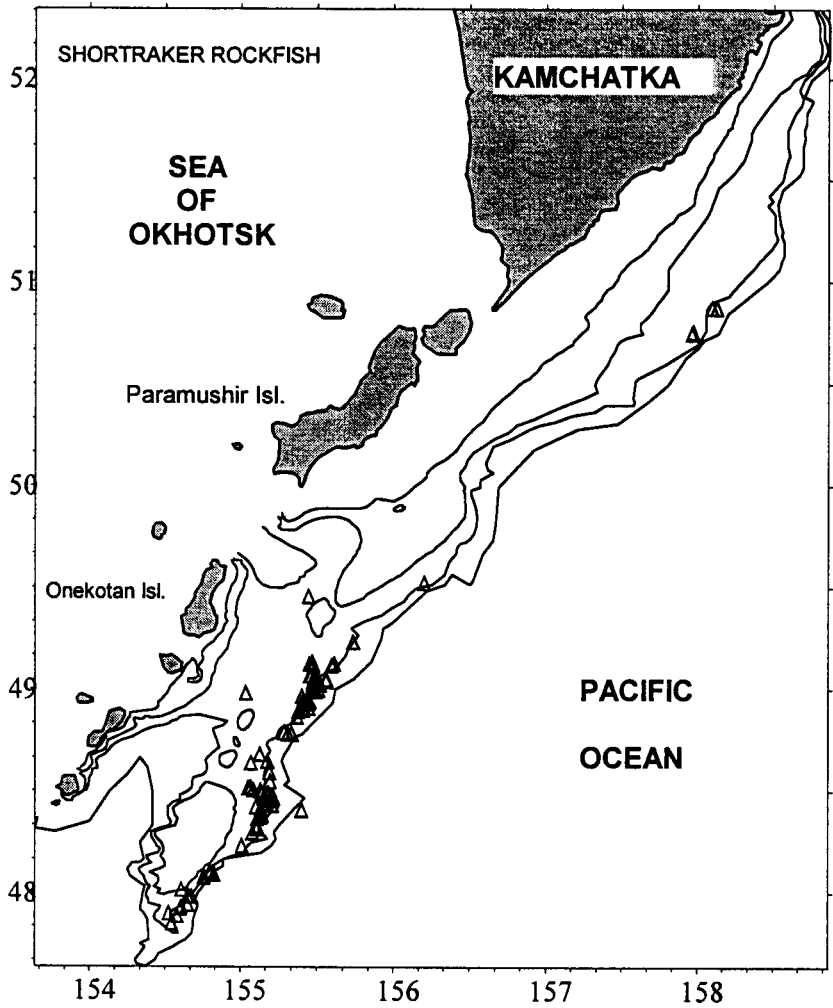


Figure 3. Capture location sites (triangles) of benthic juvenile shortraker rockfish with lengths less than 150 mm off the northern Kuril Islands and south-eastern Kamchatka.

Table 3. Relative abundance (%) of shortraker rockfish, shortspine thornyhead, and broadbanded thornyhead in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka in various depth ranges (top number = adults, bottom number = juveniles).

Species	Depth, m														
	<150	151-200	201-250	251-300	301-350	351-400	401-450	451-500	501-550	551-600	601-650	651-700	701-750	751-800	>800
Shortraker rockfish, <i>Sebastes borealis</i>	—	0.15	0.50	1.83	5.71	23.76	23.51	17.19	10.96	5.55	7.88	0.15	1.36	0.30	1.14
Shortspine thornyhead, <i>Sebastolobus alascanus</i>	0.03	—	—	—	0.03	5.68	4.52	7.99	8.74	7.83	14.90	18.91	10.37	16.74	4.25
Broadbanded thornyhead, <i>Sebastolobus macrochir</i>	—	0.06	0.08	0.71	3.22	7.41	10.63	14.48	18.72	14.64	10.04	5.69	4.31	2.19	7.81

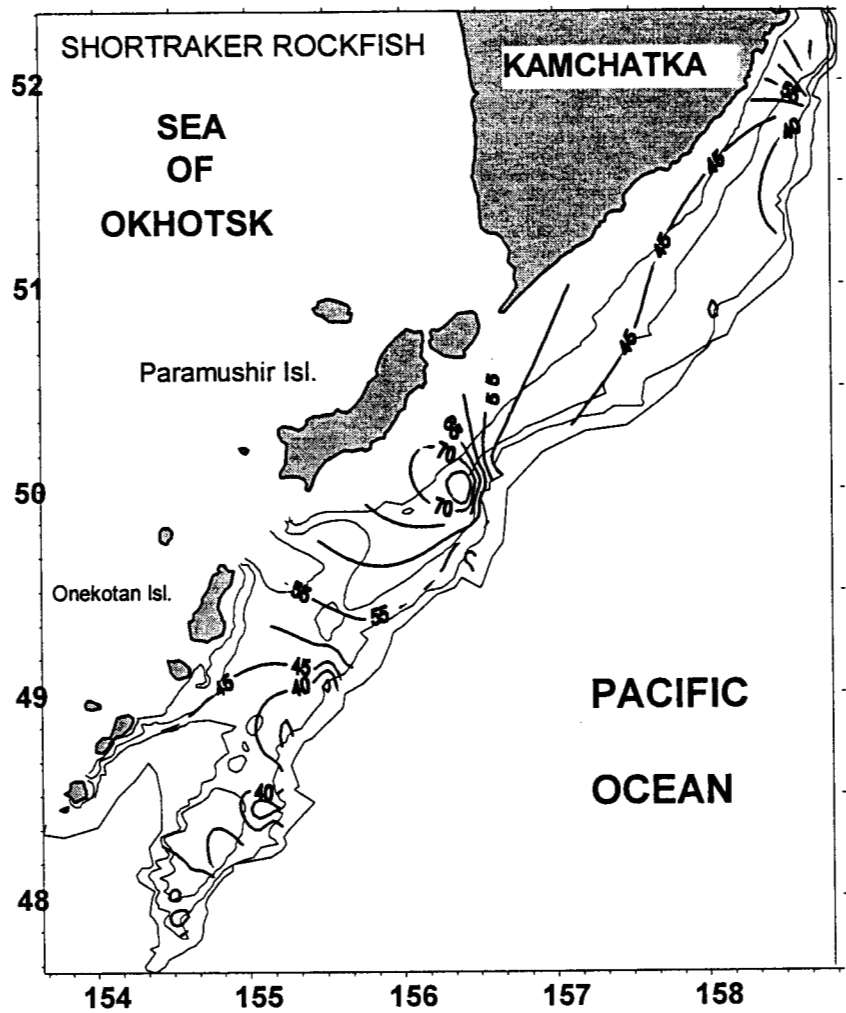


Figure 4. Mean lengths (cm) of shortraker rockfish off the northern Kuril Islands and southeastern Kamchatka.

part of the region, a localized section southeast of Onkotan Island, and the southeastern Kamchatka coast near 52°N. In each of these areas, mean body length increased from deeper to shallower waters. Shortspine thornyhead exhibited the smallest mean lengths off central Paramushir Island (Fig. 10) with mean lengths increasing to both the north and the south.

During the period of investigation, benthic juvenile shortspine thornyhead were caught at depths ranging from 357 to 615 m (mean depth 505.3 m) while broadbanded thornyhead occupied a somewhat deeper 410-645 m depth range (mean depth 527.9 m). An analysis of the vertical distribution of thornyheads shows juveniles inhabiting a narrower bathymetric range compared with the adults (Table 3) with the juveniles distributed in shallower depths than the adults. This same pattern also appears in the northeastern Pacific (Vetter and Lynn 1997). Thus the relative abundance of juvenile shortspine thornyhead in the investigated area (60.0%) reaches a maximum in 450-550 m depths while most of the adults (65.2% relative abundance) are distributed in depths deeper than 600 m. Juveniles and adult broadbanded thornyhead were most abundant in the same depth ranges.

Discussion

Shortraker Rockfish

The large-sized fishes are less abundant off the south and central Kuril Islands, in the eastern Bering Sea, and in Pacific Ocean waters of the Aleutian Islands. Maximum abundance occurs off eastern Kamchatka, the western Bering Sea, the Gulf of Alaska, and in British Columbia waters. Juveniles are most abundant off the Kuril Islands, in the eastern Bering Sea, and in the Pacific waters off the Aleutian Islands. Very few juveniles are caught off eastern Kamchatka, the western Bering Sea, the Gulf of Alaska, and British Columbia waters (Westrheim and Harling 1975, Bakkala et al. 1992, Harrison 1993, Ronholt et al. 1994, Martin 1997). Size composition of shortraker rockfish from the Aleutian Islands is heterogeneous. Smaller fishes are caught in the Pacific waters off the Aleutians where modal classes from various years vary from 35 to 44 cm with mean lengths ranging from 39.1 to 41.2 cm. During the same time periods, larger, 40-63 cm shortraker rockfish with modal lengths ranging from 47.9 to 54.8 cm were observed in the Bering Sea waters off the Aleutian Islands (Harrison 1993, Ronholt et al. 1994). Similar to observations from the northwestern Pacific, shortraker rockfish size composition in the Aleutian Islands varies considerably from year to year.

Geographic variations in size composition between different areas can be attributed to different growth rates. However, recent aging studies of shortraker rockfish show no significant differences in growth rates between fishes from the central Kuril Islands and western Bering Sea (A.A. Abramov,

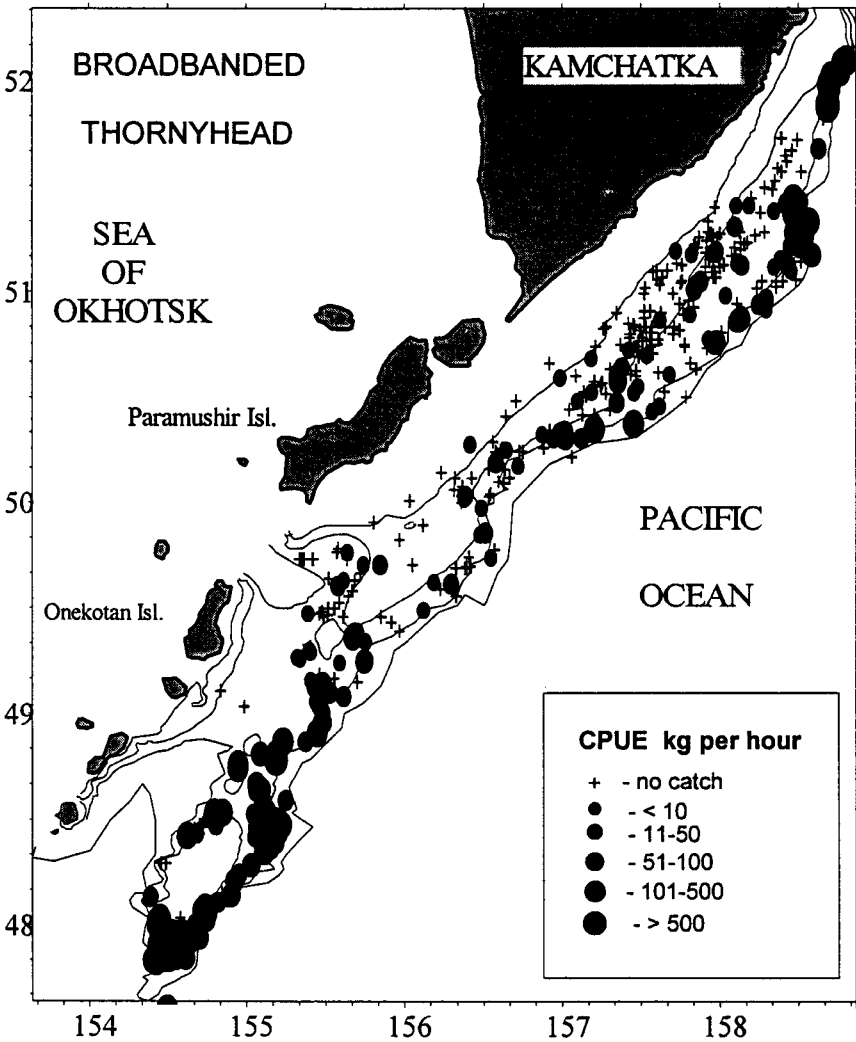


Figure 5. Distribution and relative abundance of broadbanded thornyhead categorized by CPUE (kg per hour of trawling) during the postspawning period (April-June, 1993-1999) off the northern Kuril Islands and southeastern Kamchatka.

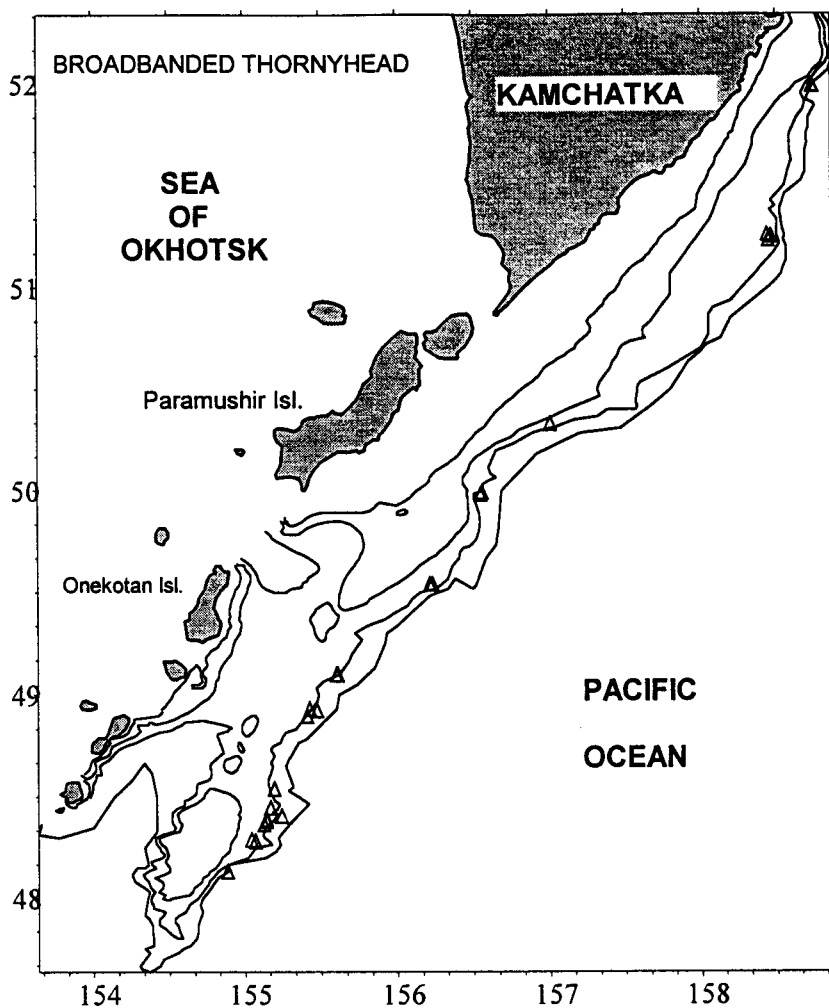


Figure 6. Capture location sites (triangles) of benthic juvenile broadbanded thornyhead with lengths less than 130 mm off the northern Kuril Islands and southeastern Kamchatka.

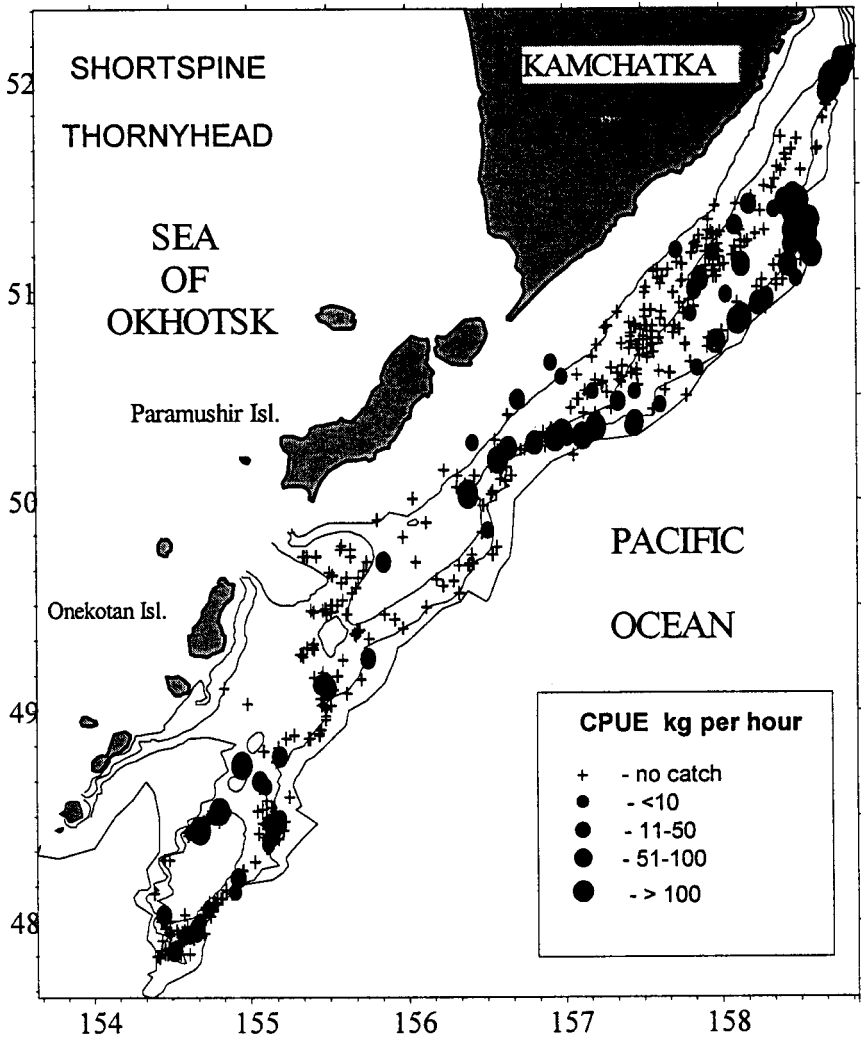


Figure 7. Distribution and relative abundance of shortspine thornyhead categorized by CPUE (kg per hour of trawling) in April-June, 1993-1999 off the northern Kuril Islands and southeastern Kamchatka.

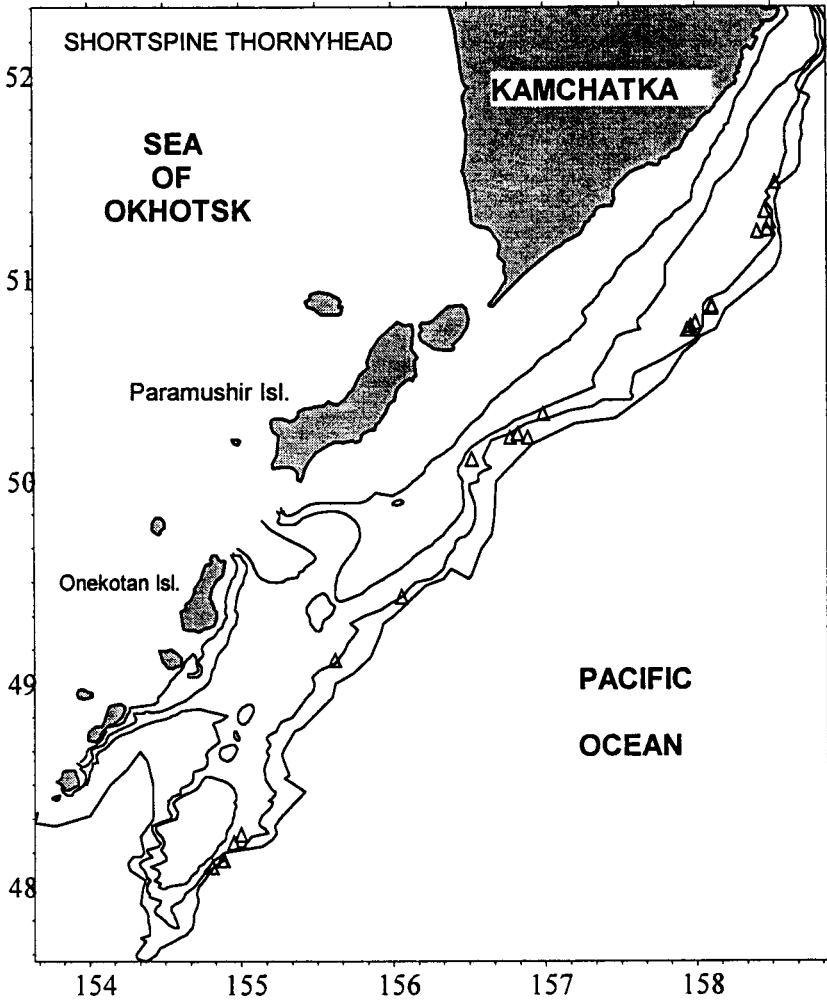


Figure 8. Capture location sites (triangles) of benthic juvenile shortspine thornyhead less than 150 mm in length off the northern Kuril Islands and south-eastern Kamchatka.

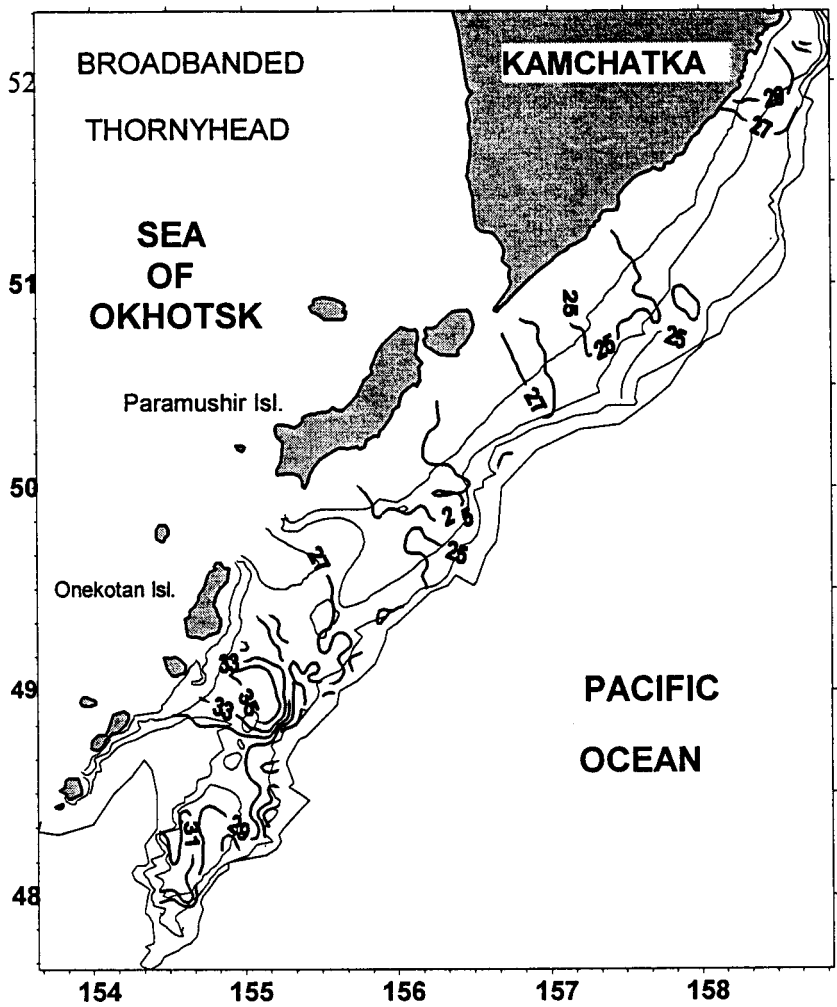


Figure. 9. Mean length (cm) of broadbanded thornyhead off the northern Kuril Islands and southeastern Kamchatka.

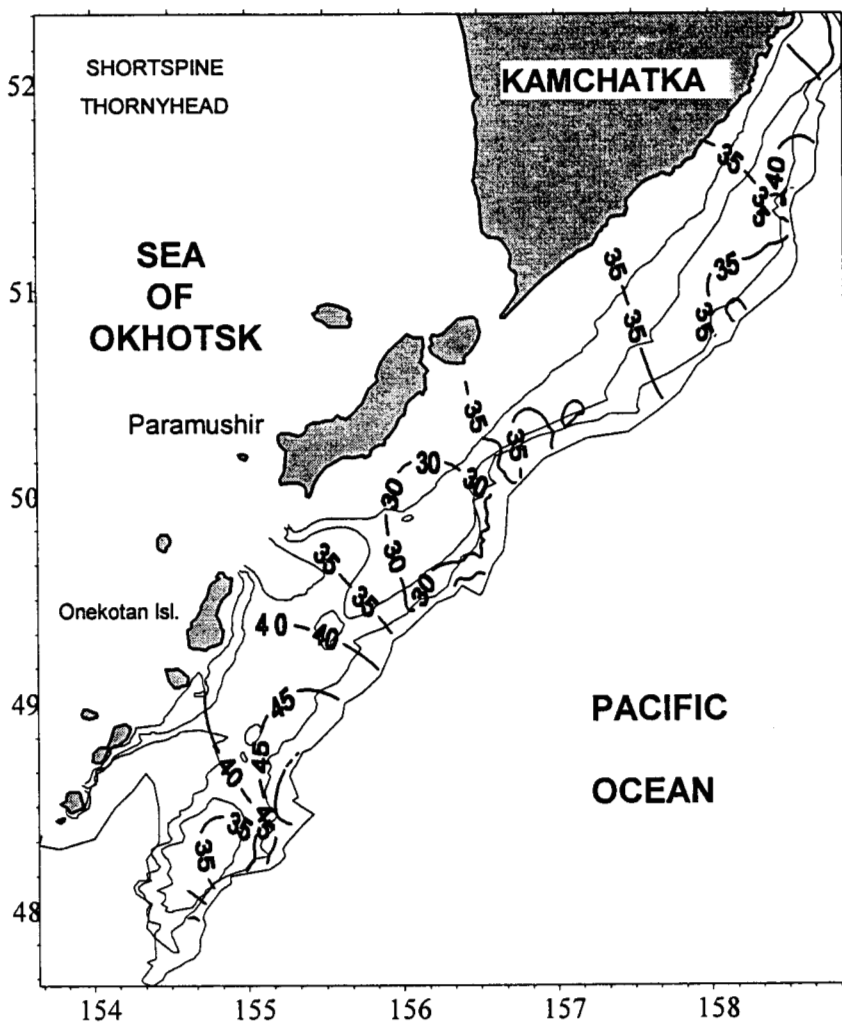


Figure. 10. Mean length (cm) of shortspine thornyhead off the northern Kuril Islands and southeastern Kamchatka.

unpubl. data) and eastern Kamchatka and the western Bering Sea (A.M. Tokranov, pers. comm.). Shortraker rockfish is a long-lived species (Beamish and McFarlane 1987) with late sexual maturation and low growth rates (McDermott 1994). Large interannual fluctuations in abundance or size-age structure variations are not pronounced. In the northwestern Pacific, seasonal and multiannual variations in size composition, taking into account the low reproductive rate and insignificant harvest rate, cannot be explained by fluctuations in abundance and, according to our hypothesis, should be related to horizontal migrations.

Size composition data, benthic juvenile spatial distribution, and ocean current patterns in the North Pacific Ocean (Favorite et al. 1976, Ohtani 1991) indicate the main habitat of shortraker rockfish is located within the Bering Sea, Gulf of Alaska, and Western Subarctic Gyre (Fig. 11). In the Bering Sea, the main spawning area is probably the continental slope from Cape Navarin and the Commander Islands and along the northwestern and central Aleutian Islands. Main reproductive areas occur along the eastern Kamchatka coast north of 52°N. Another area where spawning may occur is the Paramushir Island slope. Within the Alaska Gyre the main spawning areas are located from British Columbia to the southeastern Gulf of Alaska.

We suggest the following model may explain the pattern of shortraker rockfish migrations. The Alaska Current and Alaskan Stream transport larvae originating in the eastern Gulf of Alaska to the Aleutian Islands with some larvae being transported through several straits into the Bering Sea. In the western North Pacific, the Eastern Kamchatka current carries eastern Kamchatka larvae to the Kuril Islands and through the Kuril straits partly into the Sea of Okhotsk. Most larvae originating in the western Bering Sea are transported eastward. Some larvae are probably transported by the Eastern Kamchatka current to eastern Kamchatka and the Kuril Islands and through straits in the central Aleutian Islands into the Pacific Ocean. Some larvae and/or pelagic juveniles may linger within quasi-stationary anticyclonic eddies around seamounts, near straits, and in areas where currents form a junction. These conditions can result in temporal dependent populations that are regularly replenished by fish migrating to and from feeding areas. Taking into account the prevailing oceanographic conditions, such populations are most likely to be inherent in the Kuril and Aleutian islands areas. The consistent high abundance and small seasonal and interannual variations of shortraker rockfish size compositions off the underwater plateau in the central Kuril Islands area, and the occurrence of a quasi-stationary anticyclonic eddy around that plateau, may indicate the existence of a temporary dependent population.

In recent years, data were obtained which substantiate the hypothesis that ocean currents transport the pelagic young of rougheye rockfish (congeneric species with similar ecology and biology to shortraker rockfish; Hawkins et al. 1998). The minimum length of shortraker rockfish benthic juveniles from bottom trawl catches is about 10 cm, corresponding to an age of about 2 years (Leontiev et al. 1998). It is thought that after shortraker

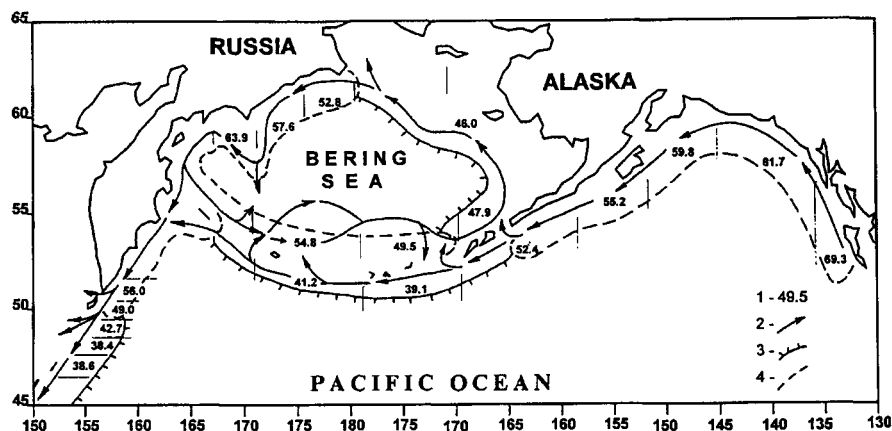


Figure 11. Mean lengths (cm) of shortraker rockfish from bottom trawl catches, locations of the main nursery and spawning areas (Bakkala et al. 1992, Harrison 1993, Ronholt et al. 1994, Martin 1997, Tokranov and Davydov 1998) and principal oceanic currents (Favorite et al. 1976, Ohtani 1991, Staben et al. 1999) of the North Pacific Ocean. 1 = mean length, 2 = direction of currents, 3 = nursery areas, 4 = reproduction areas.

rockfish larvae settle out, the adults remain relatively stationary and do not engage in lengthy migrations (Barsukov 1981, Parker et al. 2000). This conclusion, however, may only be valid for small-sized specimens. Recent investigations show that increasing size is accompanied by migratory behavior. Thus, small shortraker rockfish consume mainly benthic invertebrates and fishes (Yang 1996), while large specimens feed mostly on squids and mesopelagic fishes (Yang 1993) inhabiting the water column. To feed on squids and mesopelagic fishes, shortraker rockfish need to perform vertical migrations. We suggest that with an increase in size, this species is able to perform not only vertical, but also horizontal, migrations. In the Bering Sea, adult shortraker rockfish have been captured in deep water far from coastal waters (Balanov and Radchenko 1995). Size composition from longline and gillnet catches may also substantiate the assumption that shortraker rockfish are capable of performing horizontal migrations. These passive fishing gears are deployed in stationary locations for relatively long time periods while the spatial distribution of shortraker rockfish is characterized by sporadic movement and considerable distance between individual fish (Krieger 1992). Therefore, high CPUEs obtained in the longline and gillnet fisheries may be explained by fishes actively moving to the fishing gear. Shortraker rockfish begin to occur in longline and gillnet catches at lengths greater than 30 cm but predominantly in the 40-45 cm and larger range (Tokranov and Davydov 1998). Submersible observations (Krieger

and Ito 1999) showed that this species is able to swim at a speed of 1 km per hour, while the average speed of bottom currents in the Gulf of Alaska, Bering Sea, and eastern Kamchatka does not exceed 0.8 km per hour (Stabeno et al. 1999).

Our hypothesis cannot be substantiated by traditional tag-and-release experiments because shortraker rockfish cannot survive the barotrauma of initial capture (Moles et al. 1998). For that reason, the most promising research tools for rockfish stock structure investigations are genetic studies and the use of parasites as naturally occurring biological makers. However, none of the recently completed genetic or parasitologic studies of shortraker and rougheye rockfishes (Moles et al. 1998, S. Hawkins, NOAA, NMFS, Auke Bay Laboratory, Juneau, Alaska, pers. comm.) corroborated our hypothesis by revealing heterogeneity of these species from specimens collected from the Gulf of Alaska and Aleutian Islands regions.

Thornyheads

The ecology of both thornyhead species is similar. However, some characteristics of their spatial distributions, relative abundance, and size compositions exhibit large differences. As it is generally known, thornyheads are egg-layers with internal fertilization (Pearcy 1962) with the eggs being released within gelatinous balloons into the water column. The balloons have a positive buoyancy and float to the surface where the larvae hatch and further development occurs (Pearcy 1962, Moser 1974, Matarese et al. 1989). Anticyclonic eddies exist near the southeastern Kamachatka and Paramushir coasts and within 90-120 miles of the underwater plateau southeast of Onkotan Island. These localized eddies nearly coincide with capture sites of benthic juveniles and the locations of larger catches of postspawners. The co-occurrence of these two groups suggests that early development of the larvae and pelagic juveniles may have occurred within these eddies (primarily broadbanded thornyhead within the southern eddy and shortspine thornyhead within both northern eddies) until settlement. The locations and depths of capture of predominantly small-sized benthic juveniles may indicate that settlement of broadbanded thornyhead occurs within the deeper depths with larger fish migrating into shallower waters. The settlement of shortspine thornyhead probably occurs mostly off central Paramushir Island. From this location, fish disperse along the slope in all directions.

For thornyheads, the transition from a pelagic juvenile form to a benthic life pattern (settlement) is poorly understood. In coastal waters off Oregon, pelagic egg balloons of shortspine thornyhead are found over depths ranging from 364 to 1,820 m (Pearcy 1962) and larvae are captured within a wide depth zone over the shelf and continental slope (Moser 1974). The settlement of shortspine thornyhead juveniles occurs at lengths of 22.5-27.2 mm, mean 25 mm (Moser 1974, Wakefield and Smith 1990). Pelagic egg balloons of broadbanded thornyhead off southern Hokkaido are found in coastal waters outside the 200-m isobath (Fukataki 1963). The length of

settlement of this species is unknown. The only capture data for pelagic juveniles occurred off eastern Kamchatka (depth unknown) where lengths ranged from 21.0 to 29.8 mm, and one instance from a depth of 3,480 m off the southern Kuril Islands with a length of 67 mm (Makushok 1970, Moser 1974). In the same time period, 70-84 mm benthic broadbanded thornyhead juveniles were caught at a depth of 780 m and 107-160 mm individuals from a depth of 445 m (Makushok 1970). So, it may be suggested that settlement of broadbanded thornyhead occurs at a greater length than shortspine thornyhead (probably about 70 mm). The settlement by larger fish is also inherent in juveniles of the congeneric species longspine thornyhead (*Sebastolobus altivelis*), where settlement occurs at lengths of 42-56 mm, mean about 50 mm (Moser 1974, Wakefield and Smith 1990). These data show that broadbanded thornyhead pelagic juveniles inhabit ocean waters over deep depths and with increasing size move toward coastal waters and after settlement begin movement into shallow waters.

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Comparative Spawning Habitats of Anchovy (*Engraulis capensis*) and Sardine (*Sardinops sagax*) in the Southern Benguela Upwelling Ecosystem

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Abstract

Data on the abundance and distribution of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) eggs in the Southern Benguela upwelling ecosystem were collected during spawner biomass surveys conducted every November from 1984 to 1998. These data were used to characterize anchovy and sardine spawning habitats with respect to sea surface temperature, to compare the spatial distinction of the spawning habitats of these two species, and to provide an egg abundance time-series for each species. Sardine spawn over a wider temperature range than anchovy, and preferentially spawn in cooler water (15.2-20.5°C) than do anchovy (17.4-21.1°C). Anchovy egg distributions have been spatially stable through time, showing consistent spawning east of Cape Point. In contrast, sardine eggs were more patchily distributed through time, with both the west and south coasts being the major spawning grounds during different periods. Despite the more patchy distribution of sardine than anchovy eggs, the two species have shown a broad-scale overlap in spawning habitat during the first two-thirds of the time-series. Since 1994, however, the spawning habitats of sardine and anchovy have become markedly distinct, with sardine spawning principally off the west coast, and anchovy spawning predominantly off the south and east coasts. This spatial distinctiveness reflects changes in the species' population structure, as well as changes in habitat preference through time, and is likely to impact on egg and larval transport to the nursery grounds and subsequent recruitment strength. Over the time period studied the sardine population has increased 20-fold whereas the anchovy population biomass has shown a steady decline,

albeit with large interannual fluctuations. Biomass trends for anchovy are reflected in their egg data; both spawning area and mean egg density within the spawning area have decreased over time, resulting in a long-term decline in estimated total egg abundance. In contrast to anchovy, the sardine egg data have not shown consistent trends through time, and total egg abundance is not correlated with sardine biomass. These results are of relevance to other upwelling ecosystems where this species pair exists.

Introduction

Anchovy (*Engraulis* spp.) and sardine (*Sardinops sagax*) coexist in five of the world's large marine ecosystems (the southeastern Atlantic, the southeastern Pacific, the northeastern Pacific, the northwestern Pacific, and off southern Australia) where they dominate the landings of local fisheries and together, contribute a substantial portion of the global marine catch. Maximum catches of the two species in any one ecosystem have never occurred simultaneously (Lluch-Belda et al. 1989, 1992b; Schwartzlose et al. 1999). Analysis of fish scales preserved in anaerobic sediments from some of these regions has shown that these two genera have alternated in relative abundance in the absence of fishing over interdecadal and centennial time scales (Soutar and Isaacs 1974, Baumgartner et al. 1992). These large-scale, long-term changes in relative abundance have been termed regime shifts (Lluch-Belda et al. 1989, 1992b), and are currently the subject of much investigation and discussion (Schwartzlose et al. 1999 and references therein).

As in other ecosystems where they coexist, anchovy and sardine in the Southern Benguela have shown long-term changes in relative abundance as indexed by fisheries catch data. Sardine dominated purse-seine catches off South Africa during the 1950s and early 1960s, and landings peaked at 0.41 million tons in 1962 (Crawford et al. 1987). Thereafter, catches of sardine declined and the fishery began to use small-mesh nets to target anchovy, *Engraulis capensis*. Anchovy dominated purse-seine catches from 1965 onward, fluctuating between 41,000 and 596,000 metric tons and with an annual average catch of 254,000 metric tons over the period 1970–1997 (Barange et al. 1999). Over this period, sardine landings have ranged between 16,000 and 176,000 metric tons, and have averaged 66,000 metric tons.

Management procedures for the anchovy and sardine fisheries off South Africa initially used virtual population analysis to provide indices of abundance (Armstrong et al. 1983), but have more recently employed acoustically derived biomass estimates (Cochrane et al. 1998, de Oliveira et al. 1998). Acoustic surveys to estimate anchovy and sardine biomass in the Southern Benguela have been conducted since 1984 (Hampton 1987, 1992; Barange et al. 1999), and these have indicated a steady increase in the biomass of sardine spawners over this period. In contrast, the biomass of anchovy spawners has shown a steady decline, although fluctuations of

more than an order of magnitude have been observed. This contrasting trend in relative biomasses of these two species has led to suggestions that the Southern Benguela is currently undergoing a regime shift, with sardine now becoming more abundant than anchovy (Crawford 1998). Regime switches to sardine dominance occurred during the 1980s in the north-western (Japan) and southeastern Pacific (Peru), although catches of sardine in these regions have declined since the late 1980s (Schwartzlose et al. 1999).

Hypotheses regarding regime shifts have been divided into two categories (Schwartzlose et al. 1999). The first category proposes that continuous modifications in habitat may benefit one species over the other, and changes in factors such as food composition and temperature have been suggested as likely candidates. For example, since sardine are able to utilize phytoplankton to a greater extent than anchovy (King and Macleod 1976; van der Lingen 1994, 1999), increases in phytoplankton standing stock may promote growth of the sardine population relative to anchovy, as has been suggested by Kawasaki (1993) for the northwestern Pacific sardine. Similarly, the ability of sardine to spawn over a wider temperature range than anchovy (Lluch-Belda et al. 1991) suggests that sardine are better able to take advantage of warm conditions during the spawning season. The second category of hypotheses suggests that episodic environmental events, that trigger changes in populations and/or ecosystems, may lead to altered species dominance. Events leading to the formation of particularly strong year classes could result in rapid population growth (Kondo 1980), whereas mass mortalities, such as that recorded for sardine off Australia in 1995, could severely negatively impact population size (Jones et al. 1997).

The objective of this paper is to compare the spawning habitats of sardine and anchovy in the Southern Benguela through an analysis of egg abundance and distribution data collected over a 15-year period during annual spawner biomass surveys. While both species spawn during spring/summer (September to March), they show a temporal separation in the timing of peak spawning (Shelton 1986, Fowler 1998, Huggett et al. 1998); anchovy have a single spawning peak in October-December, whereas sardine have two spawning peaks (September/October and February/March). Although the spawner biomass surveys are timed so as to survey during peak anchovy spawning, sufficient data concerning the abundance and distribution of sardine eggs have been collected to permit a detailed comparison of spawning habitats. In this paper the spawning habitat of each species is characterized in terms of sea surface temperature, which may permit an evaluation of whether this parameter is likely to be important in initiating or sustaining regime shifts in this region. The spatial distinctiveness of anchovy and sardine spawning habitats in the Southern Benguela is examined, and discussed with reference to management of these resources. Finally, a time-series of egg abundance is presented for each species, and is compared with their respective biomass time-series. Information concern-

ing the spawning habitats of these two clupeoids may increase our understanding of how and why regime shifts occur and is likely to be of relevance to other upwelling systems where sardine and anchovy coexist.

Materials and Methods

General

Data from 15 pelagic spawner biomass surveys conducted each year during November/December over the period 1984-1998 were used in this analysis. Each survey covered an area from the South African west coast (approximately 30-33°S) to the southeast coast (approximately 24-27°E), and comprised a grid consisting of survey lines extending over the continental shelf (200 m) and positioned perpendicular to the coastline. Survey details are provided by Hampton (1987, 1992) and Barange et. al (1999). Anchovy and sardine eggs were sampled by means of vertical hauls of a CalVET net (Smith et al. 1985) deployed to 100 m or near the sea bottom (depending on bathymetry) and positioned at 5 or 10 nautical mile intervals along survey lines. An electronic temperature/depth sensor suspended below the net recorded sea surface temperature (SST) and vertical temperature profiles. Eggs collected by the CalVET net were identified and counted, and densities were standardized to number per square meter. Survey details are given in Table 1.

Characterization of Spawning Habitat with Respect to SST

Egg abundance and SST data were combined for all cruises in order to assess the preferred SST range for spawning for each species. First, the number of eggs found in each 0.1°C SST class was expressed as a percentage of the total number of eggs of that species collected over the study period. This value was then divided by the percentage frequency of occurrence of that particular SST class. The resultant quotient value was taken to reflect the selection of spawning habitat by temperature, or by any other factors associated with such temperature ranges. Assuming that fish do in fact select spawning habitat on the basis of SST, quotient values of >1 indicate positive selection, whereas values of <1 indicate that fish avoid spawning at that SST. Quotient values were plotted against SST and, because of the high interpoint variability, were smoothed using 11-point running means centered on the 6th datum.

Spatial Distributions of Anchovy and Sardine Eggs

Distribution maps of anchovy and sardine eggs were generated from data interpolation using standard Kriging routines (Barange and Hampton 1997). To assess the spatial distribution of sardine and anchovy eggs, the survey region was divided into five different predetermined continental shelf strata (Fig. 1): the West Coast, extending north of Cape Columbine; the South-

Table 1. Summary of egg data collected during the spawner biomass surveys, 1984-1998.

Year	Survey area (km ²)	No. of CalVET hauls	No. of anchovy eggs	No. of sardine eggs
1984	122,240	307	12,746	259
1985	114,834	294	12,979	216
1986	103,374	271	14,573	606
1987	139,714	441	11,818	857
1988	135,886	480	14,706	2,429
1989	112,093	361	6,996	1,646
1990	148,025	338	12,862	1,116
1991	114,192	418	17,916	1,240
1992	139,318	425	10,591	604
1993	110,660	357	9,664	631
1994	110,823	305	6,829	1,292
1995	113,065	322	6,540	1,394
1996	135,390	472	1,835	1,679
1997	124,828	286	3,649	727
1998	150,280	369	3,708	856

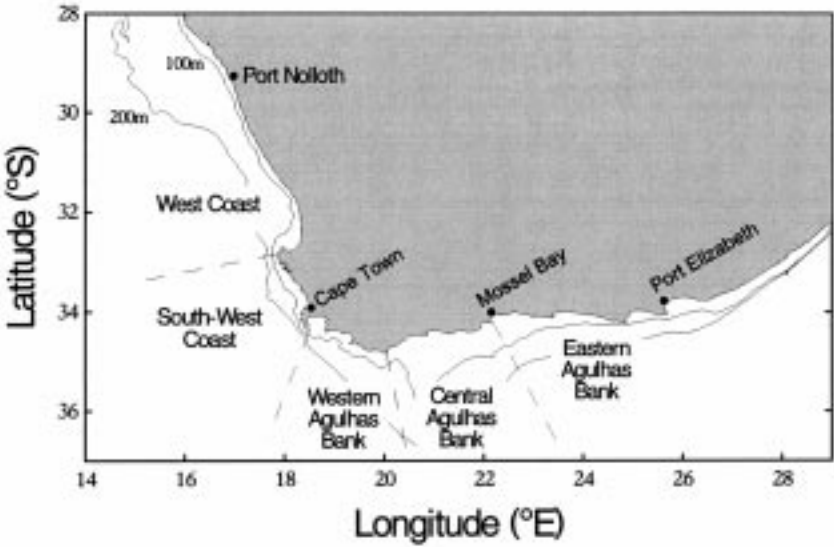


Figure 1. Site map, bathymetry, and locations of the five strata used for the egg data analysis.

West Coast, extending from Cape Point to Cape Columbine; the Western Agulhas Bank, extending from Cape Agulhas to Cape Point; the Central Agulhas Bank, extending from Cape St. Blaize to Cape Agulhas; and the Eastern Agulhas Bank, extending eastwards from Cape St. Blaize. The following parameters were calculated for each species in each stratum:

1. A = the area surveyed (expressed in m^2);
2. P = the percentage of CalVET stations at which eggs were collected (percentage positive stations);
3. G = the geometric mean density (expressed per m^2) of eggs at positive stations; and
4. T = the estimated total number of eggs, calculated from $A(P/100)G$.

Average egg density at positive stations was calculated using geometric rather than arithmetic means because the egg data were log-normally distributed. The relative importance (R) of each stratum to spawning in any one year was assessed by expressing T as a percentage of the estimated total number of eggs for that survey, i.e.

$$R = \frac{T \times 100}{\sum T}$$

Values of P , G , and R for each stratum were then plotted by year for each species.

Egg Abundance Time Series

An estimate of the total number of anchovy and sardine eggs was derived for each survey by summing the values of T for each year, and was plotted by year for each species. This egg abundance time-series was then compared with a biomass time-series derived from hydroacoustic data collected during the spawner biomass surveys.

Results

Characterization of Spawning Habitat with Respect to SST

SSTs at CalVET stations sampled during November surveys ranged from 8.8 to 23.8°C, with the majority of samples collected from waters where the SST was between 15 and 20°C (Fig. 2a). Although eggs of anchovy and sardine were collected over a similar SST range, the egg percentage/SST percentage quotient transformation (Fig. 2b) shows that a substantial difference exists between the preferred spawning temperatures of these two species. The preferred spawning range of anchovy lies between 17.4 and 21.1°C, is unimodal, and peaks between 19.5 and 20.5°C. The preferred

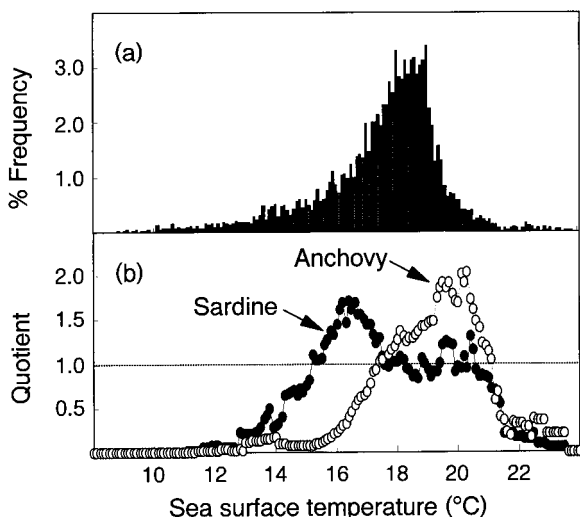


Figure 2. (a) Frequency distribution of sea surface temperature at all CalVET stations sampled during November surveys, 1984-1998; and (b) egg abundance/sea surface temperature quotients (the 11-point running means are shown) for anchovy and sardine egg samples collected during those surveys.

spawning range of sardine is somewhat larger, ranging from 15.2 to 20.5°C. The quotient curve for sardine is essentially bimodal, with a major peak from 15.5 to 17.5°C and a secondary peak between 18.7 and 20.5°C. Anchovy therefore preferentially spawn in warmer waters than do sardine.

Spatial Distributions of Sardine and Anchovy Eggs

Examples of anchovy egg distributions are provided in Fig. 3 and those for sardine are shown in Fig. 4. An obvious feature of these distribution maps is that anchovy eggs were much more abundant during November surveys than were sardine eggs. In addition to their low abundance, sardine eggs were much more patchily distributed than were anchovy eggs. For most of the time-series, areas of high (>1,001 eggs per m²) anchovy egg abundance were located over much of the Agulhas Bank, although high egg abundances were on occasion located off the West Coast (e.g., 1987; Fig. 3). Anchovy eggs found over the Agulhas Bank were generally restricted to shelf waters (<200 m), whereas those off the West and South-West Coasts were found offshore of the shelf edge. Anchovy eggs over the Central and Eastern Agulhas Banks were frequently located offshore of the cool ridge, a quasi-permanent, large-scale, subsurface thermal feature of this region (Swart and Largier 1987). High abundances of sardine eggs were limited to isolated

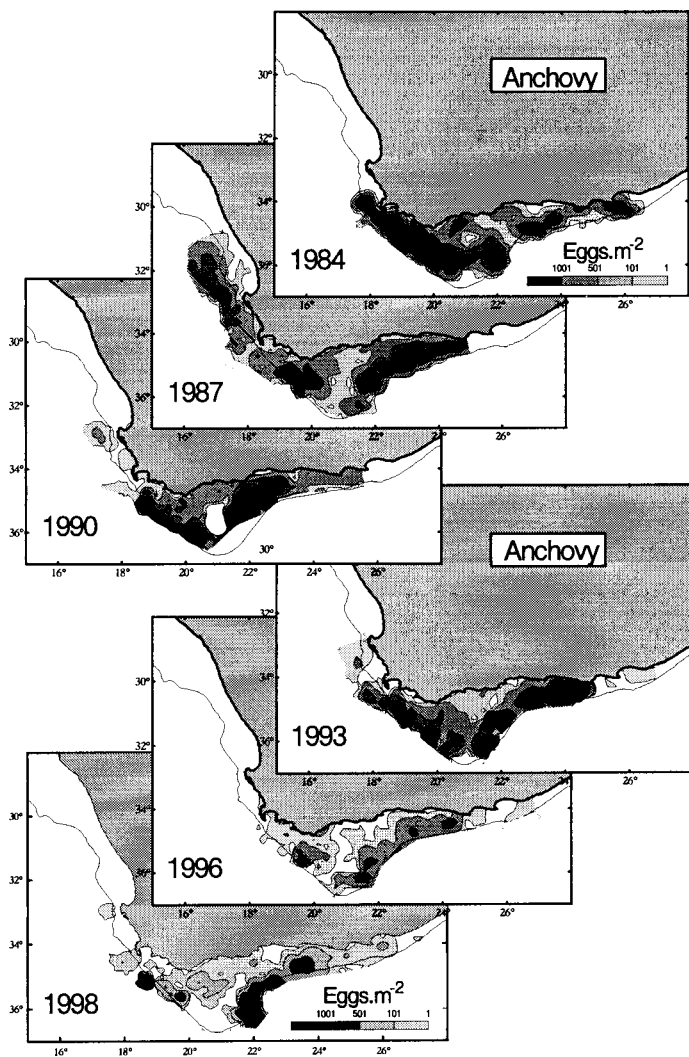


Figure 3. Surface distribution of anchovy egg density (eggs per m^2) during the spawner biomass surveys conducted in 1984, 1987, 1990, 1993, 1996, and 1998. The 200-m depth contour is shown.

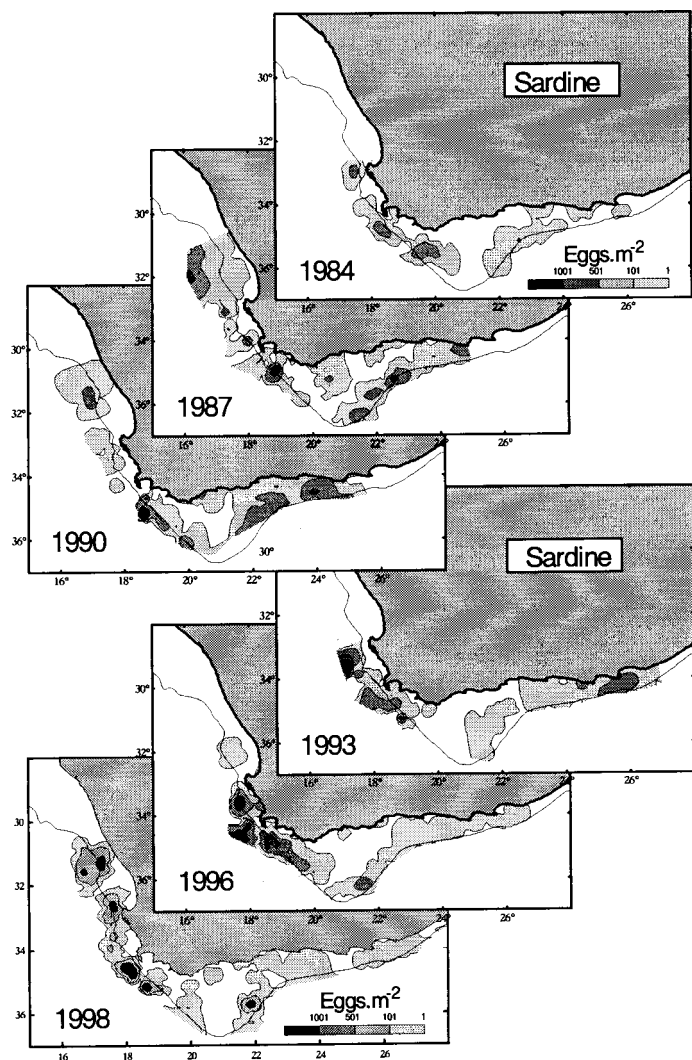


Figure 4. Surface distribution of sardine egg density (eggs per m^2) during the spawner biomass surveys conducted in 1984, 1987, 1990, 1993, 1996, and 1998. The 200-m depth contour is shown.

patches primarily off the West and South-West Coasts, and were located offshore of the continental shelf (Fig. 4).

The spawning area of anchovy, as indexed by the percentage positive stations (P), showed significant ($P < 0.05$) or weakly significant ($P < 0.1$) declines during the time period studied in all five strata (Fig. 5). Although a high percentage of stations sampled off the West and South-West Coasts contained anchovy eggs during the early years of the time-series (particularly 1986-1988), less than 20% of stations off the West Coast contained eggs during the 1990s, while for the South-West Coast this value was seldom above 50% and was also less than 20% in recent years. Values of P for anchovy eggs over the strata comprising the Agulhas Bank showed less interannual variability than data for the West and South-West Coasts, with P declining over time from about 80% to 40% for the Western and Central Agulhas Banks, and from about 60% to 30% for the Eastern Agulhas Bank. In contrast to the significant decline in spawning area shown by anchovy, percentage positive stations for sardine eggs showed weakly significant ($P < 0.1$) increases for the South-West Coast and the western Agulhas Bank, but a significant ($P < 0.05$) decline off the West Coast. The declines in P for both anchovy and sardine off the West Coast may well be an artefact of the low numbers of CalVET stations (<15) that were sampled there during the early years of the time-series. Values of P for sardine eggs off the Central and Eastern Agulhas Banks showed no trends over time, with consistent values of about 20% common for the Central Agulhas Bank, and the Eastern Agulhas Bank showing a dome-shaped pattern in P , increasing to a peak value of 60% in 1990 and declining thereafter (Fig. 5).

In addition to showing significant declines in spawning area in all five strata, the reproductive output of anchovy within its spawning area also declined through time (Fig. 6). The South-West Coast, and the Western and Central Agulhas Banks all showed a significant ($P < 0.05$) decline in geometric mean anchovy egg density, the most marked being over the Western Agulhas Bank, where densities of about 1,000 eggs per m^2 at the beginning of the time-series dropped to about 200 eggs per m^2 at the end. A weakly ($P < 0.1$) significant decline in G was observed for anchovy eggs off the West Coast. As could be seen from a comparison of Figs. 3 and 4, sardine eggs were present at much lower densities than anchovy eggs (Fig. 6), with values >200 eggs per m^2 uncommon. Although the only significant relationship observed for geometric mean sardine egg density was a declining trend for the Central Agulhas Bank, values of G were generally higher at the end of the time-series than at the beginning for the West and South-West Coasts.

Anchovy and sardine showed contrasting patterns in trends through time of the relative importance to spawning of the various strata (Fig. 7). The West and South-West Coasts were relatively unimportant to anchovy spawning, contributing a maximum of 30% to total egg abundance during 1986-1988, but $<10\%$ thereafter. The Western Agulhas Bank showed a significant ($P < 0.05$) decline in R over time for anchovy, decreasing from

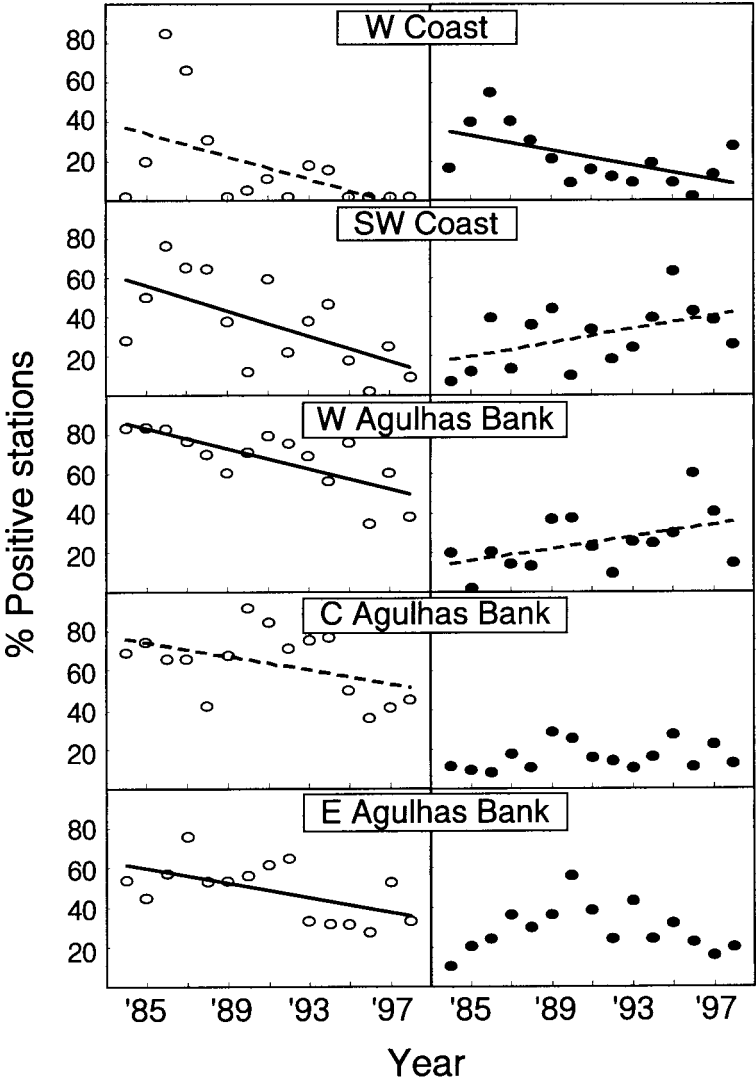


Figure 5. Scatterplots of percentage positive stations (P) against time for anchovy (circles) and sardine (black dots) in each of the five strata used in this analysis. Significant regressions are shown; solid line, $P < 0.05$; dashed line, $P < 0.1$.

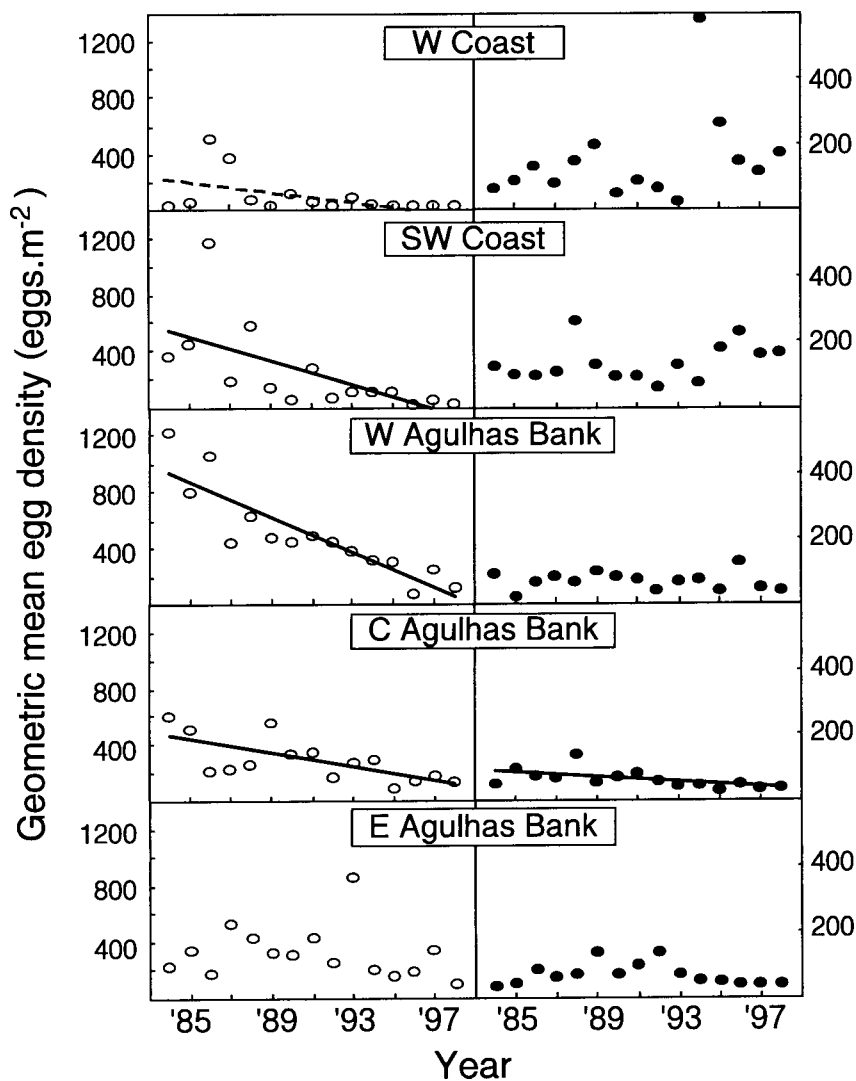


Figure 6. Scatterplots of geometric mean egg density (G) at positive stations against time for anchovy (circles) and sardine (black dots) in each of the five strata used in this analysis. Significant regressions are shown; solid line, $P < 0.05$; dashed line, $P < 0.1$. Note that the y-axes are differently scaled for anchovy and sardine.

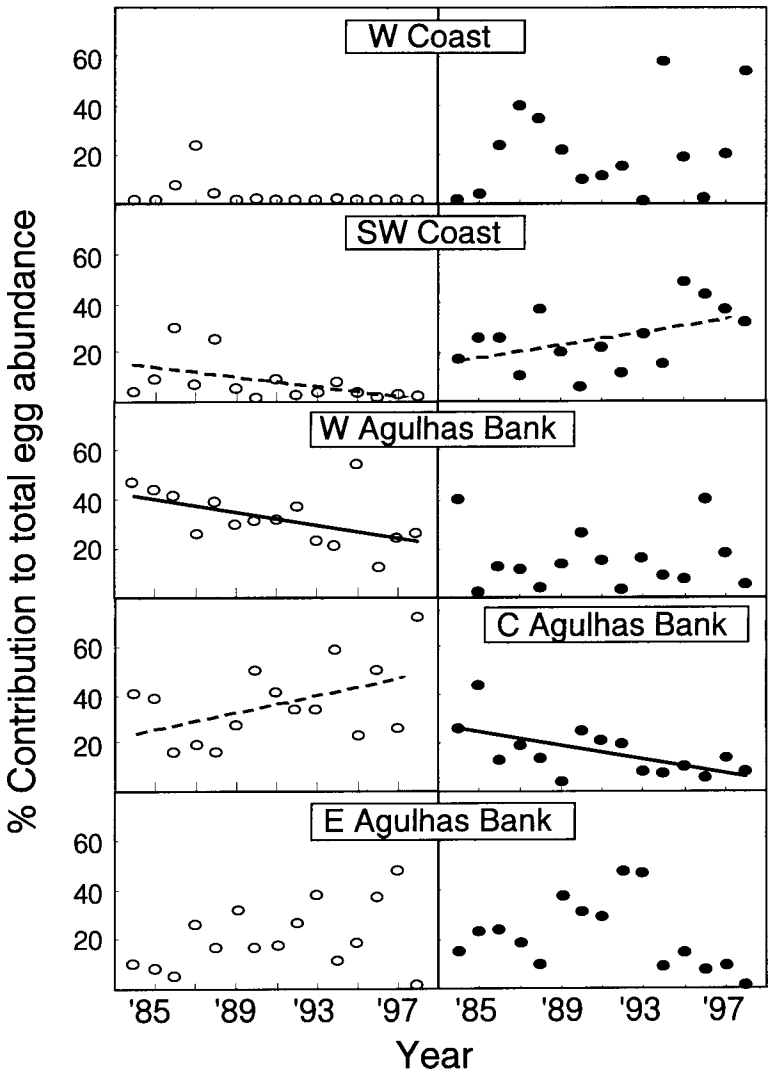


Figure 7. Scatterplots of the relative importance to spawning (R, expressed as the percentage contribution to total egg abundance during the survey) against time for anchovy (circles) and sardine (black dots) in each of the five strata used in this analysis. Significant regressions are shown; solid line, $P < 0.05$; dashed line, $P < 0.1$.

about 40% to 20% of estimated total egg production, whereas the Central Agulhas Bank showed a weakly significant ($P < 0.1$) increase in R over time. In 1998, 72% of the estimated total number of anchovy eggs were found over the Central Agulhas Bank (Fig. 7). The Eastern Agulhas Bank also showed an increasing trend in R over time, although the very low value for 1998 rendered this relationship insignificant. For sardine, the relative contribution to total egg abundance made by the West and South-West Coasts showed a high degree of variability, but a weakly significant ($P < 0.1$) trend was evident for the South-West Coast (Fig. 7). The Western and Eastern Agulhas Banks also showed high variability in R for sardine, whereas a significant ($P < 0.05$) decreasing trend for this parameter was observed for the Central Agulhas Bank.

Contouring the relative contribution to spawning by stratum through time permits temporal patterns in the abundance and distribution of the eggs of anchovy and sardine to be visualized in a single figure (Fig. 8). This figure indicates that anchovy egg distributions were most spatially stable through time, showing consistent spawning east of Cape Point. Although 30-40% of anchovy eggs were found west of Cape Point during the period 1986-1988, the Agulhas Bank was the principal anchovy spawning habitat during the rest of the time-series, with areas of intense spawning on the Agulhas Bank differing along the coast from year to year. In contrast, sardine eggs were more patchily distributed through time, with the regions to both the west and to the east of Cape Point being major sardine spawning habitat during different periods. Despite the patchier distribution of sardine than anchovy eggs, both have shown a broad-scale overlap during the first two-thirds of the time-series. Since 1994, however, the spawning habitats of these two species have become markedly distinct, with anchovy spawning principally east of Cape Point, and sardine spawning principally west of Cape Point. More than 80% of anchovy eggs have been found east of Cape Point during each survey since 1994, with most eggs being found over the Central and Eastern Agulhas Banks. In contrast to anchovy, at least 65% of sardine eggs have been found west of Cape Point during surveys since 1994.

The eastward shift in sardine egg distributions observed between 1989 and 1993, when sardine spawning was concentrated primarily on the Central and Eastern Agulhas Banks (Fig. 8), appears to have been linked to SST. A time-series of SST per stratum shows that average SSTs off the West and South-West Coasts were markedly lower than those over the Agulhas Banks during the period 1989-1993 (Fig. 9). Despite the fact that sardine are able to spawn in cooler waters than anchovy, this correspondence between sardine egg distributions and average SSTs suggests that the West and South-West Coasts may have been too cold for extensive sardine spawning during those years. This hypothesis requires better data and further testing however, with, for example, satellite data being used to estimate stratum-specific SSTs.

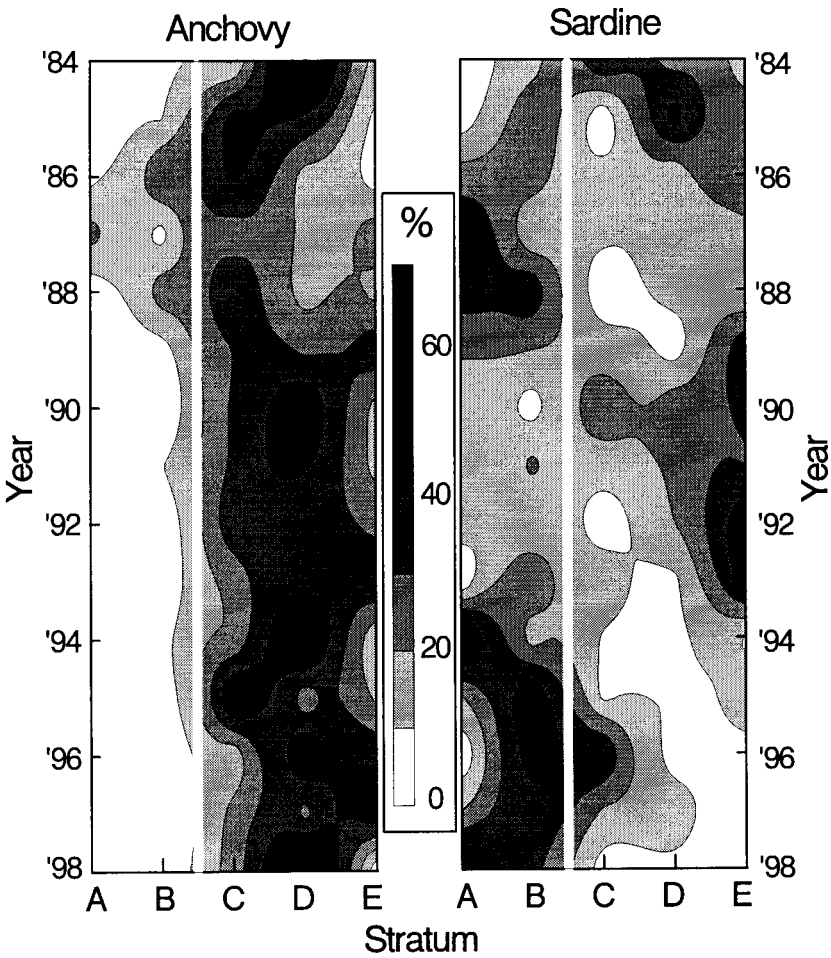


Figure 8. Changes in the patterns of abundance and distribution of eggs through time for anchovy and sardine. The x-axis represents the coastline, which has been "straightened" and divided into the five strata used in this analysis, and the y-axis represents time. The percentage contribution to total egg abundance during the survey is shown for each of five strata by year, and contouring is used to interpolate between years and strata. The vertical white line indicates the approximate position of Cape Point.

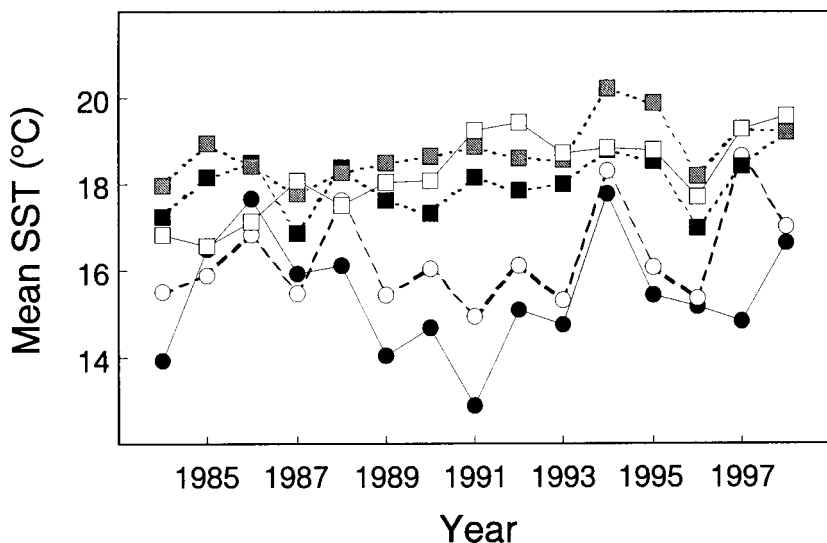


Figure 9. Time-series of mean sea surface temperature for each of the five strata used in this analysis. Black circles represent the West Coast; white circles the South-West Coast; black squares the Western Agulhas Bank; grey squares the Central Agulhas Bank; and white squares the Eastern Agulhas Bank.

Egg Abundance Time Series

The egg abundance time-series for anchovy and sardine, together with acoustically derived estimates of their respective spawner biomass over this time period, are shown in Fig. 10. Anchovy egg abundance showed a significant linear decline over the time-series ($r^2 = 0.88$; $F = 92.5$; d.f. = 1,14; $P < 0.001$), and was significantly correlated with anchovy spawner biomass ($r^2 = 0.35$; $F = 7.02$; d.f. = 1,14; $P < 0.03$). Although sardine spawner biomass increased 20-fold over the time-series, sardine egg abundance did not show a significant trend through time, nor was it correlated with sardine spawner biomass.

Discussion

Data on the abundance and distribution of the eggs of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) were collected using a CalVET net during annual spawner biomass surveys in the Southern Benguela upwelling ecosystem over the period 1984–1998. These data were used to characterize spawning habitat with respect to sea surface temperature, compare the

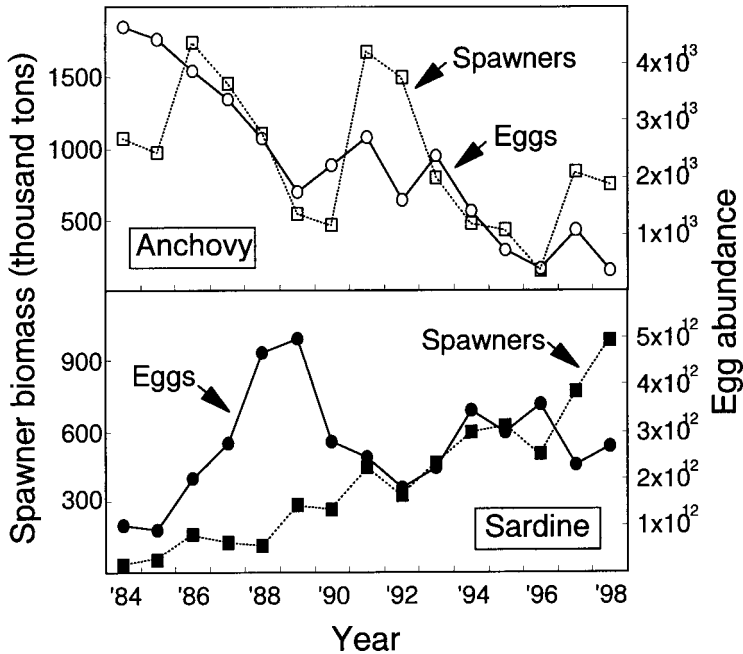


Figure 10. Time-series of estimated total egg abundance for anchovy and sardine, 1984-1998. Also shown are the time-series of relative acoustic estimates of the two species (Barange et al. 1999; Marine and Coastal Management, unpublished).

spatial distinctiveness of anchovy and sardine spawning habitats, and provide an egg abundance time-series for each species. Results obtained indicate that anchovy prefer to spawn in warmer water than do sardine; that anchovy and sardine spawning distributions no longer overlap, although this was the case prior to 1994; that anchovy spawning distribution has shifted eastward and sardine westward since 1994; and that biomass trends are reflected in the egg abundance time-series for anchovy, but not for sardine.

The egg percentage/SST percentage quotient transformation indicates that anchovy and sardine differ in their preferred spawning temperatures; anchovy prefer to spawn in warmer waters than do sardine. Although the sardine quotient curve is bimodal, the major sardine peak and the anchovy peak are well separated. A study conducted by Lluch-Belda et al. (1991), who used the egg/SST quotient transformation to examine anchovy and sardine spawning in the California Current, found similar results to those reported above; California sardine spawned over a wider SST range than

did anchovy, and the sardine quotient curve was bimodal whereas that for anchovy was unimodal. However, unlike anchovy and sardine in the Southern Benguela, the major California sardine quotient peak (at 15°C) was similar to the California anchovy quotient peak (14°C). Lluch-Belda et al. (1991) concluded that sardine were eurythermic and anchovy stenothermic, and that anchovy seemed better adapted to spawning in cooler water than sardine. While the data presented above for these clupeoids in the Southern Benguela also suggest that sardine are eurythermic compared to anchovy, they suggest that in this system, sardine should be better adapted to spawning in cooler waters than anchovy. This dissimilarity between the anchovy/sardine species pair in the Benguela and California Current systems, with sardine preferentially spawning in cooler waters in the former and anchovy preferentially spawning in cooler waters in the latter, may be partially responsible for the phase difference in cycles of abundance observed between anchovy and sardine populations in these two ecosystems. Shifts in the relative dominance of anchovy and sardine in the Southern Benguela are out-of-phase compared to this species pair in the California Current (and the other major upwelling systems), with the sardine population off southern Africa increasing and the anchovy decreasing over periods during which anchovy increased and sardine decreased off California (Schwartzlose et al. 1999). If the mechanism responsible for regime shifts between clupeoid species pairs is one of global teleconnections (Schwartzlose et al. 1999 and references therein), then the phase difference between regime shifts in the southeastern Atlantic and the other regions could plausibly be attributed to the observed differences in preferred spawning temperature between anchovy and sardine in the various systems. For example, whereas sustained warm periods have been associated with greater abundance and extended spawning of sardine in the California and Humboldt Current systems (Lluch-Belda et al. 1992a), warm periods are likely to favor anchovy rather than sardine spawning in the Southern Benguela Current system.

Anchovy egg distributions during the spawner biomass surveys have been extensively described by Armstrong et al. (1988), Shelton et al. (1993) and Roel et al. (1994). These authors considered the Western Agulhas Bank to be the major anchovy spawning area, selected by the fish because of the efficiency of transport of eggs and larvae to the West Coast nursery grounds by the shelf-edge jet current (Shelton and Hutchings 1982, Boyd et al. 1992). The data presented here suggest that the Western Agulhas Bank is no longer the major anchovy spawning area: the Central and Eastern Agulhas Banks now appear to be the most important anchovy spawning grounds. Sardine egg distributions during spawner biomass surveys were mentioned by Roel et al. (1994), but have not yet been described in any detail for this region. After conducting a geostatistical analysis on egg data from the spawner biomass survey of 1994, Barange and Hampton (1997) noted that sardine eggs were more patchily distributed than anchovy eggs, and inferred that sardine spawning was sporadic and possibly driven by local conditions.

Conversely, anchovy appeared to display a consistent spawning strategy at the population level.

The apparent eastward shift in anchovy spawning habitat over the Agulhas Bank is linked to changes in the anchovy population structure observed recently: poor recruitment over the past few years has resulted in older fish constituting a larger proportion of the population (Roel et al. 1994, Barange et al. 1999). In addition to moving eastward with age (Barange et al. 1999), older, and therefore larger, anchovy make a disproportionately large contribution to spawning. Eggs spawned over the Central and Eastern Agulhas Banks tend to be located offshore of the cool ridge where they are more susceptible to offshore advection. Boyd et al. (1992) documented regular, strong offshore flow from the southern tip of the Agulhas Bank that was likely to contribute to offshore loss of eggs; hence, they speculated that eggs spawned east of Cape Agulhas were unlikely to contribute significantly to recruitment. However, a transport model derived from Acoustic Doppler Current Profiler-derived current data has indicated that eggs spawned offshore of the cool ridge could be successfully transported to the West Coast nursery grounds (Shannon et al. 1996, Boyd et al. 1998). Concurrent with the eastward shift in anchovy spawning habitat is an apparent offshore shift of anchovy eggs on the Western Agulhas Bank, possibly due to anchovy being excluded from the inner Western Agulhas Bank by the high densities of sardine observed there in recent years (Barange et al. 1999). This eastward and offshore shift in anchovy spawning habitat is likely to increase the potential for advective loss, and therefore could have significant impacts on recruitment variability of this species.

Anchovy and sardine showed a broad-scale overlap in their egg distributions, and hence spawning habitats, for the first two-thirds of the time-series. Since 1994, however, the spawning habitats of these two species have become spatially distinct; anchovy now spawn primarily east of Cape Point while sardine spawn west of Cape Point. It is worth pointing out that 1994 was the first year of the acoustically estimated biomass time-series when the relative biomass of sardine was higher than that of anchovy (Barange et al. 1999). Recent work has shown that pelagic fish school composition reflects the relative species abundance within the pelagic community in upwelling systems (Cury et al. 2000): when sardine, sardinellas, or anchovy are abundant they tend to form pure schools, whereas when their relative abundance diminishes they mix with other species. These findings have led to the school trap hypothesis (Bakun and Cury 1999) which postulates that "a fish species driven to school together with a more abundant species must effectively subordinate its specific needs and preferences to the 'corporate volition' of a school largely driven by a different set of needs and preferences." The similarity in sardine and anchovy spawning habitat prior to 1994, and dissimilarity thereafter, may provide some evidence for the school trap hypothesis. Spatially distinct spawning habitat between anchovy and sardine has also been observed in the California Current ecosystem (Hernandez-Vazquez 1994).

Anchovy have shown consistent decreases in spawning area and spawning output within the spawning area over the time-series, a period during which the population biomass of this species has declined. These decreases have resulted in declining total egg abundance estimates from 1984 to 1998. By contrast, sardine showed no clear patterns in either spawning area or reproductive output, and no long-term increase in total egg abundance, despite substantial increases in population biomass. These results show partial correspondence with those of Barange et al. (1999), who found that while the area occupied by adult anchovy was related to stock size, no such relationship was observed for sardine. Barange et al. (1999) speculated that increases in sardine stock size were reflected in actual school densities, without a corresponding increase in the area occupied by sardine. Assuming this to be the case would explain the lack of a consistent increase in sardine spawning area. If this were true however, it could be assumed that egg density and hence reproductive output within an unchanging spawning area would increase; the data presented above do not show this.

The egg data used in this analysis were collected during spawner biomass surveys conducted in November/December, the peak anchovy spawning period. Although sardine also spawn over spring/summer, the spawning peaks of this species occur on either side of the November/December surveys (September/October and February/March). In a study examining within-season variability in the abundance and distribution of clupeoid eggs and larvae, Fowler (1998) showed evidence to suggest that sardine egg abundance was highest over the Western Agulhas Bank during August-October and January/February, while abundance was highest on the South-West Coast during November/December. Fowler's (1988) study therefore suggests that sardine do shift their spatial patterns in spawning over the spawning period, and implies that the results of this study may be biased by the timing of the surveys during which the data were collected.

An additional assumption of this analysis is that the spawner biomass surveys cover most, if not all, of the spawning habitat of anchovy and sardine. Both of these species are known to spawn in waters off the east coast (east of 28°E), with sardine eggs often being dominant in ichthyoplankton surveys in this region (Beckley and Hewitson 1994, Connell 1996) and sardine larvae being collected in light traps off Durban through most of the year (Naidoo 1998). However, because of the narrow continental shelf along the east coast, this region is considered too small to contribute appreciably to the adult stock of these species (Armstrong et al. 1991). A third factor confining interpretation of the sardine egg data is the low numbers of eggs collected for this species; whereas about 150,000 anchovy eggs were collected over the time-series, only about 15,500 sardine eggs were collected (Table 1). The data from this study are therefore likely to provide a more accurate reflection of anchovy spawning habitat than they are for sardine; consequently, less confidence can be placed in interpretations derived from the sardine egg data. Despite these reservations con-

cerning the data for sardine eggs, it was felt that the large-scale coverage and relatively long time-series of data collected permitted a meaningful comparison between the spawning habitats of these two clupeoid species.

The results discussed above have implications for the management of anchovy and sardine in the Southern Benguela. First, they suggest that our current understanding of the life history of these two species requires revision, particularly for anchovy which is considered to be relatively well understood (Hutchings 1992, 1998). For example, the assumption that the Western Agulhas Bank is the major spawning habitat for both species no longer appears correct, requiring an expansion and/or shift in the spatial focus of monitoring programs used to provide information for various models that attempt to predict anchovy recruitment strength (Cochrane and Hutchings 1995, Korrubel et al. 1998, Painting and Korrubel 1998, Richardson et al. 1998). The offshore shift in anchovy eggs, particularly over the Eastern Agulhas Bank, is likely to increase the probability of advective loss, and hence impact negatively on recruitment success. Second, apart from the potential for increased advective loss on the exposed West Coast, the implications of a westward shift in sardine egg distributions are not well understood. Third, the recent spatial separation in anchovy and sardine spawning habitats may well be linked to the regime shift between these two species currently under way in the Southern Benguela: anchovy and sardine spawning habitats became spatially distinct in 1994, the first year when the relative biomass of sardine was higher than that of anchovy. Finally, a better understanding of such shifts in relative dominance, and the mechanisms by which these shifts are initiated and sustained, can only enhance management strategies of these commercially important clupeoid species.

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Spatially Specific Growth Rates for Sea Scallops (*Placopecten magellanicus*)

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Abstract

Past analyses have shown that sea scallops (*Placopecten magellanicus*) in the Bay of Fundy exhibit differing growth rates according to area and depth of capture. Area-specific shell height-at-age estimates from the resultant growth models are routinely used in stock assessments for a number of the management areas in the Bay of Fundy. These models have been based on fitting von Bertalanffy curves to cross-sectional data and it has been assumed that this annual snapshot of growth characteristics is applicable over time for different cohorts. Data on shell height-at-age for each annular ring are also available for scallop shells for a number of years, thus providing growth information for cohorts and over time. These data are used to evaluate how consistent spatially specific growth characteristics are over time. Given that these measurements of shell height-at-age are longitudinal and hence correlated over time, nonlinear mixed effects models are used to incorporate the serial correlation into the model.

Introduction

Spatial variation in the growth of scallops, particularly for the sea scallop (*Placopecten magellanicus*) has been reported in a number of studies (e.g., Caddy et al. 1970, MacDonald and Thompson 1985, Schick et al. 1988, Robert et al. 1990, Kenchington et al. 1997). For the most part, these studies have concentrated on examining differences in growth characteristics between scallops caught at different depths because depth has been recognized as having a strong influence on almost all aspects of sea scallop growth and biology (Naidu 1991). Depth is assumed to be a proxy for differences in either temperature or food availability or both but many

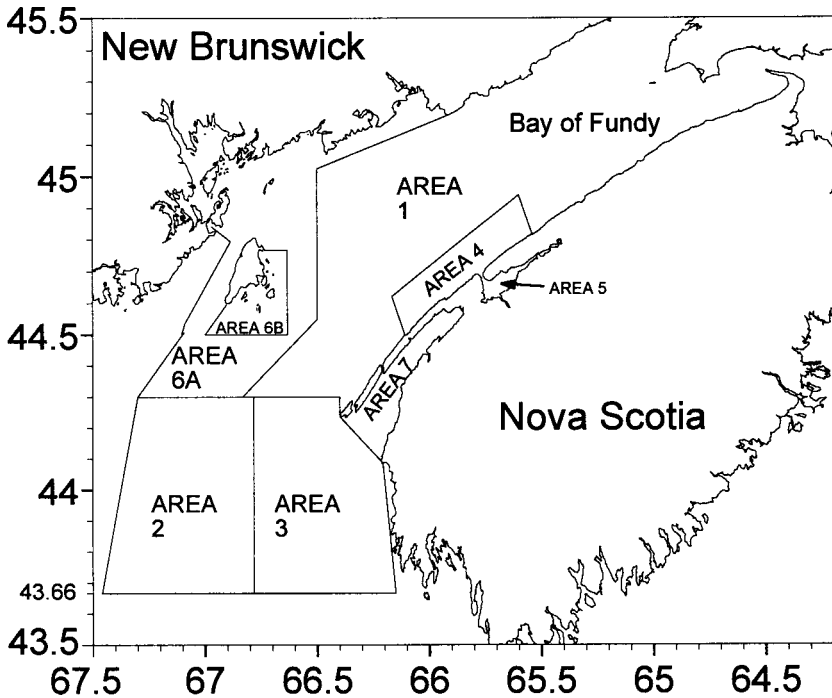


Figure 1. Scallop production areas in the Bay of Fundy as of 1 January 1997. Latitude and longitude are given in decimal degrees. Latitude 43.66 (43°40' N) corresponds to the outer boundary of the inshore scallop fishing area.

authors favor food availability as being more influential on growth rate and maximum size (e.g., MacDonald and Thompson 1985, Shumway et al. 1987).

On 1 January 1997, an area-based management plan was implemented for the sea scallop fishery in the Bay of Fundy, dividing the bay into seven scallop production areas (Fig. 1). While these areas were intended to reflect historical fishing patterns, the new management boundaries have grouped together areas where scallops were known to exhibit very different growth characteristics. However, to date management measures such as setting limits on meat count (number of adductor muscles per 500 g in the catch) and the minimum shell size which should reflect growth characteristics, are applied to an area as a whole.

Prior to the establishment of the scallop production areas, analyses of yield-per-recruit and optimum size and age of capture for scallops in the Bay of Fundy were based on growth estimates for areas where the scallops exhibited very similar growth rates (e.g., Roddick et al. 1994). Given the

change to the new areas, these analyses need to be revised to take into account spatial patterns of growth characteristics within the management areas.

In this paper we analyzed scallop growth data from one of the scallop production areas in the Bay of Fundy to investigate spatial patterns in growth. Traditionally, the most recent age and associated shell height-at-age data are used from each scallop to estimate growth parameters. However, the scallop shell contains the animal's complete growth history that can also be used to examine spatial patterns in growth that may have occurred over the lifetime of the animal.

Growth was modeled here using the von Bertalanffy growth curve, as it has been in many of the previous studies on scallop growth. One difference between our study and the other studies on the growth of scallops is that we also applied the von Bertalanffy model to the complete growth history from each scallop shell. This application of the model was done by using nonlinear mixed effects models which were developed for these kinds of repeated measures data (Lindstrom and Bates 1990). Linear forms and nonlinear forms of the mixed effects models have been used to model repeated measures of growth in grey seal pups (*Halichoerus grypus*) (linear, Bowen et al. 1992) and snapper (*Pagrus auratus*) (nonlinear, Millar et al. 1999).

Management measures such as limits on meat count and minimum shell height of scallops in the catch were based upon yield-per-recruit analyses, which in turn require a growth model. The current limits set for many of the new scallop production areas in the Bay of Fundy may not reflect the spatial variation in growth in these areas.

Materials and Methods

Data

The major source of data on abundance, growth, and shell height-at-age for scallops in the Bay of Fundy is the research surveys conducted by the Department of Fisheries and Oceans. Annual surveys have been conducted every June by the department since the late 1970s in what is now known as scallop production area 4 (Fig. 1). The survey design has varied over time but has been a consistent stratified random design since 1991. No matter what design was used, survey tows were made at randomly located stations using a gang of four Digby drags (scallop dredges) with steel rings (75-78 mm inside diameter) knitted together with rubber washers. The drags were towed for 8 minutes on the bottom. Two of the four drags were lined with 38 mm polypropylene stretch mesh to retain the smaller scallops.

From each tow, all or a sample of scallop shells were measured for height (tangential dorso-ventral measurement, Naidu 1991), the adductor muscles (meat) were removed and weighed. The shells were read for annual growth rings which are formed each winter when water temperatures

decline and the shell growth slows down causing the deposition of a dark band on the shell. Age determination can be subjective, as growth rings can be very difficult to distinguish at times. All ages in this data set were determined by one person (M.J. Lundy) in an attempt to ensure consistency. Shell height at each age for each shell was determined by measuring the height of each growth ring from the shell umbo.

For our study we chose the data collected during the June 1990 survey because these data consisted of a fairly large number of animals from which we had measurements of shell heights and ages over the whole life-span of the animal. In addition, these data had come from survey tows located in four of the strata used in the current stratified survey of this area known to have different growth characteristics. The strata labeled Centreville and Gullivers Head on Fig. 2 are generally considered to be areas of low growth rate, whereas the strata labeled Digby Gut and Delaps Cove are known to be areas where scallops exhibit high growth rates. The data used in this study are from only one survey in one year and therefore the results are intended to be illustrative and not definitive with respect to Bay of Fundy scallop populations.

In general, growth curves are estimated from the oldest ring and associated shell height from each shell. These kinds of data are referred to as cross-sectional here in that they represent size-at-age across a number of cohorts at one period in time. There were 706 animals in our data set and hence we had 706 cross-sectional measurements over the different survey strata (Table 1). Each of the 706 shells also had measurements on shell height to each annual growth ring for a total of 2,562 measurements. The literature on modeling these kinds of data where there is within-subject (scallop) and between-subject variation refers to these as repeated measurements or if measurement over time is involved, as longitudinal data.

In addition to measuring the scallops caught at each tow the depth of the tow was also recorded. Survey work was conducted during daylight hours and at least one tidal cycle was experienced. Water depths varied by 0.2-9.0 m at any one spot in the study area during June 1990 due to the strong tides in the Bay of Fundy. Therefore, all of the depths used in this study were corrected to their chart datum value using tidal height predictions supplied by the Canadian Hydrographic Service. Comparisons of the predictions for 1990 with measurements recorded during June 1990 from tidal gauges at the Parkers Cove measurement station (Fig. 2) indicated differences of less than 1 m.

Growth Models

Cross-Sectional Data

The standard three-parameter von Bertalanffy model was used here to model the growth from cross-sectional data on age and shell height (e.g., Quinn and Deriso 1999).

Table 1. Numbers of scallops measured for shell height and age by sampling stratum and measurement type. Longitudinal measurements ranged from 5 to 13 years per animal.

Stratum	Measurement type	
	Cross-sectional	Longitudinal
Centreville	120	530
Gullivers Head	80	353
Digby Gut	264	860
Delaps Cove	242	819
Total	706	2,562

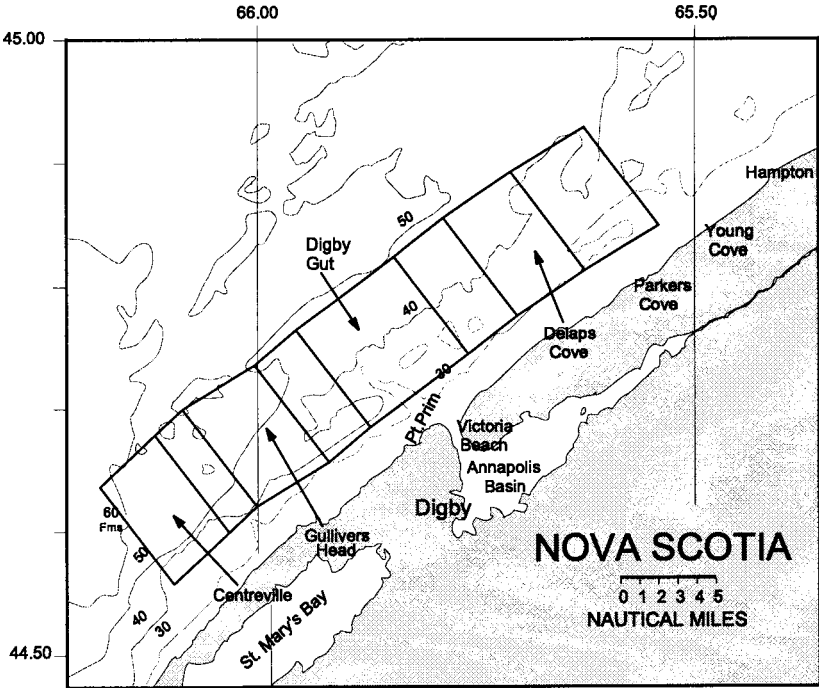


Figure 2. Scallop production area 4 in the Bay of Fundy as of 1 January 1997. Rectangles indicate strata used in resource surveys. Samples in this study are from the four strata identified by name on the map. Latitude and longitude are given in decimal degrees. Depths are measured in fathoms (1 fathom = 1.8 m). Depth contours are approximate.

$$L_{ia} = L_{\infty} \{1 - \exp[-K(a - T_0)]\} + \varepsilon_i \quad (1)$$

where

L_{ia} is shell height (mm) for scallop i at age a in years;

L_{∞} is asymptotic shell height;

K is Brody growth parameter (y^{-1});

T_0 is age at which $L_a=0$; and

ε_i is random error.

This model was fit to the data using the `nls()` function in S-PLUS (Mathsoft 1999) which uses the Gauss-Newton algorithm to estimate the parameters. The random error was assumed to be normally distributed with zero mean and constant variance.

Longitudinal Data

At the level of individual scallop shell i , the shell height at age a , $L_{i,a}$ was modeled using a von Bertalanffy curve with individual parameters.

$$L_{i,a} = L_{\infty,i} \{1 - \exp[-K_i(a_i - T_{0,i})]\}$$

The nonlinear mixed effects model approach expresses each individual parameter as being a function of a population parameter or fixed effect and an individual deviation from that fixed effect is referred to as a random effect (Lindstrom and Bates 1990). That is,

$$L_{i,a} = (L_{\infty} - l_{\infty,i}) \{1 - \exp\{-(K - k_i)[a_i - (T_0 - t_{0,i})]\}\} + \xi_{i,a} \quad (2)$$

where L_{∞} , K , and T_0 represent fixed effects and $l_{\infty,i}$, k_i , and $t_{0,i}$ are the random effects. The random effects are all assumed to follow a Normal distribution with zero mean and variance-covariance matrix $\sigma^2 \mathbf{D}_1$. For the von Bertalanffy model the variance-covariance matrix is of dimension 3×3 with diagonal elements $\sigma^2_{L_{\infty}}$, σ^2_K , and $\sigma^2_{T_0}$. The general procedure of fitting the nonlinear mixed effects model assumes that the variance-covariance matrix is a general positive definite matrix allowing the fitting algorithm to estimate covariances between the random effects.

For the longitudinal measurements made for each scallop, the random error associated with shell height at each age, $\xi_{i,a}$ is also assumed to have a normal distribution with zero mean and variance-covariance matrix $\sigma^2 \mathbf{\Lambda}_1$. The matrix $\mathbf{\Lambda}_1$ was initially set to the identity matrix when fitting the model and hence repeated measurements made on the same animal are assumed to be independent over age once the random effects have been accounted for. Serial correlation using a wide range of models can be incorporated into this matrix once the initial model has been fit to the data.

The S-PLUS (Mathsoft 1999) function `nlme()` was used to fit the nonlinear fixed effects models in this study. From our experience with using the von Bertalanffy model in the nonlinear mixed effects approach we found that the fitting algorithm was most stable when K was reparameterized as $\exp(K')$. This reparameterization ensures that the estimated growth parameter, $\hat{K} = \exp(K')$ in the model was always positive.

Results

Initial analysis of the cross-sectional and longitudinal growth data indicated that ages with shell heights less than 40 mm were poorly modeled by the von Bertalanffy model, suggesting that growth at these young ages did not follow the same pattern observed at older ages. Therefore the growth analysis was restricted to scallops greater than or equal to 40 mm which resulted in an age range of 3-13 for the cross-sectional data and 2-13 for the longitudinal data.

Cross-Sectional Growth Data

A comparison of the residuals from each area from fitting one von Bertalanffy model to the data from all areas illustrates a commonly made observation for scallop growth data from this area (Fig. 3). The resultant growth model tends to overestimate shell height-at-age in the Centreville and Gullivers Head area and underestimate in the Digby Gut and Delaps Cove area. One approach proposed by Kenchington et al. (1997) for dealing with this pattern was to fit separate growth curves for each area and based on previous studies, separate curves were used for depths shallower and deeper than 88 m (observed depth not corrected to chart datum). While such a model consisting of separate curves for areas and depth zones provides a significant improvement over using just one curve for the whole area, a total of 21 parameters are required to describe the model (model I vs. II in Table 2a).

As discussed earlier, depth has been identified as an influential variable and the residuals from the fit of the von Bertalanffy model to the data from all areas indicate a very strong linear trend with respect to depth (corrected to chart datum) (Fig. 4). This trend was characterized here by fitting a loess curve to the residuals (Cleveland and Devlin 1988). The asymptotic shell height parameter (L_{∞}) is the only linear parameter in this growth model and the residual pattern in Fig. 4 suggests that a model with L_{∞} modeled as a linear function of depth might be appropriate here.

The first model used here for L_{∞} was a quadratic relationship with depth,

$$L_{\infty} = \beta_0 + \beta_1 \text{Depth} + \beta_2 \text{Depth}^2 \quad (3)$$

While the quadratic model may capture the curvature indicated by the loess line, there also appears to be evidence of a change in the relationship at around 80-96 m. To capture this feature a model with a bilinear relationship with depth was also used for L_{∞} .

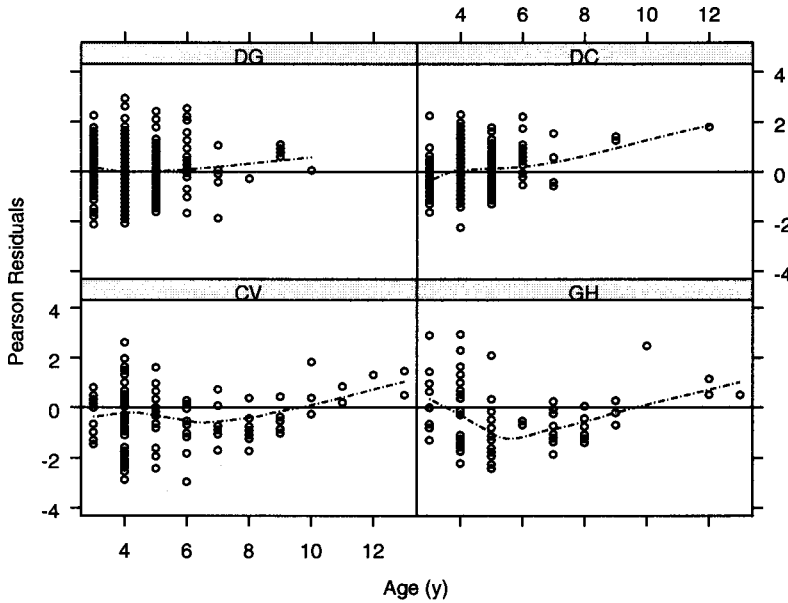


Figure 3. Scatter plot of residuals from each area based on a fit of one von Bertalanffy growth model to age and shell height measurements from 706 scallops from all areas. Data collected from the research dredge survey of the Bay of Fundy, June 1990. Panels illustrate residuals by sampling strata. Note: CV = Centreville, GH = Gullivers Head, DG = Digby Gut, DC = Delaps Cove. A loess line has been fitted to the residuals in each panel to investigate for trend.

$$L_{\infty} = \begin{cases} \beta_{0,1} + \beta_{1,1} \text{Depth, if Depth} < D_c \\ \beta_{0,2} + \beta_{1,2} \text{Depth, otherwise} \end{cases}$$

where D_c needs to be estimated but appears to be between 80 and 96 m.

The quadratic model (model III in Table 2a) explained significantly more of the variation in the data than model II. However, the additional amount of variation explained by the bilinear form of the model (model IV) over that explained by the quadratic model was significant as well. The estimate of $D_c = 90$ m was obtained by the bilinear models for a range of depths and choosing the depth which resulted in the largest model sum of squares. Comparison of parameter estimates from the von Bertalanffy model for all of the data with those for the bilinear model exhibits a greater L_{∞} when depths are less than 101 m and lower values for K and T_0 over all depths for the latter model (Table 2b). The residuals from the bilinear model do not exhibit any apparent trend with depth (Fig. 5).

Table 2. Results from fitting the von Bertalanffy growth model to the cross-sectional scallop shell height and age data using the nonlinear least-squares method.

a. Model fitting results.							
Model	Test	Residual DF	Residual SS	Model DF	Model SS	F-statistic	P-value
I.		703	26992.07				
II.	I vs. II	685	21932.30	18	5059.77	8.78	< 0.0001
III.	I vs. III	701	21392.08	2	5599.99	91.75	< 0.0001
IV.	III vs. IV	700	20772.41	1	619.67	20.88	< 0.0001

b. Parameter estimates.			
Model	L_{∞}	K	T_0
I.	113.98	0.65	1.09
IV.	131.75 – 0.12 × depth (<90 m) 144.41 – 0.30 × depth (≥90 m)	0.47	1.09

Models are: I, one growth curve for whole area; II, one growth curve for each subarea; III, one growth curve and a quadratic relationship between depth and L_{∞} ; IV, one growth curve and a bilinear relationship between depth and L_{∞} .

The curve for the predicted shell heights-at-age from the model for all of the data was not parallel with those from the bilinear model for particular depths (Fig. 6). The general shape of the all-data curve may reflect the fact that most of the data for the older ages came from the deepwater samples while the greater proportion of data on the younger ages tended to come from the samples from shallower water.

Longitudinal Growth Data

The growth trajectories for individual scallops indicate that there is strong evidence for individual variation in their respective von Bertalanffy parameters (Fig. 7). Animals that are larger (or smaller) than average at a younger age remain so as they grow older.

A nonlinear mixed effects version of the von Bertalanffy model was fit to the data portrayed in Fig. 7 both for the whole data set and within area/depth subareas as was done for the cross-sectional data. In both models, L_{∞} , K and T_0 were all defined as having fixed and random effects.

Similar to the results for the cross-sectional data, the model for area/depth subareas provided a significant improvement over the model for all areas (Table 3a). Residuals from these models were obtained for each scallop at each age by subtracting the fitted values at that level from the observations and dividing by the estimated within-scallop standard error if

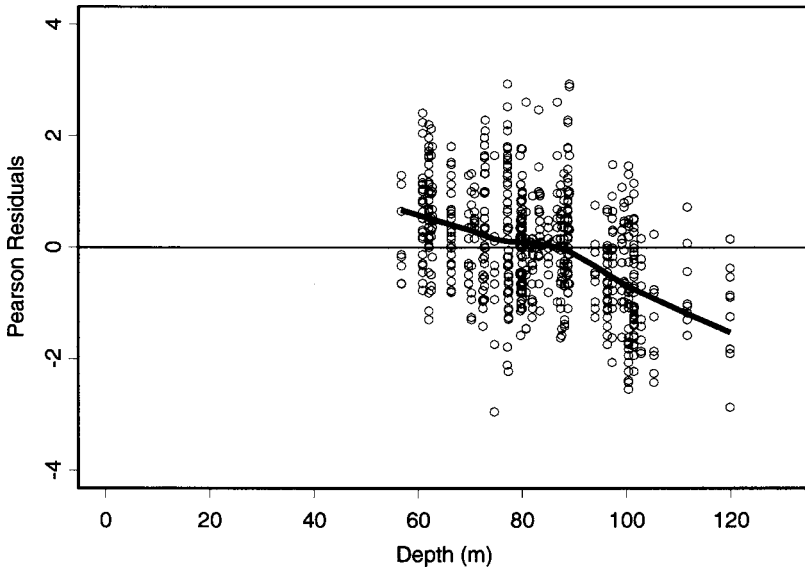


Figure 4. Pearson residuals from fit of von Bertalanffy growth model to age and shell height measurements from 706 scallops measured on research dredge surveys of the Bay of Fundy, June 1990. Residuals plotted against observed depths (corrected to chart data, see text) at dredge sites. A loess line has been fitted to the residuals to investigate for trend.

standardized residuals are required. However, given the added flexibility of allowing the von Bertalanffy parameters to vary for each individual, these residuals are probably not very informative about lack-of-fit. Instead, lack-of-fit could be ascertained from looking at the estimated random effects $L_{\infty,i}$, k'_i and $t_{0,i}$ from each scallop.

Scatter plots for each of the parameter random effects are presented in Fig. 8. Again, loess lines were used to determine if trends with depth existed in these graphs. While the panels for k'_i and $t_{0,i}$ indicate little or no trend, the very strong pattern for $L_{\infty,i}$ is striking (Fig. 8). The trend in $L_{\infty,i}$ appears to be quadratic or bilinear with an inflection point in the same depth range as noted for the cross-sectional data.

The pattern in this figure suggests that the mean of the random effects $L_{\infty,i}$, that is the fixed effect L_{∞} , is not stationary with increasing depth. Therefore, the fixed effect L_{∞} was modeled as having either a quadratic or a bilinear relationship with depth. The results from fitting these two forms of the growth model were similar to those obtained for the cross-sectional data (Table 3a). Both models provided better fits to the data with fewer parameters than either the growth model fit to all of the data or fitting individual

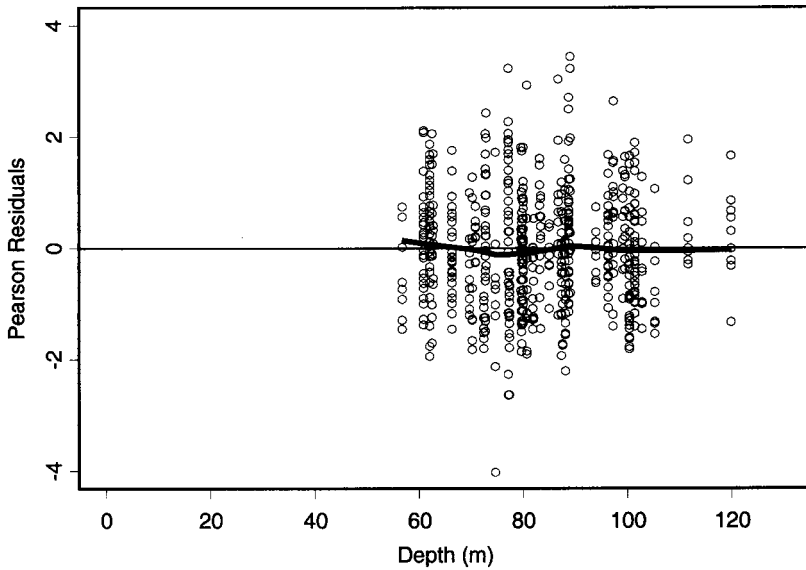


Figure 5. Pearson residuals from fit of modified von Bertalanffy growth model to age and shell height measurements from 706 scallops measured on a research dredge survey of the Bay of Fundy, June 1990. Growth model has depth incorporated as a bilinear relationship between depth and L_{∞} . Residuals plotted against observed depths (corrected to chart data, see text) at dredge sites. A loess line has been fitted to the residuals to investigate for trend.

growth curves to each area/depth combination. Also, the bilinear model was a significant improvement over the quadratic model. The scatter plot for the random effects for L_{∞} from the bilinear model shows little trend with increasing depth (Fig. 9).

Comparison of the parameter estimates from the original nonlinear mixed effects model fit to all of the data with the bilinear model shows little change in the fixed effects estimates for K' (and K) and T_0 between the two models (Table 3b). The fixed effect estimate for L_{∞} from the bilinear model was less than that from the model for all of the data for depths greater than 90 m. The slopes for the depth terms were assumed to be fixed effects only; however, the intercept term did have a random effect. The addition of the bilinear term for L_{∞} reduced the standard error, $s_{L_{\infty}}$ (intercept of bilinear relationship) of the associated random effects but did not affect any of the standard errors of the other random effects.

The hypothesis of independence between random effects was tested by setting \mathbf{D}_i to the identity matrix and refitting the bilinear model. The

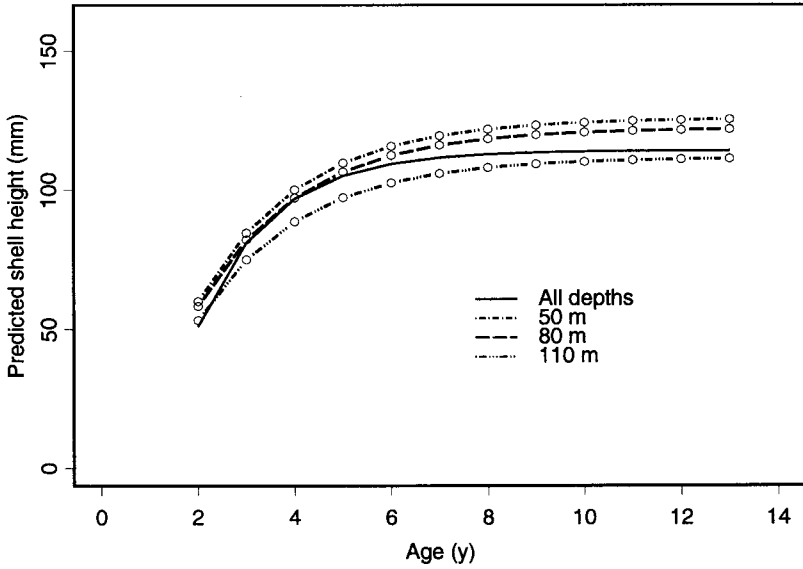


Figure 6. Predictions from modified von Bertalanffy growth model. Growth model has depth (corrected to chart data, see text) incorporated as a bilinear relationship with L_{∞} term.

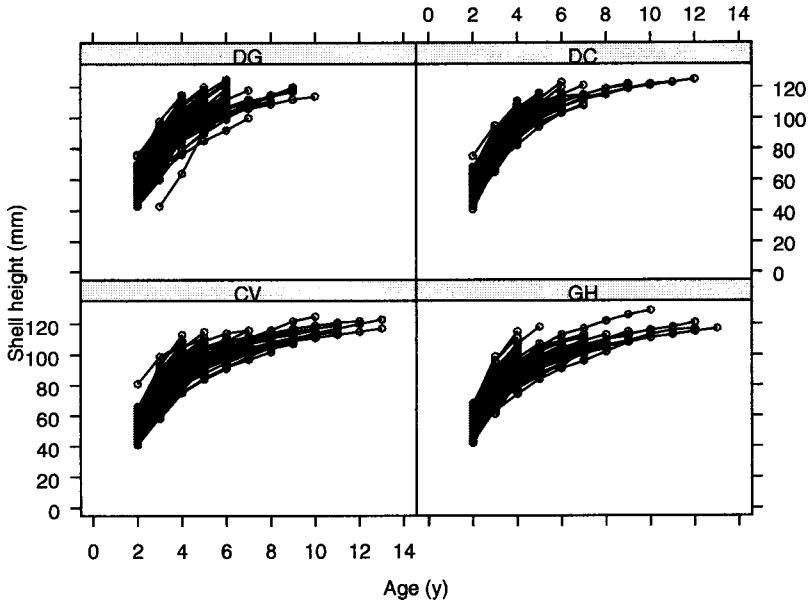


Figure 7. Scatter plot of longitudinal age and shell height measurements from 706 scallops measured on a research dredge survey of the Bay of Fundy, June 1990. Measurements from same animal are connected with lines.

Table 3. Results from fitting the von Bertalanffy growth model to the longitudinal scallop shell height and age data using a nonlinear mixed effects model.

a. Model fitting results.					
Model	Test	DF	Log likelihood	Likelihood ratio	P-level
I.		10	-7062.72		
II.	I vs. II	28	-6948.95	227.53	<0.0001
III.	I vs. III	12	-6931.69	262.06	<0.0001
IV.	III vs. IV	13	-6919.90	23.57	<0.0001

b. Parameter estimates for nlme model.								
Model	L_{∞}	Fixed effects			Random effects			
		K'	K	T_0	$\sigma_{L_{\infty}}$	σ_K	σ_{T_0}	s
I.	129.04	-0.94	0.39	0.57	12.56	0.24	0.25	1.64
IV.	147.25 - 0.18 × depth (<90 m)	-0.97	0.38	0.55	10.01	0.23	0.25	1.62
	155.48 - 0.30 × depth (≥90 m)							

Models are: I, one growth curve for whole area; II, one growth curve for each subarea; III, one growth curve and a quadratic relationship between depth and L_{∞} ; IV, one growth curve and a bilinear relationship between depth and L_{∞} .

likelihood-ratio test rejected the null hypothesis of independence (P -value < 0.0001).

Examples of predicted growth curves for selected depths appear to be parallel with the curve from the model fit to all of the data (Fig. 10). Recall that in the cross-sectional case, the predicted curve from the model fit to all of the data tended to resemble the curves for the shallower depths at the younger ages and the deeper depths for the older ages. In the case of the longitudinal data, the smaller number of older animals from the shallower depths contributes more information than was the case for the cross-sectional data. That is, all animals of age a also contribute shell heights at ages $a-1$, $a-2$, etc.

A comparison of observed and predicted shell heights by sampling strata from the bilinear form of the model does not show any area specific deviations once depth has been incorporated into the model (Fig. 11).

Yield-Per-Recruit

One of the major uses of growth data in fisheries management is to calculate yield-per-recruit and estimate reference points such as $F_{0.1}$ and F_{max} . Unfortunately, no meat weights or weights of any kind were taken during the 1990 survey. At present the only survey for which we have both shell height with meat weight data and depth corrected to chart data is the June

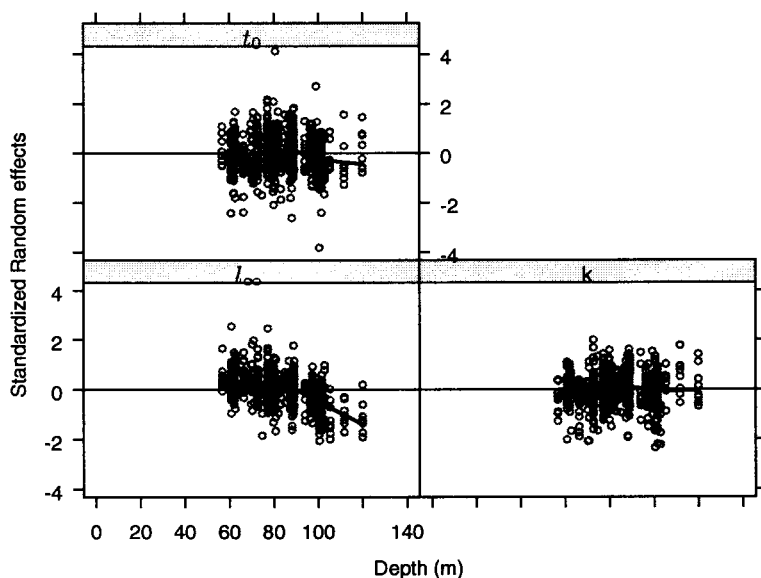


Figure 8. Scatter plot of standardized random effects for each of the parameters of the nonlinear mixed effects version of von Bertalanffy growth model fitted to longitudinal age and shell height measurements from 706 scallops measured on research dredge survey of the Bay of Fundy, June 1990. Random effects are plotted against observed depths (corrected to chart data, see text) at dredge sites. A loess line has been fitted to the data to see if any trend exists in the random effects.

1996 survey of the same area. Given that our analyses are intended to be illustrative we used the 1996 meat weight data to calculate yield-per-recruit. Preliminary analysis of a regression of the natural logarithm of meat weight on the natural logarithm of shell height indicates that a depth effect similar to those observed in the growth data analyzed here was also apparent in the meat weight data (S.J. Smith, unpubl. data). The study of these data is ongoing but indications are that modeling the intercept of the regression as a bilinear function of depth with a break point at 90 m provides the best fit. A full analysis of these will not be presented here but predicted meat weights at shell heights by depth were used to estimate mean weight-at-age for the growth models analyzed in this report.

The Thompson-Bell model for yield-per-recruit (Ricker 1975) was chosen here with the selectivity curve used in Roddick et al. (1994). Estimates of $F_{0.1}$ for cross-sectional growth curves are higher than those from the longitudinal growth curves for comparable depths (Table 4). The cross-sectional models also indicate that this optimal level of fishing mortality will result in the average age of scallops in the catch being 1 year younger

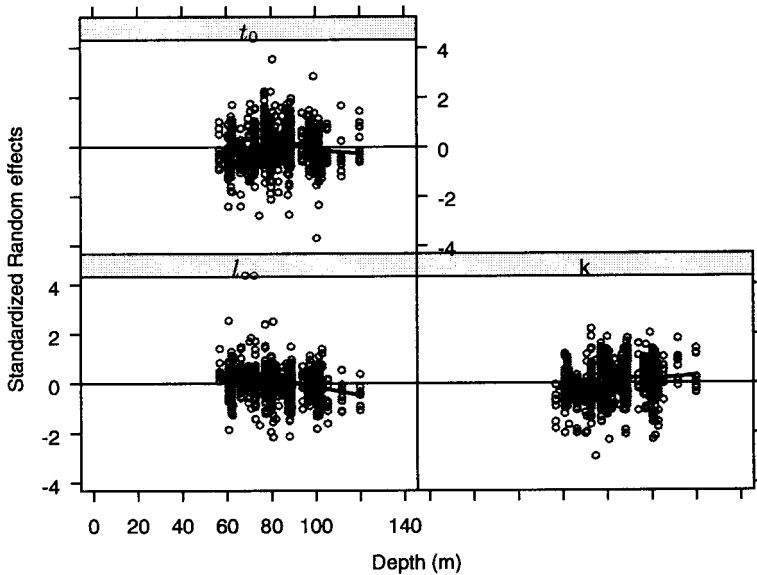


Figure 9. Scatter plot of standardized random effects for each of the parameters of the nonlinear mixed effects version of von Bertalanffy growth model modified to include a bilinear relationship between depth and L_∞ . The model was fitted to longitudinal age and shell height measurements from 706 scallops measured on research dredge survey of the Bay of Fundy, June 1990. Random effects are plotted against observed depths (corrected to chart data, see text) at dredge sites. A loess line has been fitted to the data to see if any trend exists in the random effects.

than expected from the longitudinal model. As a result meat counts and mean meat weights were also less for the cross-sectional models compared to the longitudinal models. Within model type, mean age in the catch was the same for each $F_{0.1}$ but the expected mean weight was smaller for the deeper depths.

Note that neither the counts nor the meat weights presented here take into account the substantial meat growth that occurs from June to the fall. In recent years the fishery has opened in October and closed when the total allowable catch has been taken, usually in November.

Discussion

The finding that depth appears to have a significant effect on growth in scallops is not a new one as indicated by the literature cited in the introduction to this paper. Scallops appear to grow slower or have a smaller asymptotic size, or both, the deeper they are found (Caddy et al. 1970,

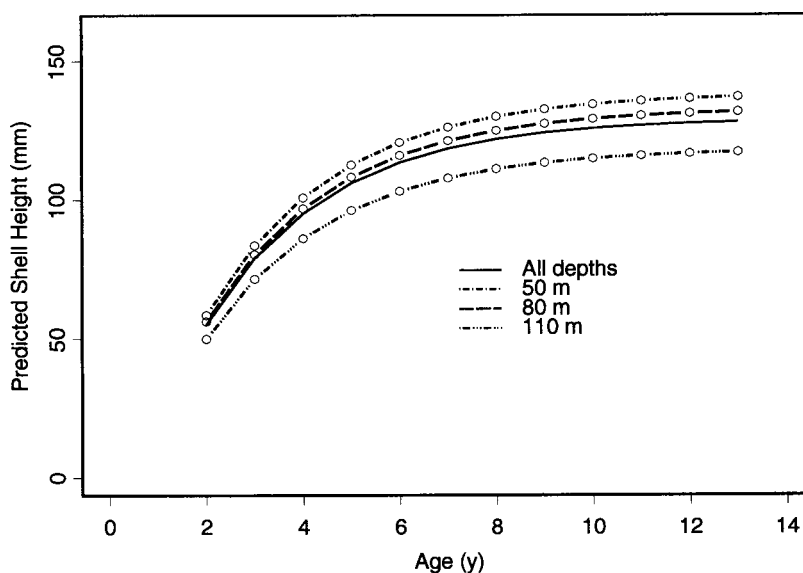


Figure 10. Predictions of population curves from modified mixed effects von Bertalanffy growth model. Growth model has depth incorporated into L_{∞} term as a bilinear equation.

MacDonald and Thompson 1985, Schick et al. 1988, Robert et al. 1990, Kenchington et al. 1997). Barber et al. (1988) also noted that scallops had lower fecundities in deeper water than scallops in shallower waters with respect to the number of eggs spawned.

Most of these studies on depth and growth suggested that lower availability of food at the deeper depths may be the controlling factor. A comparison of gut contents from scallops caught at 20 m and 180 m showed that there were differences in the species composition of algae consumed by the scallops at the two depths (Shumway et al. 1987). Pelagic species and benthic species were equally abundant in the gut contents of scallops from 20 m but the pelagic species were outnumbered by benthic species in the 180 m sample. While the authors did not report on possible nutritional differences between pelagic and benthic species of algae, they suggested that the seasonal availability of algae during blooms was probably more beneficial for animals in shallow water than in deep water.

Food availability may also be a function of the water currents in the area. The Bay of Fundy has a highly complex system of currents given the large tides in the area but unfortunately there has been little detailed work on the currents in this area (J. Loder, Bedford Institute of Oceanography, Ocean Sciences Division, Dartmouth, Nova Scotia, pers. comm.). Predic-

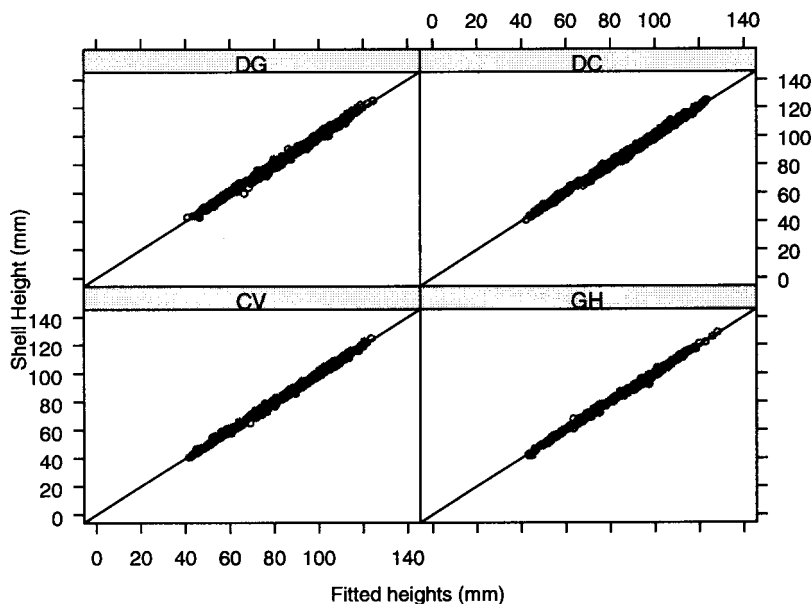


Figure 11. Scatter plot of observed shell heights versus fitted values for nonlinear mixed effects version of von Bertalanffy growth model modified to include depth. Model was fitted to longitudinal age and shell height measurements from 706 scallops measured on a research dredge survey of the Bay of Fundy, June 1990. Panels refer to sampling strata. Note: CV = Centreville, GH = Gullivers Head, DG = Digby Gut, DC = Delaps Cove.

tions from oceanographic models show that the velocity of tidal currents decrease with distance and depth from the Nova Scotia shore into the Bay (J. Loder, unpubl. data). Lacking direct observation we can only speculate that lower velocity currents may transport lower amounts of food to the deeper depths.

The fact that the 90 m depth is important for both the cross-sectional and longitudinal data and the preliminary finding that it is also important for the 1996 cross-sectional meat weight and shell height relationship suggests that it is probably a constant feature for this area. As such this depth may be a point where there is a dramatic decrease in current velocity due to boundary layers or some other feature. The 90 m depth appears to be specific to this area of the Bay of Fundy. Lundy and Smith (1999) analyzed the residuals from the von Bertalanffy model for cross-sectional data from the Brier Island/Lurcher Shoal area at the mouth of the Bay of Fundy and found that the breakpoint for the residuals corresponded to a combination of depth and westward location. In this case, there appears to be a relationship between the residuals and the location of a frontal zone.

Table 4. Predictions from Thompson-Bell yield-per-recruit model for scallop growth data.

Method	Depth (m)	$F_{0.1}$	Mean meat weight (g)	Mean meat count/500 g	Age
Cross-sectional	All	0.22	11.24	44	4+
	50	0.20	14.09	35	4+
	80	0.20	13.67	37	4+
	110	0.22	6.91	72	4+
Longitudinal	All	0.19	12.89	39	5+
	50	0.18	16.45	30	5+
	80	0.19	15.40	32	5+
	110	0.21	7.35	68	5+

If food availability is the underlying cause for the differences in growth with depth then it may be quite natural to model these differences as a function of the maximum size L_{∞} . Beverton and Holt (1957) suggested that in the von Bertalanffy model, when applied to weights-at-age, the parameter for maximum size W_{∞} is proportional to the cube of the ratio of the coefficients of anabolism and catabolism, while K is proportional only to catabolism. Changes in food supply would solely affect the rate of anabolism and such a change would then only be reflected by changes in W_{∞} .

Originally the von Bertalanffy model had been defined to describe the growth of a single animal (see Southward and Chapman 1965). In the application of this model to measurements from a group of animals, individual variability was assumed to be characterized by the ϵ_i term in equation 1. As such, this term acts as a catchall for the cumulative effects of individual genetic variability and environmental effects. Individual variability in growth might be more appropriately characterized as having individual growth parameters (Sainsbury 1980). Sainsbury predicted that if this situation exists then the estimate of K from equation 1 would be greater than the actual mean K over the population. Therefore the estimated size at age from equation 1 would underestimate the true size at age. However, this latter prediction was based on assuming that there was no individual variability in T_0 and that L_{∞} and K were independent. Our analysis indicates that neither of these assumptions was true. While the growth parameter from equation 1 is higher than from equation 2 as predicted by Sainsbury (1980), the estimated size at age from the latter is not greater than the former over all ages due to the differences in all of the parameters for both models and the correlation between the parameters.

Although Sainsbury (1980) suggested that the amount of bias in the estimated size-at-age might not be large enough for concern given the typical

range of variation in individuals of most fish populations, the results of Table 4 appear to warrant concern here. The results of the yield-per-recruit for the longitudinal data are more optimistic than those from the cross-sectional data by suggesting that meat yields will be higher and that the mean age of the scallops in the catch will be one year older at $F_{0.1}$.

The difficulty we encountered in fitting shell height-at-age for animals less than 40 mm in both types of data may be due to the fact that many of those animals were not or had just become sexually mature. While scallops may become sexually mature as early as 1 year old (23-35 mm) their fecundity is low relative to their mass (Young-Lai and Aiken 1986). Day and Taylor (1997) recommended that the von Bertalanffy model not be used for growth up to and including age-at-maturity because the model does not acknowledge the change in resource allocation at maturity. In addition, because the curve is asymptotic the model does not accurately represent the growth trajectory of an animal during its prereproductive stage of life when all of its energy is dedicated to growth. Our situation was further complicated by the use of the 38 mm liner in the survey drags which precluded the representative sampling of small scallops and probably resulted in the catch of the faster-growing individuals at the younger ages.

Scallops are largely sedentary creatures and therefore the fishery can be spatially selective targeting areas with higher growth rates until densities are reduced to below commercially viable levels. The strong relationship between growth and depth presented here means that spatial targeting can be facilitated by simply knowing the depth you are fishing at within the scallop production area. The imposition of any or all of meat count limits, minimum meat weights, or minimum shell size would only increase the degree of targeting.

Under the current management system for scallop production area 4, the only enforceable control on the size composition in the catch is the monitoring of meat counts. In practice, a range of meat sizes is allowed in the catch as long as the average meat count from two monitoring samples meets the regulated count. Under this regime, fishing in the lower-growth areas will occur and catches from high- and low-growth areas are "blended" to meet the regulated count.

The practices of targeting and blending result in differential fishing mortality with depth. Depending upon the degree of these practices, the population of scallops in the whole management unit may not correspond to the fished population. Initial expectations of productivity based on the whole population may greatly overestimate the actual productivity as higher growth areas are targeted and fished down. In recent years, the major recruitment to scallop production area 4 has been in the deeper areas and we have realized that we probably underestimate fishing mortality when using survey indices calculated from the whole management area (Smith and Lundy 1998). Accurate estimates of fishing mortality and productivity will require more specific knowledge on the spatial behavior of the fishing fleet.

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Spatial Distribution and Recruitment Patterns of Snow Crabs in the Eastern Bering Sea

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Abstract

Data from summer trawl surveys and spring commercial fisheries from 1978 to 1999 were analyzed to understand the spatial dynamics of snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea. Males were generally more dispersed than females. Mean sizes at maturity for females increased from north to south and slightly from shallow to deep water. Some crabs appeared to move gradually from shallow water in the northeast to deeper water in the southwest during ontogeny. Centers of distribution of mature females and large males have gradually moved to the northwest over time since the late 1970s. Newshell mature females were broadly distributed during years of high abundance but were concentrated in the north during years of low abundance. Recruits (newshell male and immature female crabs <45 mm carapace width) to the middle, eastern, or southern areas may have better opportunities to grow to commercial sizes than those to the north. During the past 22 years, recruitment has been periodic: strong recruitment occurred every 4-7 years. However, extremely low recruitment in recent years may interrupt this pattern. Questions remain about the degree of stock separation, the total geographic range of the stock, and the loss of oldshell males from the survey stock due to emigration or high natural mortality.

Introduction

Snow crabs (*Chionoecetes opilio*) are widely distributed in the Bering Sea, extending as far north as the Chukchi Sea and Arctic Ocean (Wolotira et al.

1977). Within the eastern Bering Sea, mean sizes of mature males and females increase with decreasing latitude or increasing depth (Otto 1998). Large males are found in high abundance primarily in the southern part of the eastern Bering Sea and in a band along the outer margin of the continental shelf (Somerton 1981) where the snow crab fishery in the eastern Bering Sea occurs.

Snow crabs in the eastern Bering Sea currently support one of the largest and most valuable fisheries in the United States. The Japanese fleet first harvested snow crabs as bycatch in the 1960s until 1973 when a directed fishery was initiated. The catch gradually increased through the 1970s (Otto 1990). Total catch was relatively small until the directed domestic fishery was developed in the late 1970s. The Magnuson Fisheries Conservation and Management Act prohibited fishing for snow crabs in 1980. The domestic fishery expanded quickly in the late 1980s, and catch peaked in 1991 at 0.15 million t (Morrison 1999). Annual ex-vessel value peaked in 1994 at US\$192 million (Morrison 1999). Catches have fluctuated widely during recent years, tracking the abundance of large male crabs estimated by the National Marine Fisheries Service (NMFS) trawl surveys (Stevens et al. 1998). Because of the low abundance estimated in the 1999 summer survey, the catch quota (12,900 t) for 2000 was the lowest in the last two decades.

The objectives of this study were to conduct an exploratory analysis on the spatial distribution of snow crabs in the eastern Bering Sea and to examine spatial recruitment patterns. Annual spatial data by size and sex were mapped to identify spatial distribution patterns. Annual centers of abundance of different size groups of males and females were computed, and relationships between crab carapace size, depth, and latitude examined. Finally, size frequencies of male and female crabs were followed over time to identify strong and weak year classes.

Methods

Summer trawl survey data for snow crabs in the eastern Bering Sea from 1978 to 1999 were obtained from NMFS. Before 1978, the survey covered a limited area that does not fully represent the snow crab stock. The survey employs a systematic design where a 20×20 nautical mile grid was overlaid on the eastern Bering Sea. One 0.5-hour trawl tow was usually made per 400 square nautical miles. Multiple tows (usually two tows) have been conducted for a single station for small areas around the Pribilof Islands and St. Matthew Island. Occasionally, multiple tows were conducted at stations with an extremely high catch of red king crabs (*Paralithodes camtschaticus*) or blue king crabs (*P. platypus*). Surveys occurred from May 20 to September 3, primarily during June-July (Table 1). After 1978 over 300 stations were surveyed, with the total number of tows ranging from 349 to 522 each year dependent on the number of stations with multiple tows and the number of stations surveyed north of St. Matthew Island.

More than 16,000 snow crabs were caught and measured each year. For the purpose of estimating total population abundance, we stratified the surveyed stations based on number of tows commonly conducted for a station. Specifically, 18 multiple-tow stations around the Pribilof Islands were regarded as one stratum, and 9 multiple-tow stations west of 173°W near St. Matthew Island were grouped together as another stratum. All other stations were treated as one station per stratum. An abundance index for each station was computed as crabs per square nautical mile, and total population abundances by size group, sex, and shell condition were estimated for the whole eastern Bering Sea using the "area-swept" method (Alverson and Pereyra 1969).

Annual station abundance indices (by size and sex) were mapped to identify spatial distribution patterns and to reveal spatial recruitment patterns. Abundance indices for periods with similar spatial patterns were averaged and contrasted with abundance indices during periods with different patterns. Spatial patterns during periods with strong recruitment were contrasted with those during periods with poor recruitment. For the purpose of this study, we defined recruitment as newshell male and immature female crabs <45 mm carapace width (CW). This definition is arbitrary but approximately reflects an index of cohort strength sampled up by the survey gear. Annual centers of distribution for three size groups of males and for immature, newshell mature, and oldshell mature females were computed by averaging locations (in longitude and latitude) weighted by abundance to illustrate the change in distribution and recruitment over time. Annual crab indices from all surveyed stations were used to compute centers of distribution. Mean carapace sizes and crab densities for males and mature females for each station were plotted over depth and latitude to examine their relationships, which were revealed by the LOWESS (locally weighted regression scatter plot smoothing) procedure with the fraction parameter (f) equal to $2/3$. Size frequencies of males and females were plotted over time to identify strong and weak year classes.

Commercial catch data by fishery statistical area from 1985 to 1999 were obtained from the Alaska Department of Fish and Game. Mean catches by statistical area from January to June from 1985 to 1999 were mapped to show spatial distributions. The fishery was typically opened from January to June throughout 1991 and from January to March thereafter.

Results and Discussion

General Spatial Distribution

Spatial distribution of snow crabs is both size- and depth-dependent (Figs. 1-3). Small males and immature females generally occur in the northeastern part of the eastern Bering Sea in relatively shallow water. Mean crab body size increases toward the southwest or with depth. Mean female size at maturity increases from north to south, and slightly from shallow to deep water. These findings are consistent with those derived by Somerton

Table 1. Catch sampling of eastern Bering Sea snow crabs in NMFS trawl surveys from 1978 to 1999. Numbers of males caught are classified by three carapace width intervals, and numbers of females caught are classified by immatures, newshell matures (NS-M), and oldshell matures (OS-M).

Year	Sampling of dates	No. of stations	No. of tows	Number of males				Number of females			
				Empty tows	Total measured	Caught		Total measured	Caught		
						<50 mm	50-90 mm		>90 mm	Immature	NS-M
1978	5/20-8/18	254	314	76	16,843	24,853	24,932	10,631	28,149	32,278	14,411
1979	5/22-8/27	377	522	213	21,774	100,587	49,709	11,880	133,606	77,654	34,483
1980	5/22-7/30	327	386	97	15,892	24,887	41,869	10,984	21,886	120,497	62,659
1981	5/22-7/20	303	386	89	17,118	9,148	41,104	4,358	7,889	44,306	37,171
1982	5/29-8/01	333	349	63	23,380	3,341	58,155	7,396	2,806	53,297	36,006
1983	6/07-8/06	329	375	86	20,928	14,050	40,263	8,644	4,821	14,815	42,539
1984	6/09-8/10	329	435	116	19,899	20,884	20,259	11,158	6,367	18,888	16,554
1985	6/06-9/03	330	358	95	12,734	9,179	8,668	5,107	3,680	9,891	804
1986	6/04-8/06	330	383	100	14,250	21,555	21,070	5,205	5,007	38,897	6,023
1987	5/27-7/30	340	380	105	24,485	71,212	69,509	10,819	10,351	122,702	22,299
1988	6/01-8/06	353	396	118	21,566	36,685	76,187	11,898	9,408	34,000	23,595
1989	6/04-8/14	362	439	150	25,293	21,722	81,749	14,286	9,917	20,153	129,161
1990	6/01-8/06	355	401	110	24,834	15,313	57,050	35,929	9,489	37,505	76,332
1991	6/01-8/07	365	372	65	27,536	66,727	61,357	27,000	12,758	91,370	105,623
1992	6/05-8/03	332	361	98	18,886	53,738	33,654	12,096	9,438	65,116	36,012
1993	6/04-7/26	351	393	110	20,722	93,848	74,812	9,100	9,313	102,194	39,487
1994	6/03-7/24	351	396	122	22,478	95,547	96,878	5,767	14,374	75,255	16,924
1995	6/04-7/24	351	382	104	17,837	27,401	107,966	6,981	8,389	39,323	56,558
1996	6/08-7/28	348	375	102	22,022	6,434	78,871	16,029	6,186	9,302	54,009
1997	6/07-7/26	348	376	84	26,892	2,597	39,219	22,455	6,432	5,237	60,372
1998	6/09-8/05	348	380	75	21,208	7,023	19,953	15,338	6,717	10,653	5,144
1999	5/23-7/20	348	380	86	12,869	3,412	8,820	5,934	4,693	3,857	16,645

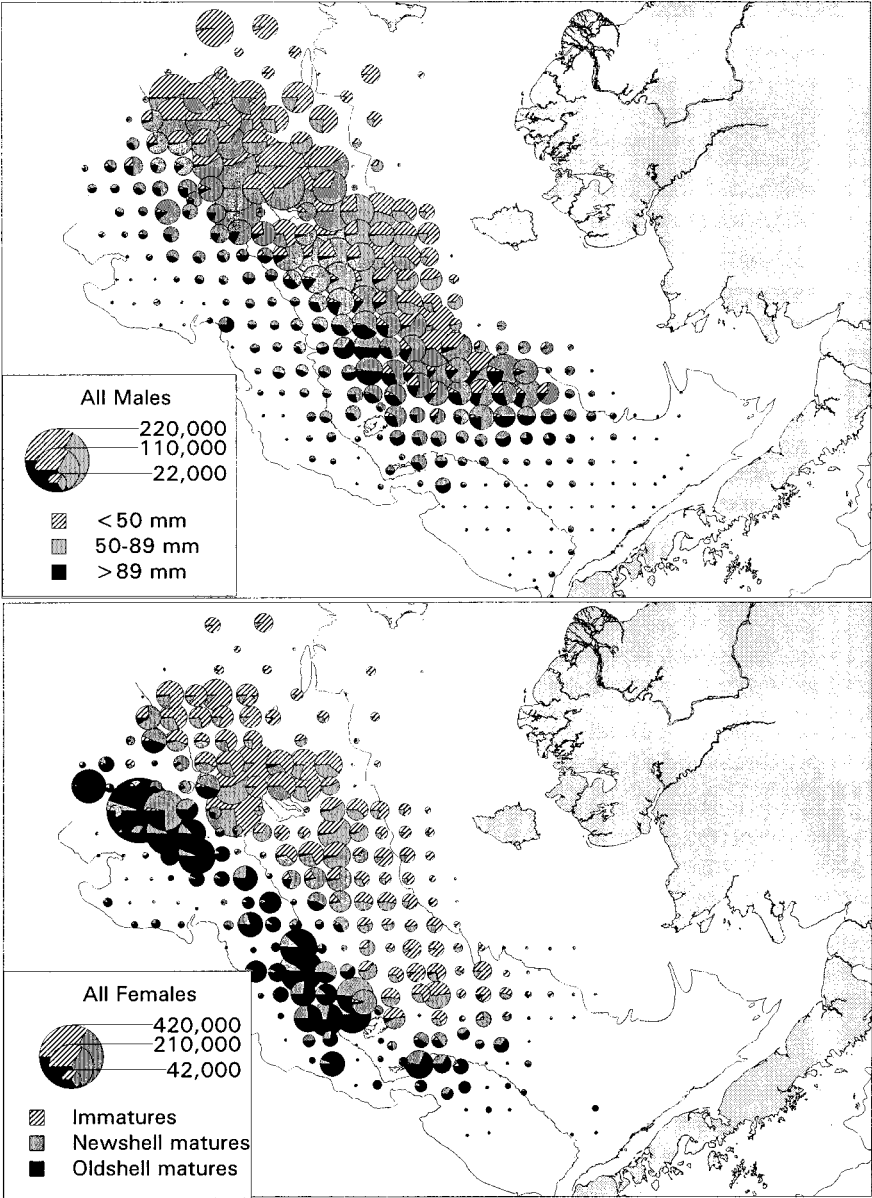


Figure 1. Distributions of male (upper panel) and female (lower panel) snow crabs in the eastern Bering Sea derived from NMFS summer trawl survey data from 1978 to 1999. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.

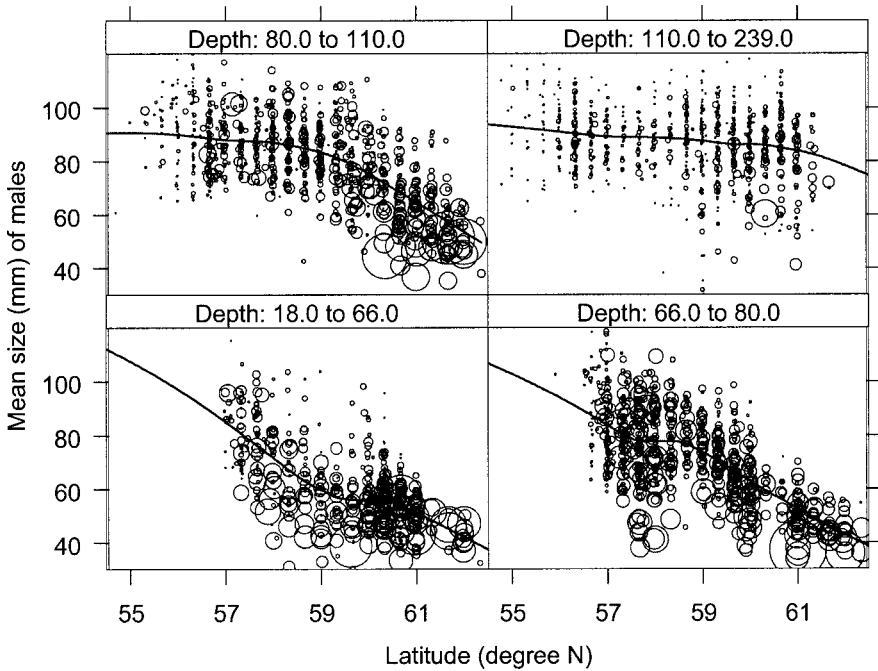


Figure 2. Mean carapace width (mm) of male snow crabs in the eastern Bering Sea for each survey station as a function of latitude and depth (m) from 1978 to 1999. Circle sizes are proportional to crab density, and solid lines are LOWESS smoothing curves with the fraction parameter (f) equal to $2/3$.

(1981) using only trawl survey data in 1979 and Otto (1998) using trawl survey data from 1989 to 1994. Both Somerton (1981) and Otto (1998) conducted a limited study on spatial distributions of eastern Bering Sea snow crabs by plotting general distribution of different size groups of crabs and computing mean sizes of mature crabs as a function of longitude, latitude, or depth. Our study not only used a much longer time series of data but also examined spatial distribution patterns by shell condition, and the mean sizes of males and mature females as a function of a combination of abundance, location, and depth. For females, the molt to maturity is the final, or terminal, molt. Oldshell mature females, which generally have been mature for at least 1 year, mostly occur in deep water and concentrate within a smaller area than other groups of crabs. Males were more abundant than females in Bristol Bay (southeastern Bering Sea). The paucity of small crabs in Bristol Bay indicates that a substantial number of snow crabs in Bristol Bay probably immigrate from the north. It appears that, during ontogeny, crabs gradually move from shallow water in the northeast to deep water in the southwest.

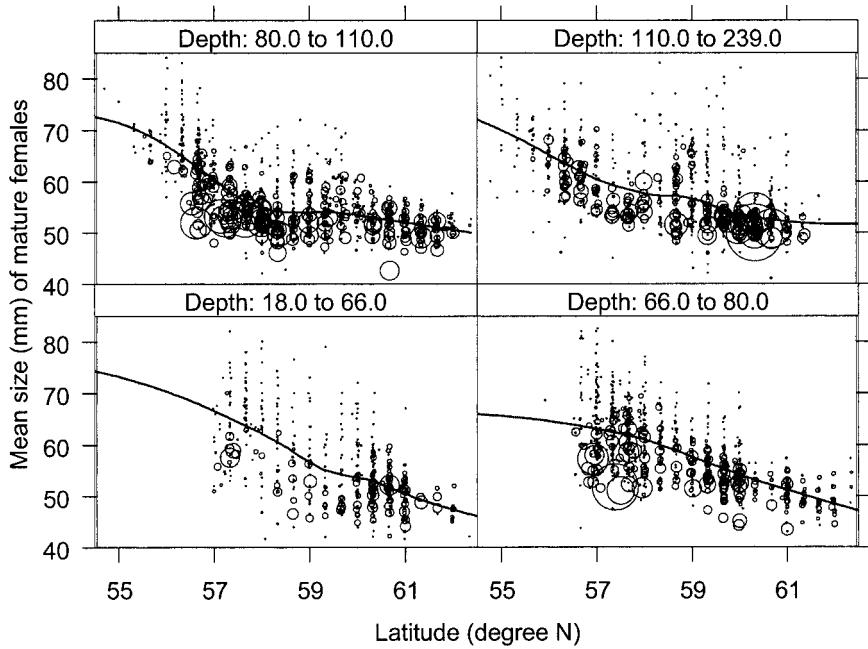


Figure 3. Mean carapace width (mm) of mature female snow crabs in the eastern Bering Sea for each survey station as a function of latitude and depth (m) from 1978 to 1999. Circle sizes are proportional to crab density, and solid lines are LOWESS smoothing curves with the fraction parameter (f) equal to $2/3$.

Commercial catches occurred primarily between 100 m and 200 m and within the survey area (Fig. 4). Some catches, however, were made in deep water outside the survey area. Most catches were taken during January–March, and the fishery shifted to the northwest during May and June (Fig. 4). The low catch in the southeast during May and June was partially due to area closures and partially due to prospects for higher catch rates to the northwest as the ice edge retreats in spring.

Body size is related to depth and latitude in snow crabs and other crab species in the Bering Sea. During the 1985 trawl survey, mean carapace widths of snow crabs were 34.4 mm for males and 33.2 mm for females in Norton Sound versus 47.2 mm for males and 38.8 mm for females in the northeast Bering Sea (Stevens and MacIntosh 1986). On average, the Norton Sound survey area is about 1.5° north of the survey area in the northeast Bering Sea. Within a similar depth range, Chukchi Sea snow crabs were generally larger for the southern stations (within $68\text{--}70^\circ\text{N}$) than for the northern stations (within $70\text{--}72^\circ\text{N}$) in 1990–1991 (Paul et al. 1997). Female snow crabs in the Chukchi Sea are about 50 mm CW at 50% maturity (Jewett

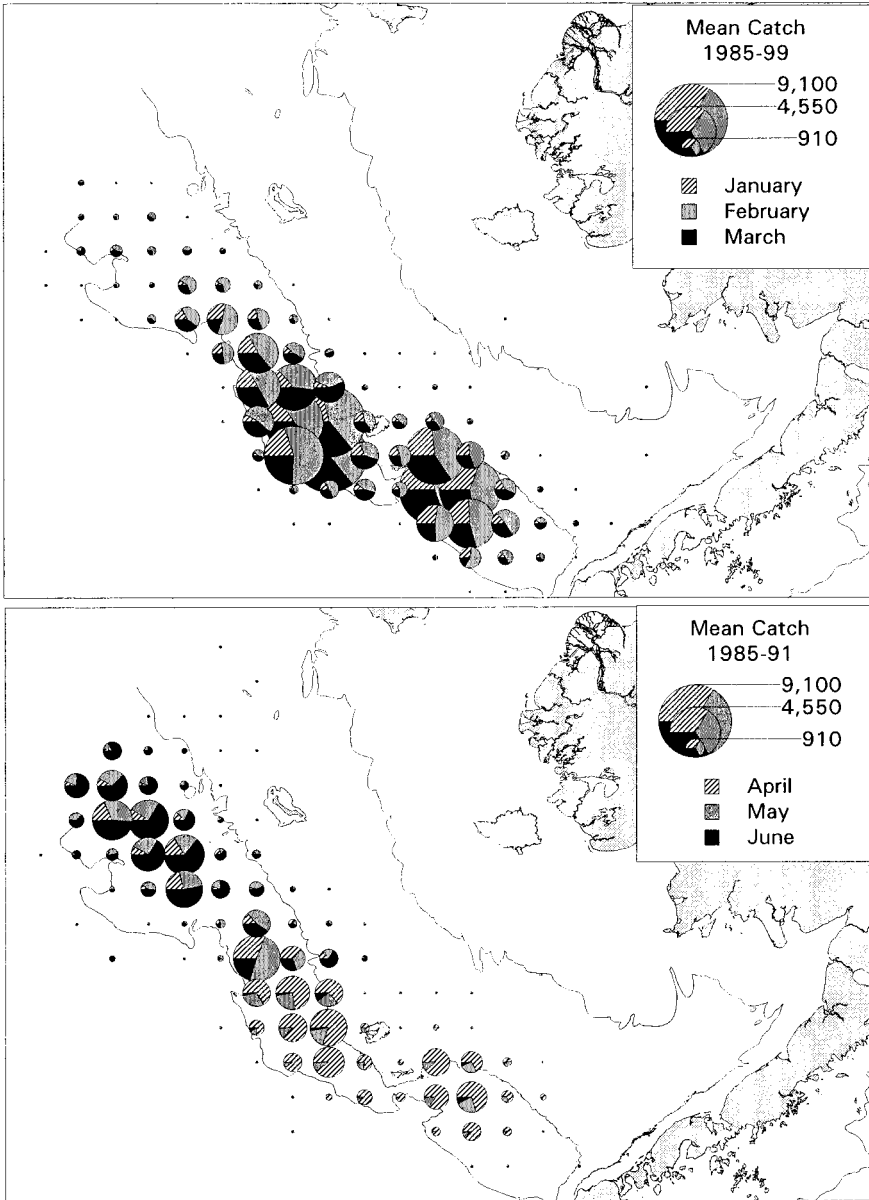


Figure 4. Distributions of commercial catch (in a unit of 1,000 crabs) by statistical area during January, February, and March from 1985 to 1999 (upper panel) and during April, May, and June from 1985 to 1991 (lower panel) for eastern Bering Sea snow crabs. Most areas in the southern part of the eastern Bering Sea were closed to fishing during May and June.

1981), similar to the mean CW of 46 mm for mature females (Paul et al. 1997). This size range (46-50 mm CW) was similar to the mean size of mature females in the northeast Bering Sea (Stevens and MacIntosh 1986) and the northern part of the eastern Bering Sea (Fig. 3) and smaller than those in the southern part of the eastern Bering Sea (Fig. 3). In the southwestern Gulf of St. Lawrence, snow crab size increased with increasing depth (Desrosiers et al. 1982). In the eastern Bering Sea, mature blue king crabs are generally larger at the Pribilof Islands than at St. Matthew Island (Stevens et al. 1998), and mature female red king crabs from the Pribilof Islands are larger than those in Bristol Bay. Norton Sound red king crabs are the smallest of these three red king crab stocks (Otto et al. 1990).

Smaller crab body sizes in the northern area may be attributed to lower molting probabilities for a given size and/or smaller growth increments per molt. For two blue king crab stocks in the eastern Bering Sea, the molting probability for a given size is much lower for the St. Matthew Island stock than for the Pribilof Islands stock (Otto and Cummiskey 1990). Both growth increment and molting probability are lower for red king crabs in Norton Sound than in Bristol Bay (Weber and Miyahara 1962, Brannian 1987). For juvenile red king crabs, growth is positively related to temperature (Stevens 1990); therefore, crabs in warmer southern areas have higher growth rates than those in colder northern areas. Temperature may, therefore, influence size differentiation of mature snow crabs in different parts of the eastern Bering Sea.

The broad, continuous distribution of snow crabs over the eastern Bering Sea makes it difficult to identify separate stocks. Using survey data from 1975 to 1979, Somerton (1981) concluded that management subareas, defined by either longitude or latitude based on size differences, are ineffective because there is no clear-cut separation line to divide the subareas. Within the eastern Bering Sea, there is little genetic difference among snow crabs at St. Matthew Island, the Pribilof Islands, and in Bristol Bay, and little genetic differentiation was found even between snow crabs in the eastern Bering Sea and North Atlantic (Merkouris et al. 1997). Current fisheries regulations divide the eastern Bering Sea (Bering Sea District) into two management subareas: the Eastern Subdistrict (north of 54.6°N and east of 173.0°W) and the Western Subdistrict (north of 54.6°N and west of 173.0°W) (ADF&G 1998). Area-swept estimates of abundance from all surveyed areas are used to set the catch quota and to determine reference points for overfishing (NPFMC 1998). Questions remain whether size differentiation of mature snow crabs within the eastern Bering Sea is large enough to separate the stock into multiple substocks, and whether smaller-sized mature crabs in the northern part of the eastern Bering Sea, which may not recruit into the exploitable stock, should be included for estimating harvestable biomass and overfishing levels.

Changes in Distribution Over Time

Change in crab distribution can be simply illustrated by plotting annual distribution centers from the survey data. Centers of small crab (males <50 mm CW and immature females) abundance were generally located in the northwest portion of the standard survey area during the mid- and late 1990s and in the middle or east during 1985 and 1986 (Fig. 5). It appears that centers of distribution of mature females and large males have moved gradually to the northwest since the late 1970s (Fig. 5). During the mid-1970s, snow crabs were abundant in the southern part of the eastern Bering Sea, but we cannot compute the overall centers of distribution because the surveys did not extend sufficiently to the north. Comparing distributions of mature females in the late 1970s and late 1990s illustrates this dramatic change (Fig. 6). During 1978-1979, newshell mature females were widely distributed and centered in the middle of the standard survey area at 50-100 m, and oldshell mature females were generally found in the south (Fig. 6). During 1998-1999, newshell mature females generally were in the northeast and oldshell mature females in the northwest (Fig. 6). Generally, males were more dispersed than females. Oldshell males, which can be used to approximate relatively old crabs, were concentrated in the middle and south during 1978-1979 and extended to the north considerably during 1981-1999, especially crabs ≥ 90 mm CW (Fig. 7).

One possible cause of the northward movement since the late 1970s is the regime shift in climate and physical oceanography that occurred in 1976-1977. A measure of the regime shift is the intensity of the Aleutian Low, which generally intensified from 1977 to 1988 (Beamish and Bouillon 1993; Adams and Bond 1999; Zheng and Kruse 2000). During this period of intensification, seawater temperatures were generally warmer, which could cause snow crabs to concentrate in the colder northern area. Distributions of red king crabs in Bristol Bay also showed a northward movement from the 1970s to the 1980s (Hsu 1987). Small male and immature female snow crabs generally concentrate in the northeast and do not show dramatic changes in spatial distribution over time.

Fishing can also affect the spatial distribution of crabs. Because the most valuable and accessible resources were depleted first, Orensanz et al. (1998) speculated that overfishing might have caused serial depletion of crustacean stocks in the Gulf of Alaska. However, we do not believe that fishing pressure has played an important role on the changes in spatial distribution of eastern Bering Sea snow crabs for several reasons. First, harvest rates were relatively low during the late 1970s and early 1980s when the change in distribution occurred. Second, large snow crabs were not depleted in the early 1980s in the southeastern area, which was most easily accessible to the fleet. Large crabs continued to move into the southeastern area during the summer and expanded their range into the northwestern area. Finally, because of their smaller size and incomplete spatial overlap with commercial-size males, mature females were subject

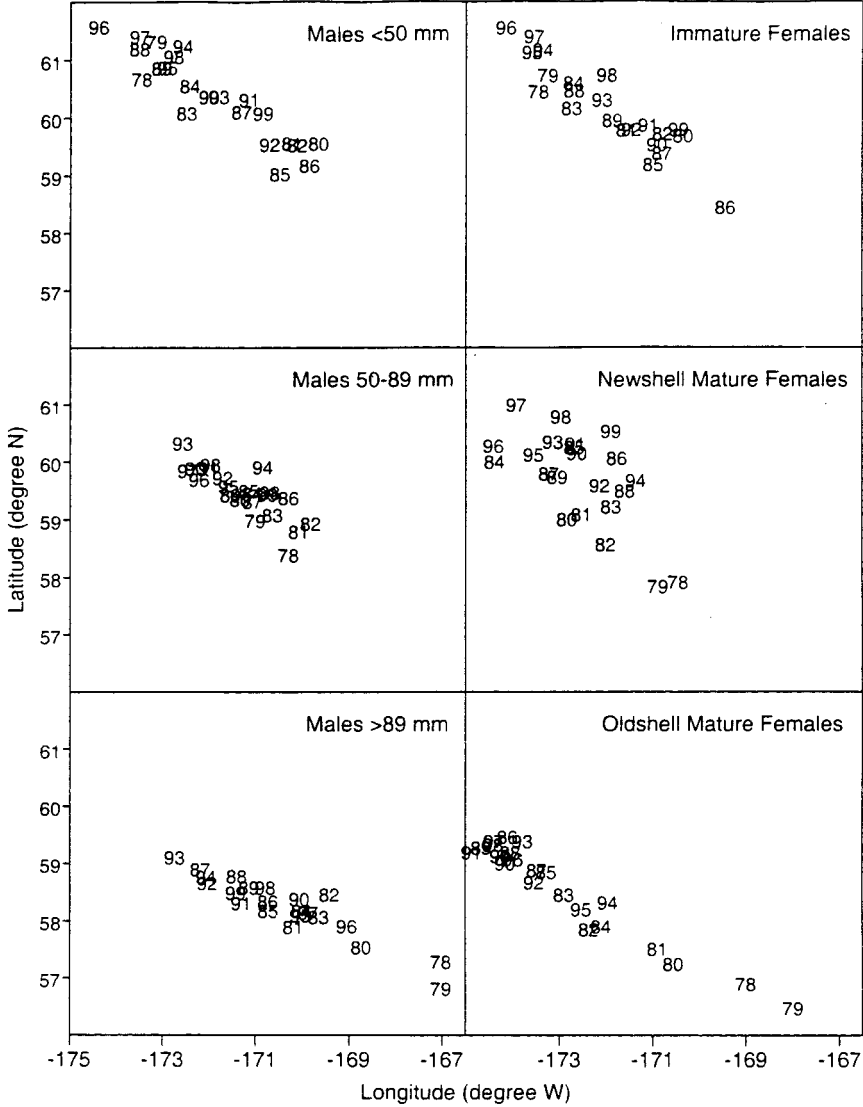


Figure 5. Centers of distribution of eastern Bering Sea snow crabs derived from NMFS summer trawl survey data from 1978 to 1999. Years are plotted as data points.

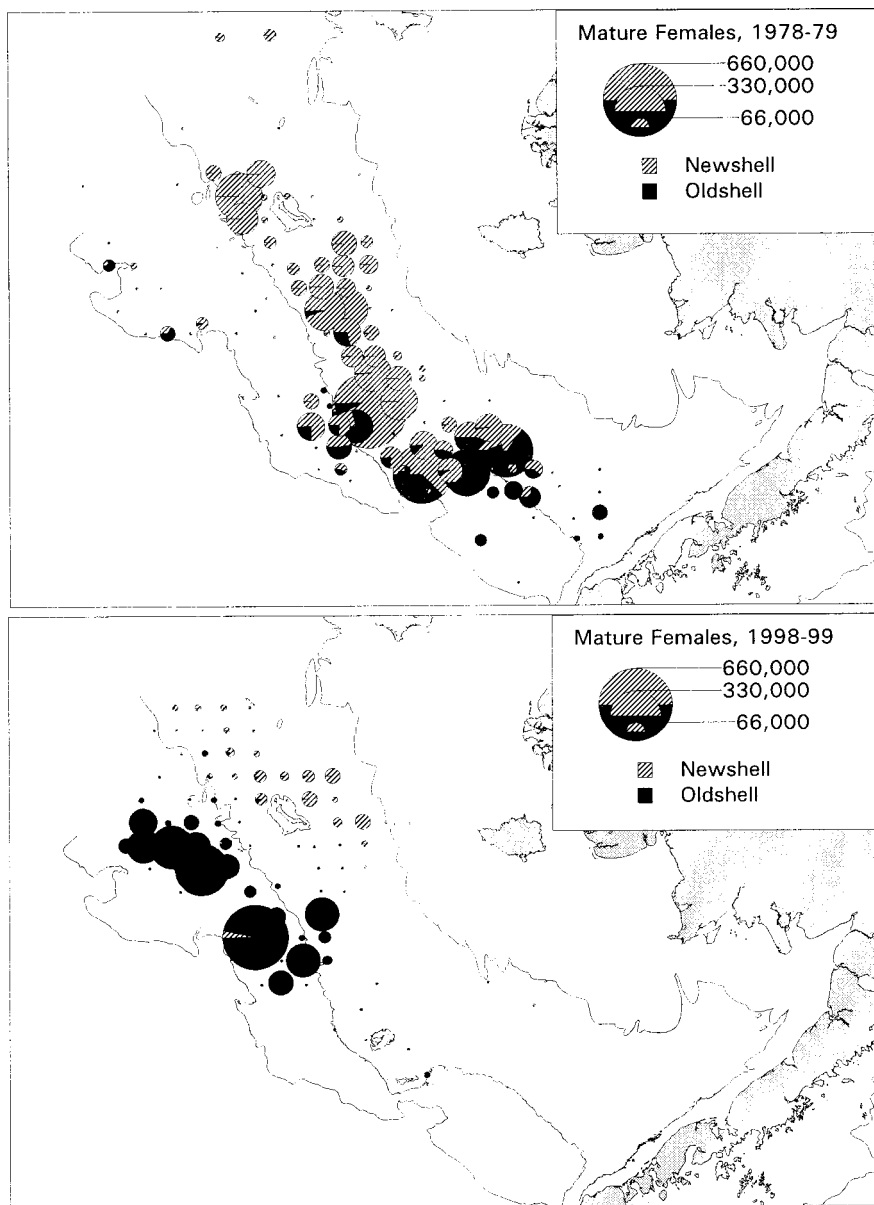


Figure 6. Distributions of mature female snow crabs in 1978 and 1979 (upper panel) and in 1998 and 1999 (lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.

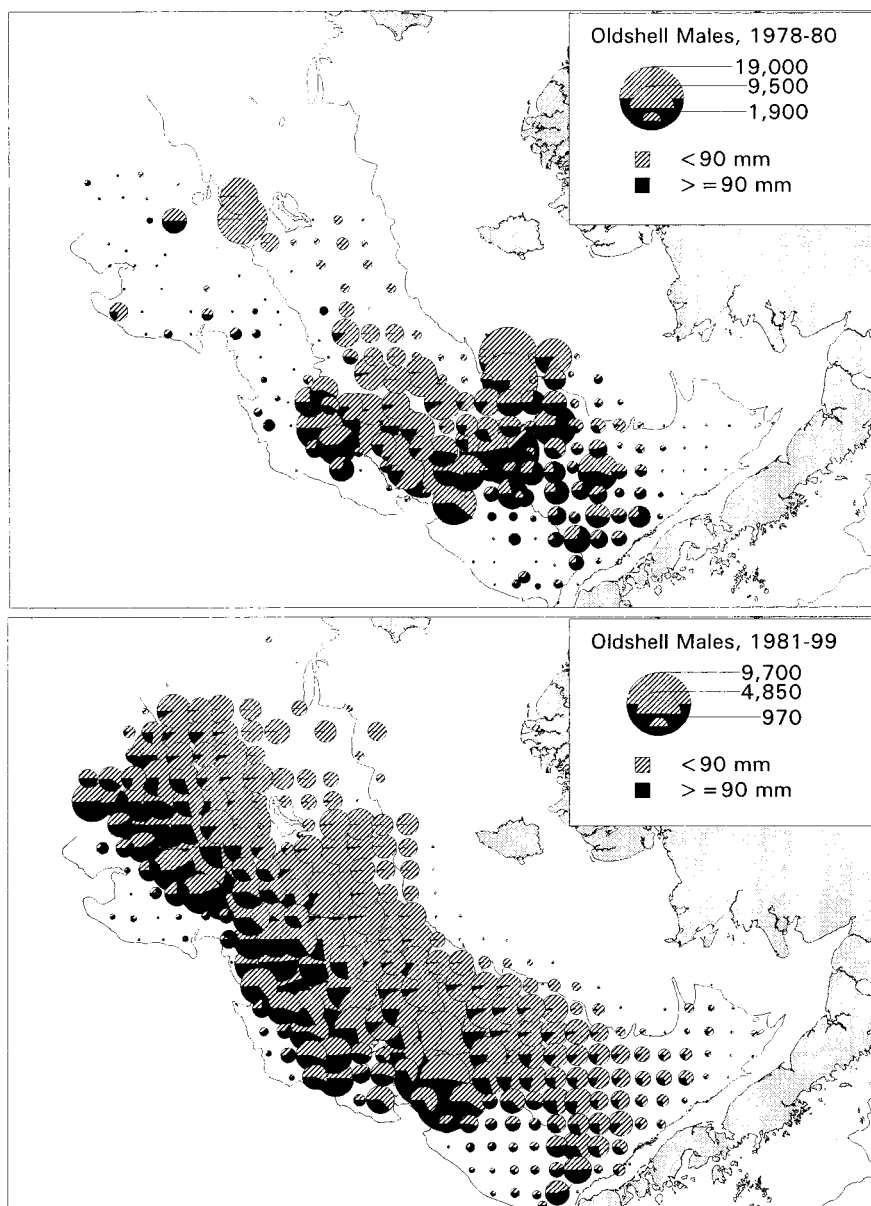


Figure 7. Distributions of oldshell male snow crabs from 1978 to 1980 (upper panel) and from 1981 to 1999 (lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.

to low fishing mortality, yet their spatial distribution changed more than that of large males.

Recruitment Patterns

Recruitment to the eastern Bering Sea snow crab stock was periodic. High abundances of juvenile crabs (<45 mm CW for males and immature females) recruited to the survey gear during 1978-1979, 1986-1987, and 1991-1994, but there was little recruitment during 1981-1982, 1989-1990, and 1995-1998 (Fig. 8). Therefore, strong recruitment tends to occur every 4-7 years. The last 5 years was the longest period with low recruitment. In 1999, the biomass of mature crabs fell below the overfished level defined in the fishery management plan (NPFMC 1998; Bob Otto, NMFS, Kodiak, pers. comm.). Stock rebuilding depends on strong recruitment events. If no strong recruitment occurs in the next 2 years, this recruitment pattern will have been broken, and it will be difficult to use historical patterns to project the future recruitment.

There are approximately 20 survey stations north of 61.2°N, but only a few of these were surveyed each year since 1978 (Stevens et al. 1998). Except in 1979, few crabs were caught in these northern stations before 1988 (Fig. 8). The high abundance of small crabs in these northern stations in the 1990s is due to more stations being surveyed and a concentration of small crabs in the northern part of the standard survey area during this period. How many small crabs move to the north or west beyond the survey area is unknown, as few crabs north of 61.2°N reach harvestable size (Fig. 8). The current size limit is 78 mm CW (ADF&G 1998), but processors prefer a minimum size of 102 mm CW for economic reasons. Therefore, the annual catch quota is based on the abundance of male crabs ≥ 102 mm CW (Stevens et al. 1998).

The estimated highest abundance of crabs ≥ 102 mm CW occurred in 1991, the year of record catches (Stevens et al. 1998). These crabs most likely recruited to the <45 mm CW size group during 1985-1987. The recruitment during 1991-1994 was also the strongest since the stock has been surveyed (Fig. 8); however, the proportion of these crabs that grew to 102 mm CW in the survey area by 1997-1999 was much smaller than the proportion of recruits from the 1985-1987 period. The locations of small crabs were generally centered more in the southeastern areas during 1985-1987 than during 1991-1994; this suggests that recruits in the middle, eastern, or southern areas may have a better chance to grow to a large size than those in the north. It may be that the increased probability of attaining large commercial sizes in the middle and southern areas is attributable to temperature-dependent growth of juvenile crabs.

Similar to small males, high abundance of immature females occurred during 1978-1979, 1986-1987, and 1991-1994, and high abundance of newshell mature females generally occurred a year later (Fig. 9). Because females do not molt after maturity, the abundance of oldshell mature

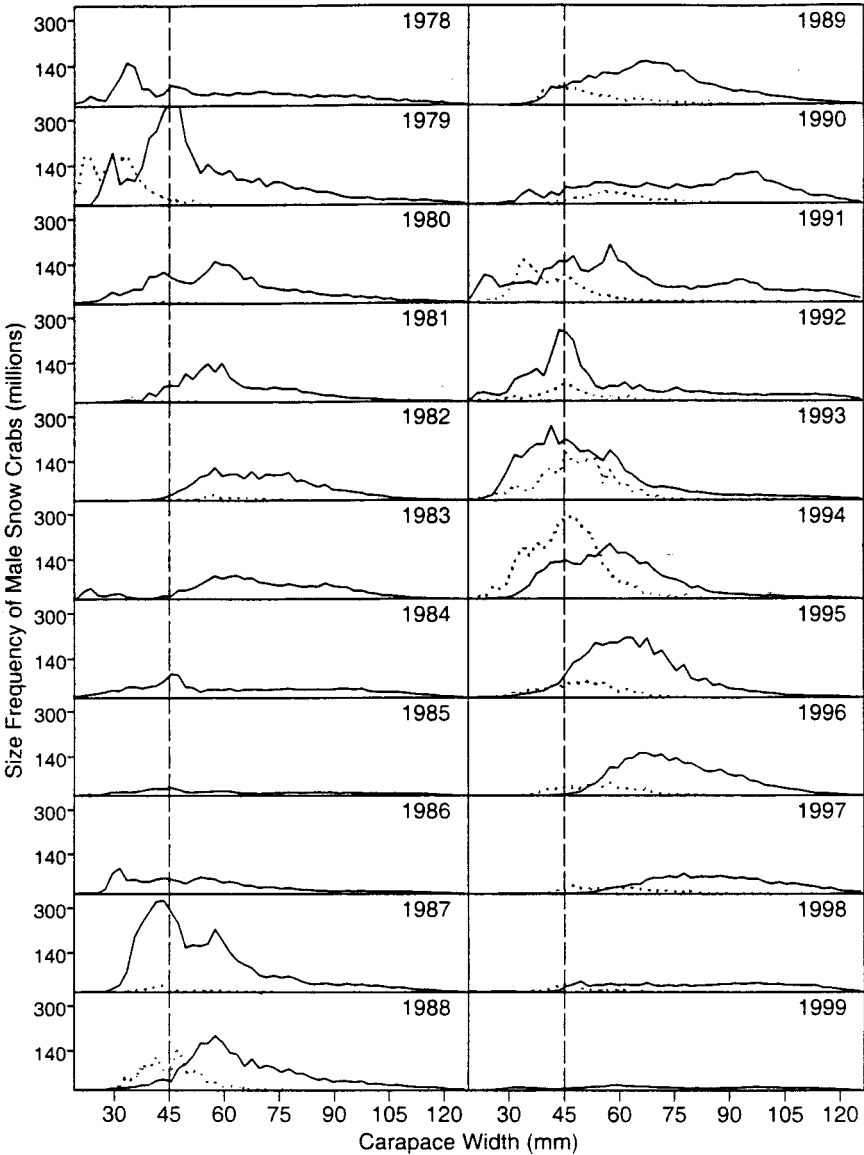


Figure 8. Size frequency distribution of area-swept estimates of male snow crab abundance in the eastern Bering Sea. Solid lines represent abundances south of 61.2°N, dotted lines represent abundances north of 61.2°N, and the two vertical dashed lines indicate 45-mm carapace width.

females can be used as an index of survival after maturity. Based on abundances of oldshell mature females during 1981-1983, 1989-1991, and 1996-1998, high natural mortality rates did not occur within the first 3 years of maturity (Fig. 9). The large decline in oldshell female abundance from 1983 to 1984, 1991 to 1992, and 1998 to 1999 may be due to senescence. With extremely low abundance of immature females from 1996 to 1999, the population will continue to be depressed until a strong cohort occurs.

Comparison of spatial distributions of crabs during periods with high and low abundances helps us understand the recruitment patterns. As expected, immature females and small males were more dispersed during periods of high abundance than during periods of low abundance (Fig. 10). These crabs were generally concentrated at 50-100 m and did not occur in high abundance in Bristol Bay (Fig. 10). Newshell mature females were broadly distributed during years of high abundance but concentrated in the north during years of low abundance (Fig. 11). Contraction of spatial distribution during periods of low crab abundance was much greater for mature females than for large males. According to MacCall's (1990) "basin model," the range of a stock expands or contracts around its center as a function of overall abundance and large-scale changes in density-independent factors. Although snow crab distributions in the eastern Bering Sea expand and contract as a function of overall abundance, their population centers change over time. The closest fit to the "basin model" is mature females since the early 1980s with its center around the northwestern part of the standard survey area. Male snow crabs, regardless of abundance, gradually move to deeper water toward the southwest as they grow.

Although the causes are not well understood, periodic or quasiperiodic recruitment patterns are common in many crab and fish stocks. For Bristol Bay red king crabs, strong recruitment occurred in the mid- and late 1970s, and weak year classes occurred in the late 1980s and early and mid-1990s (Zheng et al. 1995). Recruitment in red king crab stocks in the northern Gulf of Alaska and along the Aleutian Islands was strong during the late 1970s and has been weak since the mid-1980s (Zheng and Kruse 2000). Recruitment to eastern Bering Sea blue king crab stocks was strong in the mid- and late 1970s, weak in the mid-1980s, and relatively strong in the early and mid-1990s (Zheng and Kruse 2000). Year classes for Bristol Bay Tanner crabs (*Chionoecetes bairdi*) from 1968 to 1989 showed a strong cyclic behavior with 13- or 14-year periodicity (Zheng and Kruse 1998). Recruitment in Tanner crab stocks in the northern Gulf of Alaska was strong in the mid-1970s but has been weak since the early 1990s (Zheng and Kruse 2000). The recruitment periodicity of snow crabs in the northwest Gulf of Saint Lawrence is 8 years (Sainte-Marie et al. 1996), whereas periodicity for Dungeness crabs (*Cancer magister*) off northern California is about 10 years (Higgins et al. 1997). Recruitment of many fish stocks has periodicities ranging from 10 to 26 years (Koslow 1989). Therefore, the apparent recruitment period for the eastern Bering Sea snow crab stock is

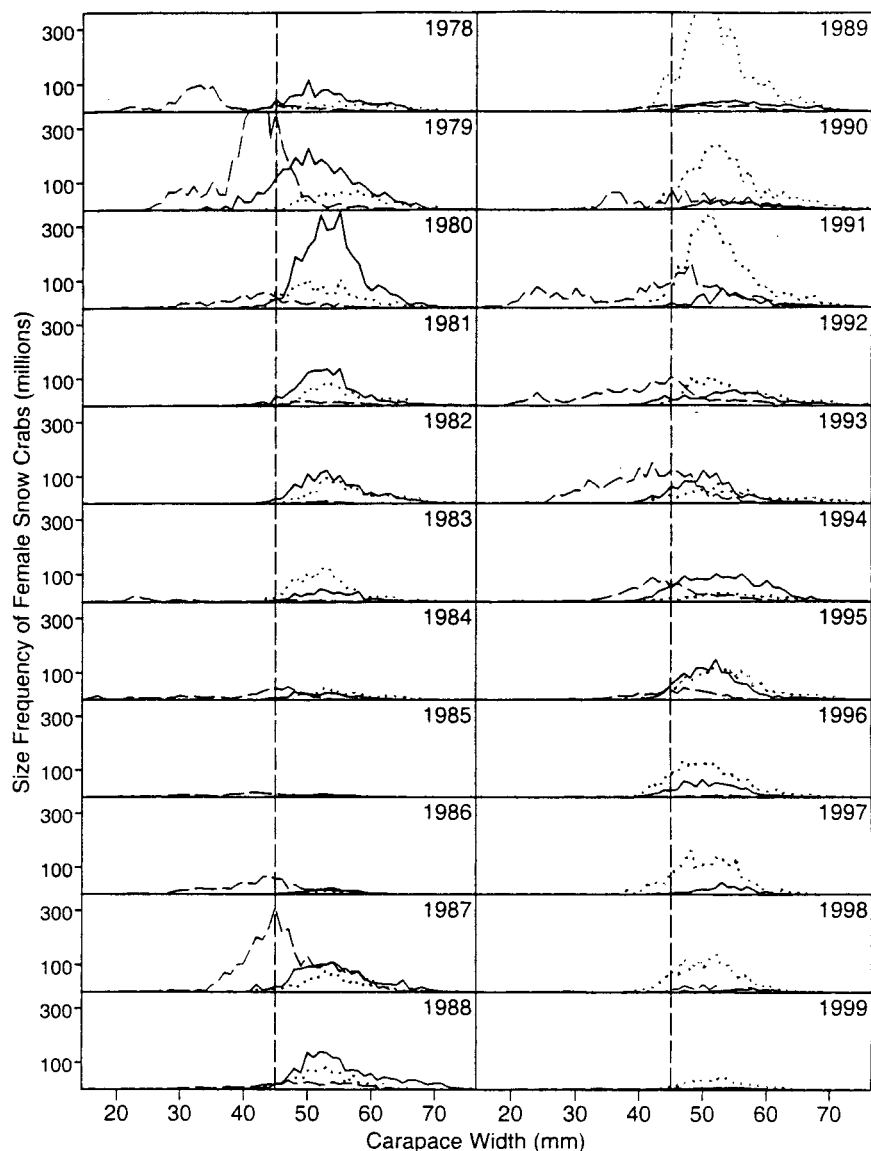


Figure 9. Size frequency distribution of area-swept estimates of female snow crab abundance south of 61.2°N in the eastern Bering Sea. Dashed lines represent immature crabs, solid lines represent newshell mature crabs, dotted lines represent oldshell mature crabs, the two vertical dashed lines indicate 45-mm carapace width.

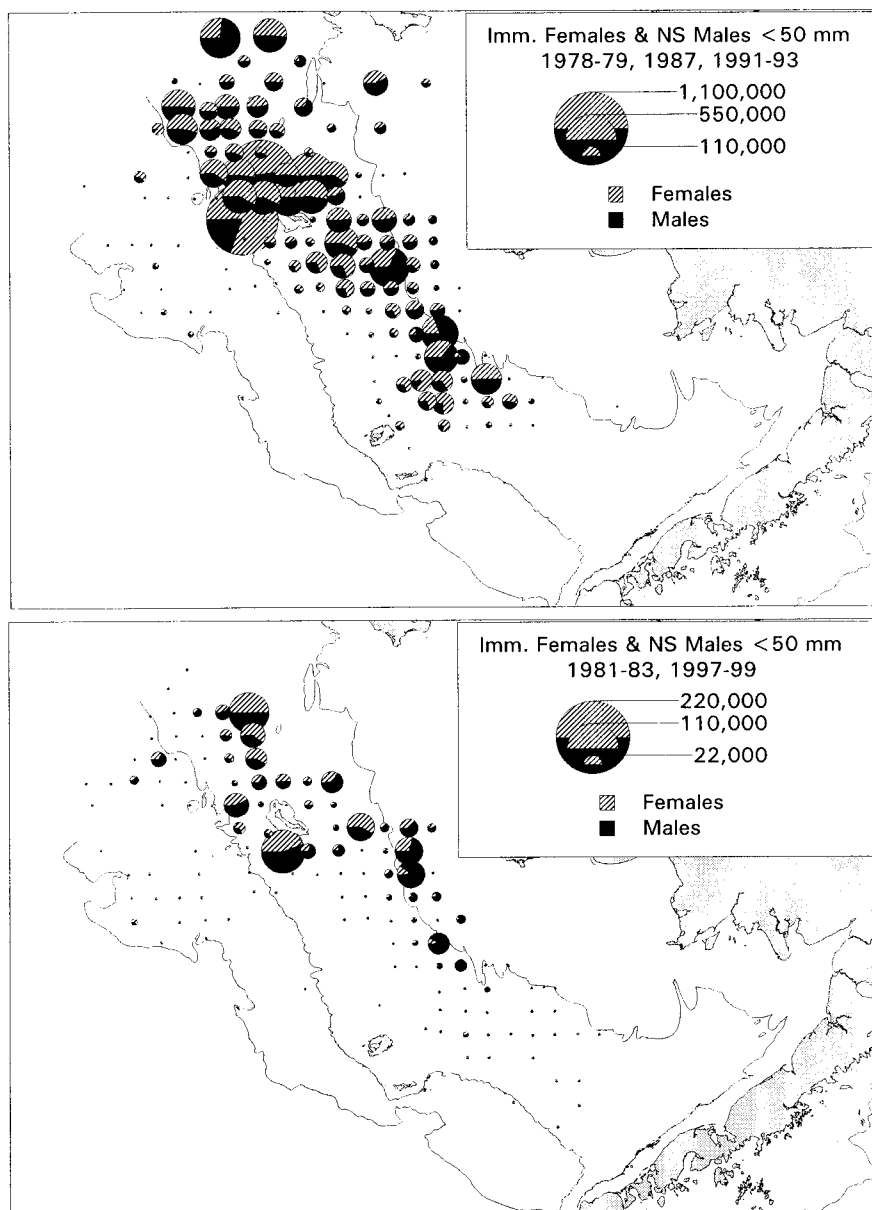


Figure 10. Distributions of immature female and newshell male (<50 mm carapace width) snow crabs during years of high abundance (1978-1979, 1987, and 1991-1993; upper panel) and low abundance (1981-1983 and 1997-1999; lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.

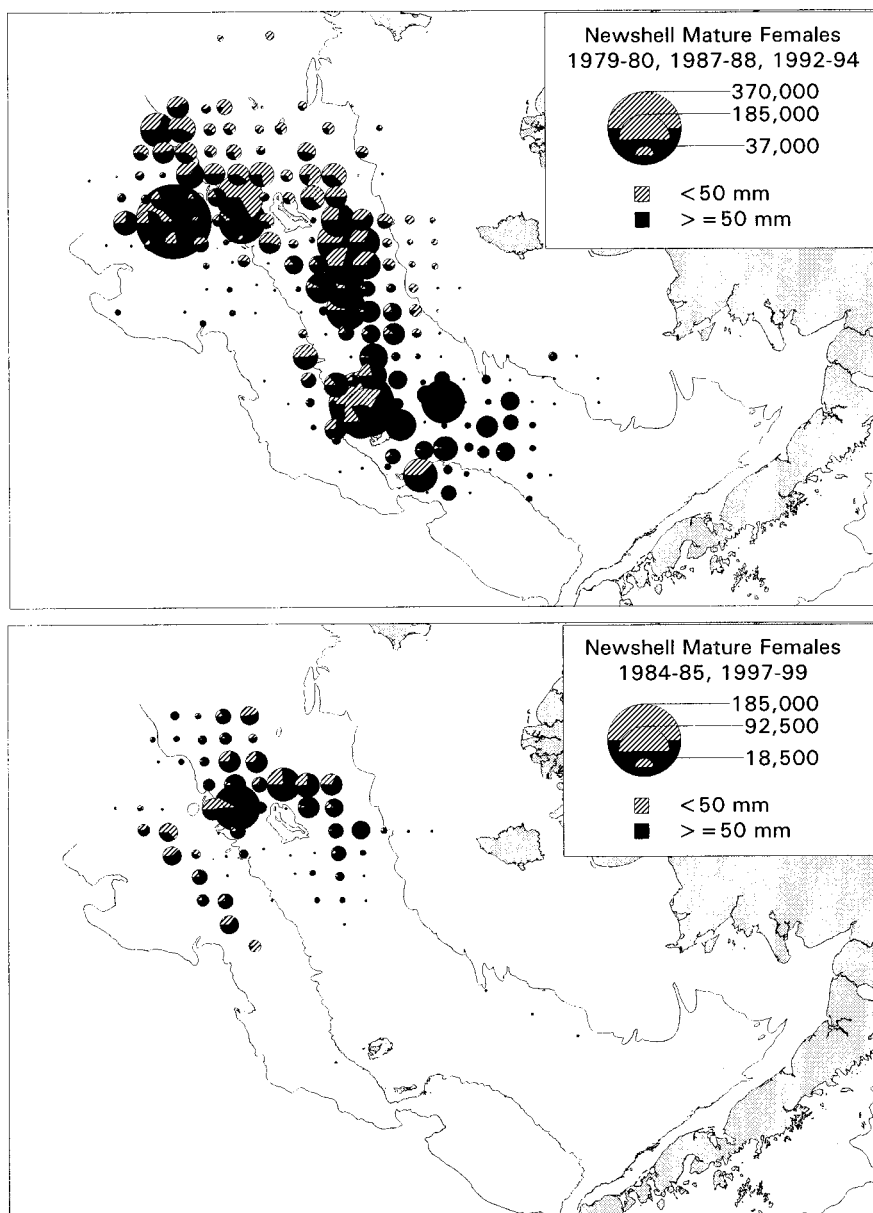


Figure 11. Distributions of newshell mature female snow crabs during years of high abundance (1979-1980, 1987-1988, and 1992-1994; upper panel) and low abundance (1984-1985, and 1997-1999; lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.

among the shortest observed for crab and fish stocks. The sharp contrast between strong cohorts and recruitment failures is another feature of snow crabs in the eastern Bering Sea. Because of very high natural mortality (Otto 1998), eastern Bering Sea snow crabs cannot sustain long periods of very weak recruitment without sharp declines in abundance. If strong cohorts do not occur during the next 2 years, this stock may fall to abundance levels that are much lower than the lowest level previously observed.

Although the summer trawl survey and spring commercial catch data provide important information about abundance and dynamics of snow crabs in the eastern Bering Sea, our study raises some important questions about the crab distribution with respect to the standard survey area. One line of questioning is concerned with snow crabs in the northernmost (north of $\sim 61^{\circ}\text{N}$) survey stations with respect to exploitation. Is this a juvenile rearing area? Do these crabs move south during ontogeny or do they remain in the north as a separate stock? Based on the general pattern of southwesterly movement with ontogeny, some of these crabs, if they move at all, may move to deep water west of the survey area because southward movement is blocked by the shallow water surrounding St. Matthew Island. If crabs from these stations move out of the standard survey area, or if they do not grow to commercial size owing to cold temperatures, they should be excluded from yield calculations. A second line of questioning concerns the distribution of snow crabs on and off the shelf with respect to the areas routinely surveyed. What proportion of the stock exists in waters deeper than those routinely surveyed? How deep do snow crabs occur? Older mature males seem to disappear from the surveyed area at high rates. Do they migrate off the shelf or do they suffer higher mortality? What is the contribution of deepwater snow crabs to the reproductive stock? Extending the trawl survey to additional stations to the northwest and to deep waters off the shelf, augmented with pot surveys if necessary, may help answer these questions. Answers to these questions will not only lead to better estimates of stock abundance, but they will also facilitate the development of optimal harvest strategies.

Acknowledgments

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Yelloweye Rockfish (*Sebastes ruberrimus*) Life History Parameters Assessed from Areas with Contrasting Fishing Histories

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Abstract

Experimental manipulation of rockfish (*Sebastes*) stocks has been proposed to accelerate the learning process for fishery stock assessments. In this study, fishers' anecdotal knowledge of fishing history is used retrospectively as a surrogate for experimental manipulation, to examine the spatial impacts of fishing on yelloweye rockfish (*S. ruberrimus*). This project was undertaken jointly with the hook and line industry in British Columbia, Canada, as a first attempt at a research collaboration to assess yelloweye rockfish status in a northern and southern area of the coast and at specific sites that fishers identified as heavily and lightly fished. Chartered longline fishing vessels conducted research surveys at the study sites in September 1997 and May 1998. Samples of yelloweye rockfish from the sites were examined for differences in age composition, growth, and size and age at maturity. In addition, commercial logbook data corresponding to the sites were analyzed to determine whether catch rate information was consistent with the research surveys.

Yelloweye rockfish populations showed symptoms consistent with their respective fishing histories. Age distributions were remarkably truncated at one of the heavily fished sites relative to the lightly fished sites. Northern sites, with the shorter exploitation history, yielded larger commercial catch rate observations than the southern sites. This result illustrated that past harvest activities could be detected in sedentary, long-lived rockfish populations and that biological data are capable of assessing the effects. However, the possible ambiguity of results was also demonstrated when alternative explanations for the results could not be discounted.

Introduction

In British Columbia (B.C.), Canada, a hook and line fishery targeting rockfish (*Sebastes*) catches up to 22 species with quillback (*S. maliger*), copper (*S. caurinus*), and yelloweye (*S. ruberrimus*) rockfish traditionally dominating the landings. In recent years, nontraditional deepwater species such as redbanded (*S. babcocki*), roughey (*S. aleutianus*), and silvergray (*S. brevispinis*) rockfishes have been increasing in proportion. This fishery shares features with many recreational and artisanal fisheries in that fishing vessels operate close to shore and the catch is diverse, with small individual landings marketed to local live or fresh fish retailers.

The fishery has progressed northward along the coast of B.C. over the last 20 years, moving from areas close to local markets to more distant fishing grounds. Declines in rockfish populations in the more accessible southern grounds likely occurred through the serial depletion of local reef areas. Fishers typically maintain high catch rates by continually moving to new fishing reefs. This fishing tactic can have two effects. First, from an assessment perspective, the apparent stability (hyperstability) of catch rates can mask population declines when data are aggregated over large management areas (Hilborn and Walters 1992). Second, from a fisher perspective, the effect of local depletion on overall abundance may appear to be minimal because they can maintain catch rates by moving and hence have the impression of a large population size. In addition, a high participant turnover within the B.C. hook and line rockfish fleet has eroded the historical frame of reference required for the appropriate evaluation of spatial trends in fishing success. New participants find it difficult to accept harvest restrictions as they have been able to find fish and achieve monthly limits in the last few years and have had no comparable experience over the last 20 years.

Assessment and management of nearshore rockfishes (*Sebastes* spp.) is complicated by the constraints imposed by their life history (Leaman 1991) and a lack of information on biological parameters such as maximum age, natural mortality, and size and age at maturity (Love et al. 1990). Catch and effort data from the B.C. fishery required for stock assessment are temporally limited and are reported for areas defined on a large spatial scale (Haigh and Richards 1997). A logbook program was initiated in 1986 but biologists and managers have not used logbook data extensively largely due to the uncertainty in whether catch rate measures abundance (Fox and Starr 1996). Population data such as age distributions and maturity schedules are sparse in B.C., with only a few species and locations sampled in any year.

In general, rockfish abundance cannot be assessed using conventional tagging studies because rockfishes possess a closed swim bladder that is susceptible to barotrauma. Acoustic methods or swept-area trawl surveys are of limited use for nearshore species because of their close association with rocky bottom, although some progress has been made on semipelagic rockfishes (Stanley et al. 2000). These restrictions have led to new approaches using submersibles and video cameras for in situ estimation of

abundance combined with habitat quantification (Richards 1986, O'Connell and Carlile 1993, Palsson 1998, Wakefield et al. 1998). These new methodologies remain expensive relative to traditional sources of fishery-dependent catch and effort data.

Passive collection of fishery-dependent data for long-lived rockfishes is unlikely to provide timely information on stock status (Walters 1998). Fishing experiments over space and time have been proposed to accelerate learning about fish population response to harvest (Walters 1986, 1998; Walters and Collie 1989; Leaman and Stanley 1993); however, few experiments have been implemented for rockfishes. Prospects for experimentation are poor since the managing agency and industry stakeholders must commit to a long-term proposition (Leaman and Stanley 1993) given that the lag between the experimental intervention and the detection of a response can be at least 10-20 years (Francis 1986, Leaman 1991). Thus, consideration should be given to retrospective studies that use fishing history as a surrogate for experimental manipulation. For the data-limited nearshore rockfishes in B.C., traditional fishery-dependent data sources have not provided a time series of spatial contrast in harvest because of an absence of data and poor spatial resolution of the data.

In this paper, we describe a project undertaken in collaboration with the rockfish hook and line industry to use experienced fishers' knowledge on specific fishing areas and their fishing histories retrospectively to enhance the data collection for stock assessment and evaluate yelloweye rockfish population response to harvests. Yelloweye rockfish have been a target species in the hook and line fishery since its inception. Given that these fish are long-lived and sedentary, past fishing harvests in spatially discrete areas could be evident in the remaining population.

Experienced fishers from the hook and line fleet were asked to identify a "heavily" fished site and a relatively "lightly" fished site in both the southern and northern portions of B.C. Commercial vessels were chartered to conduct research fishing for yelloweye rockfish at the selected sites. Biological samples were obtained to allow comparison of population parameters. Based on the site classification provided by fishers, we expected to find a truncated age spectrum and a reduced size or age at maturity at the heavily fished sites relative to the lightly fished ones. Catch rates were also expected to be lower at the heavily fished sites. The northern sites were expected to show less fishing impacts than the southern sites due to their relatively short fishing history.

Logbook data corresponding to the study sites were then examined to evaluate whether commercial catch rate data were consistent with the results of the research fishing charter. If consistency could be demonstrated among logbook data, research charter data, and industry opinion on fishing history, then fishers may be more willing to provide detailed information in their logbooks. Collected over the long term, this information might reveal differential impacts of fishing at a spatial scale commensurate with localized depletion of yelloweye rockfish populations.

Methods

Data Collection

Experienced fishers were consulted and they identified sites off the west coast of Vancouver Island and the west coast of the Queen Charlotte Islands (Fig. 1). West coast Vancouver Island sites included waters adjacent to Triangle Island (area bounded by 50°42' to 50°51'N and 129°00' to 129°20'W) and Top Knot (area bounded by 50°28' to 50°32'N and 128°12' to 128°19'W). The Top Knot site was considered by industry to be the most heavily fished site over the last 20-30 years primarily because of its proximity to home ports and shelter from foul weather. The Triangle site is farther offshore and is frequently subject to inclement weather conditions without many safe anchorages. Sites in the Queen Charlotte Islands included Tasu (area bounded by 52°40' to 52°47'N and 132°00' to 132°16'W) and Flamingo (area bounded by 52°03' to 52°12'N and 132°13' to 132°27'W). Fishers reported that the Flamingo site was sheltered, easily accessible, and one of the first areas heavily fished in the Queen Charlotte Islands as the fleet moved northward along the B.C. coast during the late 1980s. The Tasu site was designated as lightly fished due to its isolation and exposure to the weather.

Commercial longline vessels were chartered to conduct targeted fishing for yelloweye rockfish in September 1997 and also in May 1998. Longline gear was standardized to a 500-hook string with a hook spacing of approximately 2.4 m. Size 14/0 circle hooks with a swivel and perlon were clipped onto the groundline (snap gear). Hooks were baited with whole California squid (*Loligo opalescens*). Gear was set and soaked for a 2-hour period delimited by the time that the first anchor was deployed and the time that the last anchor was retrieved. The number of sets ranged from 20 at the Top Knot site to 34 at the Triangle site.

The date, time, duration, position, and minimum and maximum depths fished were recorded for each set. The catch was identified to species for all sets and the number of each species was recorded. For sets where biological sampling was required, all yelloweye rockfish were sampled at sea for fork length (millimeters), sex, and maturity stage. The sagittal otoliths were excised for later age determination using the burnt otolith section method (MacLellan 1997). Maturity state was determined macroscopically and fish were partitioned into one of seven maturity stages (Westrheim 1975). Weights of individual fish could not be determined at sea because conditions aboard the charter vessels precluded accurate weighing.

Maturity Analyses

Maturity ogives were fit to age and size data using logistic regression (Hosmer and Lemeshow 1989). For these analyses, fish at maturity stages 1 and 2 were treated as immature and fish at stages 3-7 were treated as mature. Maturity was therefore a binary response with the probability of a mature fish given by the logistic function

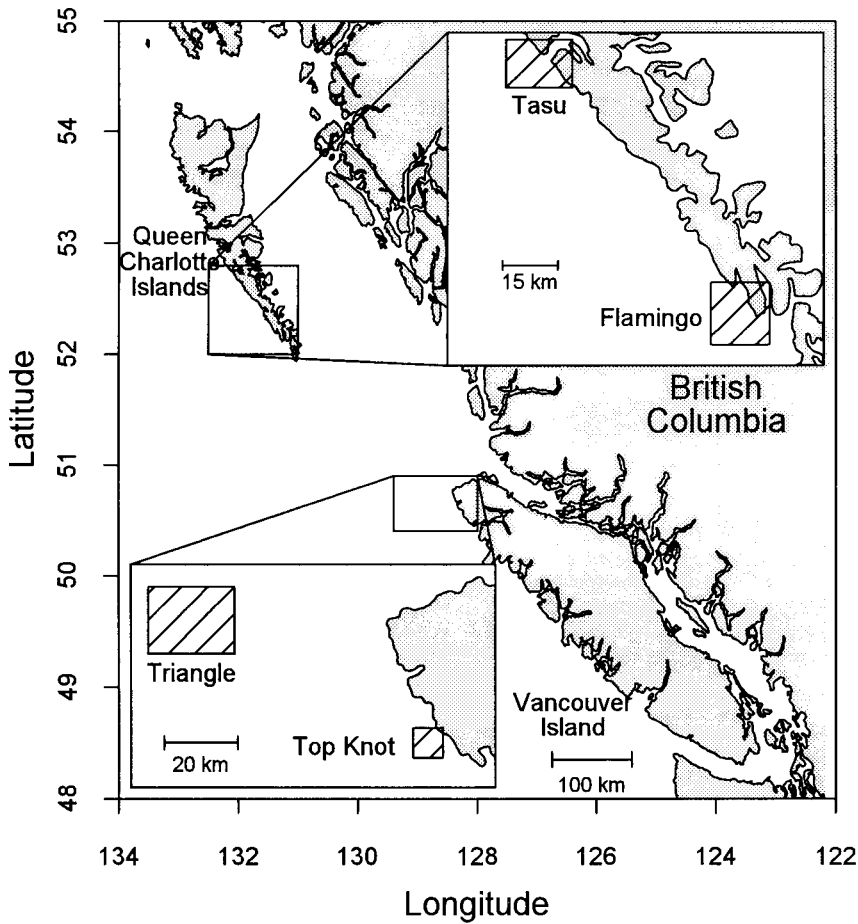


Figure 1. Coastal British Columbia with the locations of the Flamingo, Tasu, Top Knot, and Triangle study sites identified (insets).

$$\pi(x_i) = \frac{\exp\left(\sum_{j=0}^p \beta_j x_{ij}\right)}{1 + \exp\left(\sum_{j=0}^p \beta_j x_{ij}\right)}, \quad (1)$$

where $x = (x_{i0}, x_{i1}, \dots, x_{ip})$ is a list of p explanatory variables, $i = 1, \dots, n$, and $x_{i0} = 1$. The logit transformation (Hosmer and Lemeshow 1989) yields the logistic linear regression

$$\log\left(\frac{\pi(x_i)}{1 - \pi(x_i)}\right) = \sum_{j=0}^p \beta_j x_{ij}. \quad (2)$$

Nominal scaled variables, or factors, with $k = 1, \dots, K$ levels can be represented by $K-1$ design variables. Age and length were treated as continuous explanatory variables, while the study site was considered a factor variable with four levels. The probability of maturity was modeled as a function of age, or length, and site. Allowing interaction between age (length) and site permitted a model with essentially a separate linear regression for each site

$$\log\left(\frac{\pi(x_i)}{1 - \pi(x_i)}\right) = \beta_0 + \tau_k + \beta_k x_{ik}, \quad (3)$$

where τ_k is a factor variable representing the sites. The hypotheses of interaction between age (length) and sites were tested to determine equality of regression slopes using likelihood ratio statistics (Hosmer and Lemeshow 1989). Age (length) at 50% maturity was computed by inverting a simple logistic regression of maturity on age (length) with $\pi(x_i) = 0.5$ and solving for the value of the explanatory variable.

Growth Analysis

Growth curves were estimated using a model proposed by Schnute (1981) that incorporated a variety of growth forms, including von Bertalanffy (1938) growth. Subsequent description of the growth model (Appendix 1) follows the notation of Schnute (1981). The model involves six parameters, two of which are fixed at arbitrary ages τ_1 and τ_2 , with the restriction that $\tau_2 > \tau_1$. If $Y(t)$ is the size of a fish at time t , then y_1 is the size of a fish at time τ_1 and y_2 is the size of a fish at time τ_2 with $y_2 > y_1 > 0$. Two additional parameters, a and b , determine the shape of the growth curve by controlling the acceleration (deceleration) in growth from times τ_1 to τ_2 . Specialized growth forms are obtained by applying constraints to the parameters a and b . For example, specialized von Bertalanffy growth is obtained by the constraints

($a > b, b = 1$). Schnute (1981) provided the necessary equations to compute classical parameters for the age at time 0, τ_0 , and the expected asymptotic size, y_∞ , where they exist. Growth curves among areas were compared using likelihood ratio methods as reviewed recently by Quinn and Deriso (1999).

Logbook Data

Although commercial logbooks have been collected since 1986, compliance with recording exact location and depth fished was poor until about 1994 (Haigh and Richards 1997). Beginning in 1994 about 75% of the recorded fishing sets included geo-referencing and depth information. Data were included in the analysis if the fishing position was within the boundaries of one of the four study sites, and the reported depth was less than 250 m, to coincide with the fishing conducted by the charter vessels. Some records might be erroneously included or excluded from the analysis due to the limits of the spatial resolution of the data recorded. This filtering effectively limited valid logbook records to 1994 through 1998 data where a total of 79, 172, 136, and 302 sets qualified at the Flamingo, Tasu, Top Knot, and Triangle sites, respectively. Because of the short time span covered by the qualified data and the small sample size in some site-by-year combinations, the data were pooled over time for subsequent analysis.

Results

Age and Maturity Analyses

Aging data are summarized in Table 1. The youngest yelloweye rockfish caught at the survey sites ranged in age from 7 to 14 years and the oldest fish ranged in age from 35 to 115 years. Very young fish may not be vulnerable to the gear or were not available at the survey sites. The median age was less than the mean age for all sites and both sexes indicated positive skewness. The fall 1997 samples included a greater component of older fish than spring 1998 samples for all sites except Top Knot. Inspection of the quartiles suggested that the age distribution at the Top Knot site was most severely skewed in comparison to the other sites, with the majority of Top Knot fish less than about 20 years of age. Data were pooled by sex and sampling time to produce the age-frequency histograms shown in Fig. 2. A nonparametric kernel density estimate (Silverman 1986) is shown as a solid line overlaid on each histogram. The Top Knot age distribution was sharply truncated at about age 30 relative to the other sites where, in contrast, fish were distributed to at least 80 years of age. At each site there was a large mode of fish centered on age 20 as fish become fully vulnerable to the gear.

The sex ratio varied considerably among sites during each sampling period (numbers by sex in Table 1). Females were dominant at all four sites in the fall 1997 survey, while males were dominant in the spring 1998 survey with the exception of the Tasu site. Inspection of the median, mean,

Table 1. Summary of yelloweye rockfish age and maturity by year, sex, and study site.

Site	Year	Sex	<i>n</i>	Min	1st quartile	Median	Mean	3rd quartile	Max
Flamingo	1997	F	239	9	17.0	24	30.57	40.00	93
	(8)	M	144	14	18.0	25	30.76	39.00	81
	1998	F	107	11	18.0	20	26.92	36.50	82
	(9)	M	140	9	18.0	21	26.61	28.00	67
Tasu	1997	F	238	9	16.0	23	30.99	41.00	115
	(11)	M	123	9	18.0	24	29.63	39.00	87
	1998	F	123	8	17.0	19	23.50	25.00	83
	(9)	M	110	10	17.0	19	23.83	25.75	67
Top Knot	1997	F	93	7	15.0	17	19.98	19.00	60
	(8)	M	84	8	16.0	17	18.50	18.00	48
	1998	F	88	9	17.0	19	19.59	21.00	49
	(12)	M	127	9	17.5	19	19.20	21.00	35
Triangle	1997	F	275	8	21.0	35	36.57	44.50	98
	(9)	M	133	13	19.0	24	30.27	39.00	84
	1998	F	204	10	18.0	22	28.42	35.00	88
	(13)	M	288	9	18.0	21	23.80	26.00	84

The sample size (*n*) and minimum (Min), maximum (Max), median and mean ages are listed along with the quartiles of the age distribution. The number of 500-hook longline sets fished is indicated in parentheses below each year.

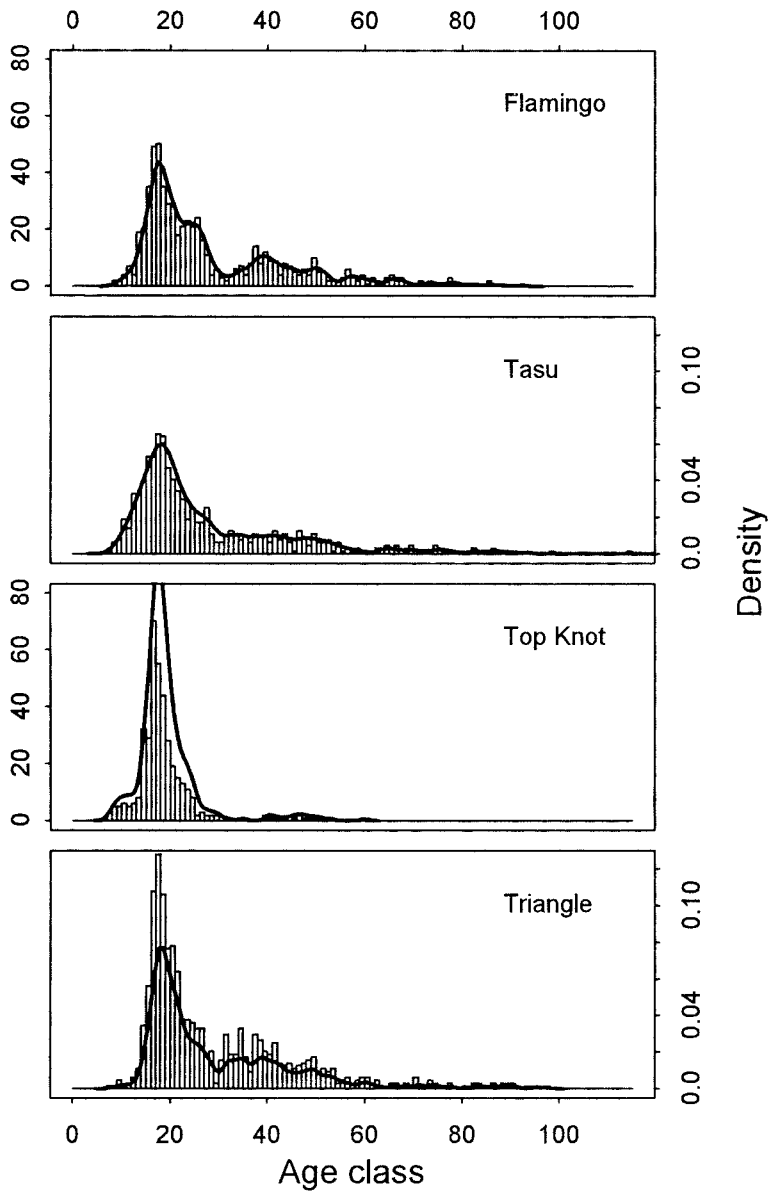


Figure 2. Age-frequency distributions for yelloweye rockfish at the four study sites. Each panel shows an age-frequency histogram with a kernel density estimate overlaid as a solid line.

and 3rd quartile in Table 1 suggests a lower relative abundance of old females in spring at the Flamingo, Tasu, and Triangle sites. These differences in sex ratio may be related to the seasonal behavior patterns of rockfish since the bias in the sex ratios is consistent among sites for both the fall and spring sampling periods. Rockfish copulate in the fall, delay fertilization, then release live larvae in the spring. Sex-specific patterns of movement on a seasonal basis have not been documented for yelloweye rockfish; however, seasonal depth-related movement on a small spatial scale is known for other rockfish species (Matthews 1990).

Due to the prevailing bathymetry, fishing at the Top Knot site was restricted to a range of about 35-100 m. The depth restriction introduced possible confounding of the age differences with depth, since deeper fishing was possible at the other sites. However, plots of depth of fishing against age for each site (Fig. 3) showed that the first 100 m sampled at the Flamingo and Triangle sites included fish up to 80 years of age. Thus, it seems that shallow depths fished at Top Knot do not preclude the occurrence of fish older than 60 years. Sample size could also have affected the results at Top Knot, where about half the specimens were obtained relative to the other sites due to the lower catch rate.

The oldest fish observed at Top Knot was 60 years of age (Table 1). An ad hoc investigation of the effect of sample size on the upper tail of the age-frequency distribution was conducted by drawing 1,000 random samples from the age-frequency distribution observed at Triangle (Fig. 2). Samples of size 400 and 200 were selected to simulate the sample sizes obtained in a single year at Triangle and Top Knot, respectively. Of the 1,000 simulated age distributions of sample size 400, 1,000 included fish older than 60 years of age and 995 included fish older than 70 years of age. The 1,000 simulated age distributions of sample size 200 contained fish older than 60 years in 996 cases, and fish older than 70 years in 913 cases. Thus, a sample of 200 fish, similar to the sample size obtained at Top Knot, should include fish older than 70 years if they are present in the population. We concluded that the absence of fish older than 60 years at Top Knot was unlikely to be an artifact of the lower sample size.

Independent simple logistic regressions of maturity on age (length) were computed for each site to produce the estimates of age (A_{50}) and length (L_{50}) at 50% maturity listed in Table 2. Only data from female yelloweye rockfish sampled in May 1998 were used in these calculations. The maturity stage of the female gonad is less ambiguous in spring since larvae are either still present or have recently been extruded. A multiple logistic regression of maturity against age and site was fit to determine whether differences existed among the sites. A model that included an age-by-site interaction was compared to one with only the main effects of age and site. The interaction term was not significant ($\chi^2_{0.053} = 2.617$, $P = 0.454$), which suggested a model with a common slope coefficient for age but different intercepts for each site. The intercepts differed since the main effect of site was significant ($\chi^2_{0.053} = 8.476$, $P = 0.037$). Inspection of the estimates

Table 2. Age (years) and length (cm) at 50% maturity for yelloweye rock-fish sampled at the study sites.

Site	A_{50}	L_{50}
Flamingo	20.3 (17.6, 23.0)	49.1 (47.4, 50.8)
Tasu	18.9 (17.5, 20.5)	48.5 (47.0, 49.9)
Top Knot	16.5 (13.1, 18.4)	42.1 (40.0, 43.7)
Triangle	17.2 (14.3, 18.9)	42.4 (40.1, 44.0)

95% Confidence intervals are indicated in parentheses.

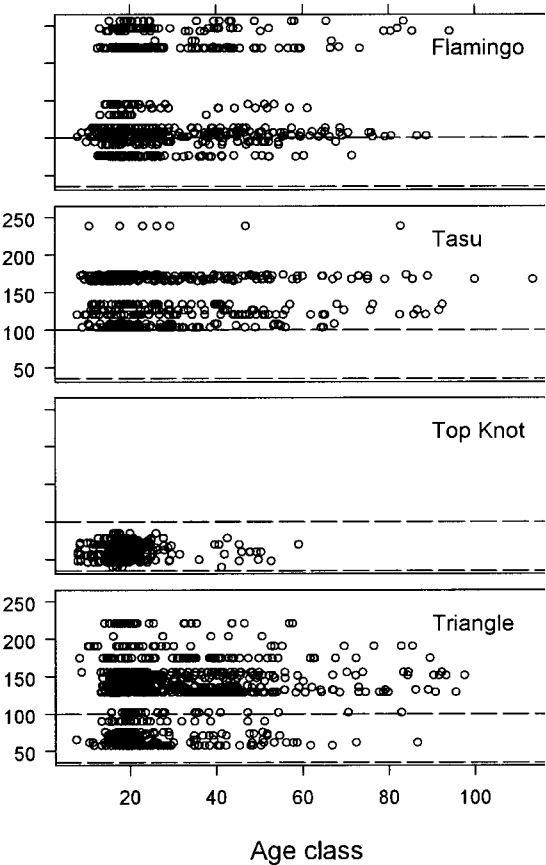


Figure 3. Depth caught as a function of age for fish sampled in 1997 and 1998 at the four study sites. The horizontal dashed lines in each panel correspond to the depth interval sampled at the Top Knot site. The observations have been randomly offset along the depth axis to expose the density of the observations.

of A_{50} and associated confidence intervals suggested that Flamingo and Tasu estimates were older than Top Knot and Triangle estimates. To test for a difference, the main effect of site was replaced by a factor that compared Flamingo and Tasu against Top Knot and Triangle, i.e., Queen Charlotte Island sites against Vancouver Island sites. A significant difference was found between the two groupings ($\chi^2_{0.05,1} = 7.036$, $P = 0.008$).

Similar results were found for the analysis of maturity against size and sites. The interaction between size and site effects was not significant ($\chi^2_{0.05,3} = 4.939$, $P = 0.176$), while the main effect of site was significant ($\chi^2_{0.05,3} = 50.4$, $P < 0.001$). As before, a model with a common slope coefficient for size but different intercepts for each site was adequate. Inspection of L_{50} estimates and associated confidence intervals in Table 2, once again, suggest that the Flamingo and Tasu data be compared to the Top Knot and Triangle data. The difference between the two groups was significant ($\chi^2_{0.05,1} = 49.2$, $P < 0.001$), with fish from the Queen Charlotte Islands sites larger at 50% maturity than fish from the Vancouver Island sites.

Growth

Exploratory plots of the length-at-age relationship by sex and year (not shown) suggested little difference in the growth pattern between fish sampled in 1997 and 1998. Consequently, data were pooled from each sampling period to produce the length-at-age plots shown in Fig. 4. Growth curves were fit to the data for each site and sex using Schnute's (1981) model, assuming additive normal errors and with $\tau_1 = 10$ and $\tau_2 = 60$. The values of a and b were not subject to constraints for these fits; i.e., the full model was fit (Appendix 1). The growth curves are shown as solid lines in each panel of Fig. 4 with the corresponding parameter estimates and their standard errors listed in Table 3. At the Flamingo, Tasu, and Triangle sites, the strong tendency for rockfish growth to asymptote early in the life span is evident. For the Top Knot site, the relative absence of fish over about 20 years of age, and the complete absence of fish older than 60 years of age, distorts the growth curves to the point where there is no growth asymptote for males.

Inspection of the standard errors for b indicated that it is the least precisely known parameter in the model. Residual plots (not shown) showed no obvious lack of fit or patterns that would suggest a multiplicative error structure. Estimates of size at age 10 (y_1) and age 60 (y_2) were similar among the sites. To determine whether the growth form could be simplified, the model was applied to the data with the constraints ($a > 0$, $b = 1$), which corresponds to von Bertalanffy growth. The hypothesis that $b = 1$ was tested for each site and sex independently by comparing the observed likelihood ratio statistic to $\chi^2_{0.05,1} = 3.84$ for significance (Table 3). Growth of female yelloweye rockfish at the Flamingo site, and of males at the Top Knot and Triangle sites, was best explained using the full model rather than the specialized von Bertalanffy model. Regardless of the model used, the standard errors of parameter estimates were relatively large for the Top Knot fits,

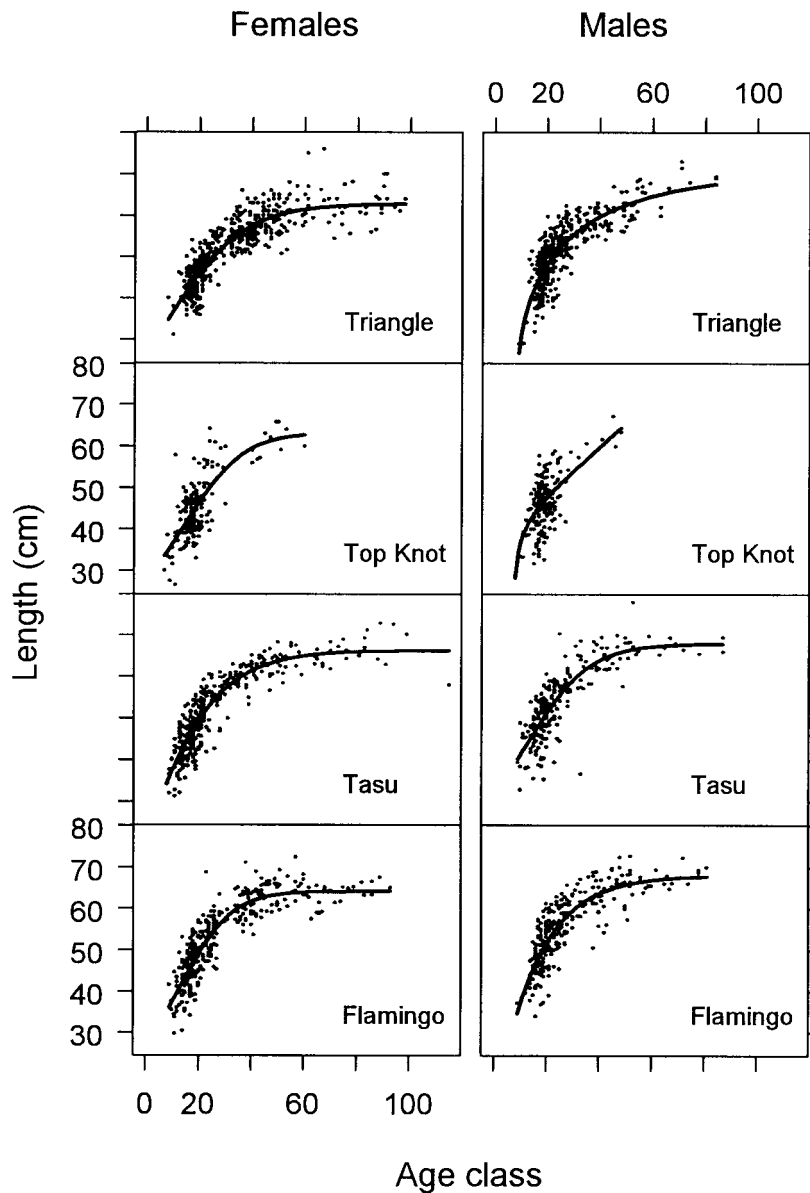


Figure 4. Length at age for yelloweye rockfish males and females from the four study sites. The solid line in each panel indicates the growth curve obtained using Schnute's (1981) model.

Table 3. Summary of parameter estimates and standard errors (SE) from growth model fits.

Site	y_1	S.E.(y_1)	y_2	S.E.(y_2)	a	S.E.(a)	b	S.E.(b)	τ_0	γ_∞	σ^2	n	$\ln L$	χ^2
Females														
Flamingo	37.3	1.00	63.9	0.53	0.114	0.027	-2.742	1.848	—	64.20	16.28	353	993.29	6.81*
Tasu	37.5	0.79	65.0	0.49	0.066	0.015	0.055	1.161	-42.83	66.38	14.41	338	930.53	0.760
Top Knot	36.5	1.17	62.8	2.87	0.103	0.109	-3.093	6.428	—	63.30	23.88	181	544.00	0.578
Triangle	36.7	1.01	61.6	0.36	0.063	0.013	-0.451	1.246	—	63.25	13.78	512	1398.09	1.67
POOLED	36.6	0.92	66.2	0.46	0.049	0.012	1.239	0.898	-2.54	68.89	22.21	1176	3485.02	761.8*
Females														
Flamingo	35.2	0.84	64.3	0.47	0.062	0.005	1	—	-2.29	65.69	16.59	353	996.69	—
Tasu	37.0	0.64	65.0	0.47	0.054	0.004	1	—	-4.84	67.05	14.45	338	930.91	—
Top Knot	36.0	0.99	64.6	2.08	0.037	0.009	1	—	-9.52	69.83	23.95	181	544.29	—
Triangle	35.7	0.74	61.6	0.34	0.049	0.004	1	—	-6.69	64.08	13.83	512	1398.93	—
POOLED	36.8	0.61	66.2	0.44	0.052	0.003	1	—	-4.87	68.59	22.20	1176	3485.06	771.5*
Males														
Flamingo	36.8	2.19	66.9	0.68	0.066	0.020	0.894	1.529	-2.96	68.03	17.75	288	822.85	0.005
Tasu	41.4	1.29	67.3	1.00	0.092	0.038	-2.725	3.085	—	68.03	22.39	222	660.10	2.18
Top Knot	37.0	1.38	71.8	5.51	-0.068	0.052	7.993	2.920	7.71	—	23.34	211	631.75	5.34*
Triangle	31.5	1.55	64.9	0.68	0.022	0.011	3.724	0.668	7.85	71.85	17.03	455	1290.61	8.11*
POOLED	37.1	0.50	63.0	0.28	0.070	0.009	-0.575	0.776	—	64.29	18.06	1384	3958.44	1,106.38*
Males														
Flamingo	36.7	1.41	66.9	0.63	0.065	0.007	1	—	-1.88	68.10	17.75	288	822.85	—
Tasu	40.0	1.10	67.7	0.88	0.049	0.007	1	—	-7.31	70.39	22.62	222	661.19	—
Top Knot	37.4	1.30	65.1	4.14	0.040	0.017	1	—	-9.27	69.38	23.94	211	634.42	—
Triangle	35.1	1.19	64.1	0.69	0.058	0.007	1	—	-3.13	65.85	17.34	455	1294.67	—
POOLED	36.3	0.40	63.1	0.26	0.052	0.002	1	—	-5.76	65.34	18.14	1384	3961.07	1,095.9*

Pooled label indicates the fit with common parameters by sex. Significant likelihood ratio test statistics (χ^2) are denoted by asterisks.

and for y_2 in particular due to the absence of older fish. Differences in growth among areas were examined independently for each sex by comparing the sum of the likelihood values over sites to the likelihood value obtained by pooling the data over sites and fitting a model with a common parameter set $\Theta = (\tau_1, \tau_2, y_1, y_2, a, b)$ and unequal variances, σ_i^2 , $i = 1, \dots, 4$. For both the full and constrained model there were significant differences in the parameter sets $\Theta_i = (\tau_1, \tau_2, y_1, y_2, a, b)$ among the sites (Table 3, row labeled "Pooled").

Catch Rates

The number of yelloweye rockfish caught on each set by the charter vessels was plotted against depth (Fig. 5). Catch rates at Top Knot were lower and less variable than catch rates at other sites. The largest catch rates were observed at about 150 m depth with the exception of the Top Knot site where all fishing occurred at depths less than 100 m. Given the typically skewed distribution of catch rate data, and the unequal variance among sites, a nonparametric Kruskal-Wallis test (Conover 1980) was used to test the hypothesis that the catch rate distribution functions were identical among sites. The test was significant ($\chi^2_{30,05} = 11.34$, $P < 0.01$), indicating that at least one site tended to yield larger catch rates than at least one of the other sites. A multiple comparison procedure described by Conover (1980) was used to conduct pairwise comparisons of the sites and confirmed that no differences among distributions could be detected for the Flamingo, Tasu, and Triangle sites and the Top Knot catch rate distribution differed from the other sites.

Plots of catch rates against depth for the 1994-1998 commercial log-book data (Fig. 6) showed patterns similar to those observed for the survey data (Fig. 5). Depths of up to 150 meters fished at Top Knot failed to yield catch rates as large as those observed from similar depths at the Triangle and Flamingo sites. The test of identical catch rate distribution functions among sites was rejected (Kruskal-Wallis $\chi^2_{30,05} = 32.25$, $P < 0.01$). Pairwise multiple comparisons showed that a difference in distribution functions existed between the Top Knot and Triangle sites, and that both differed from the Flamingo and Tasu sites. No difference in catch rate distributions was detected between the Flamingo and Tasu sites.

Discussion

We are entering a period where greater collaboration with the B.C. hook and line industry on rockfish assessment problems is possible, provided mutual confidence in the experimental process is maintained. The lack of an abundance-based assessment for nearshore rockfishes in B.C. has resulted in low industry confidence in recommended catch limits. At the same time, industry is eager for a larger role in the collection and analysis of data for stock assessment. For fisheries where little historical fishing information is available, using firsthand knowledge about the development

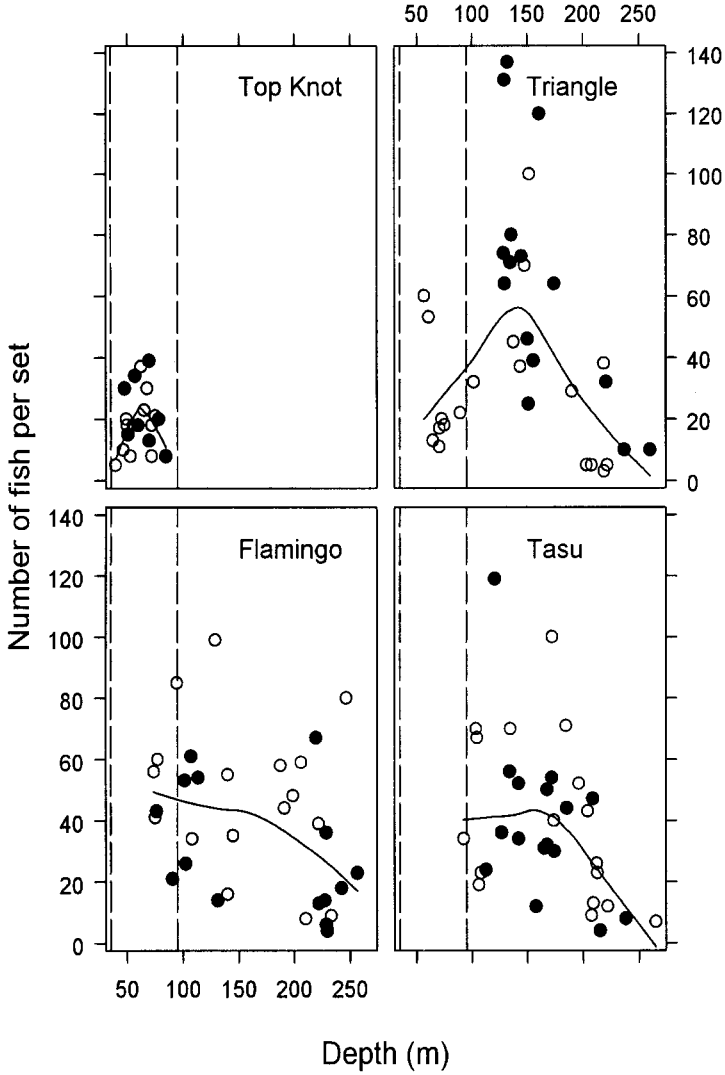


Figure 5. Research catch rates (number of yelloweye rockfish per set) as a function of depth at the four sites in 1997 (open circles) and 1998 (closed circles). The trend line (solid line) in each panel was computed using loess regression. Vertical dashed lines delimit the depth range sampled at the Top Knot site.

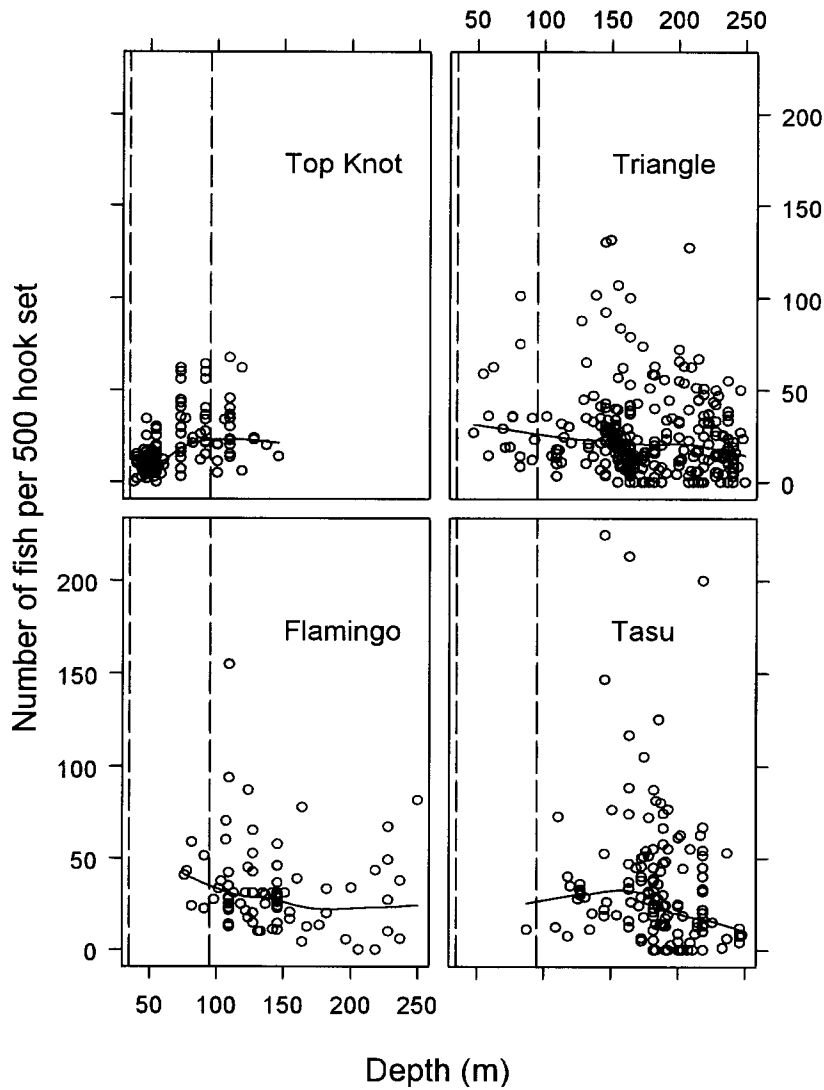


Figure 6. Commercial catch rates (number of yelloweye rockfish per 500-hook set) as a function of depth at the four study sites. The trend line (solid line) in each panel was computed using loess regression. Vertical dashed lines delimit the depth range sampled at the Top Knot site.

of the fishery from experienced fishers can be a valuable source of information on rockfish distribution, their preferred habitats, and historical population levels. This anecdotal information can be utilized in retrospective analyses where harvest-related processes can be investigated. Fishers also express their own scientific skepticism that inevitably enriches the experimental design (Stanley et al. 2000). Their involvement may also bring them a full appreciation of the investment in project design and the data collection required to show clear results. Furthermore, they make it possible to carry out projects by contributing to the costs of research and data collection either directly or through the provision of vessel time and technical support.

Although the results obtained at the Top Knot site were consistent with expectations, the truncated age structure is difficult to interpret in the absence of data to support a sequential population analysis or an absolute abundance estimate. The difficulty lies in distinguishing whether the observed age structure is a result of juvenation of the population due to excessive fishing or a result of increased recruitment to a particular site. Alternatively, age-dependent emigration of fishes either spatially, or by depth, could explain a truncated age distribution sampled from a discrete locality.

Like the interpretation of the age distributions, it is hard to attribute biological significance to statistical differences in maturity and growth estimates without a modeling framework to evaluate long-term population implications. The more recent exploitation of Queen Charlotte Island sites relative to the Vancouver Island sites may contribute to the differences observed in the maturity estimates. Growth comparisons among the four sites detected differences in the growth parameters. However, much of the difference can be attributed to the lack of older fish at the Top Knot site where there were insufficient data to define a growth asymptote for old male fish and estimates of size at age 60 were poorly determined.

Although logbook data have been collected since 1986, the completeness of the data was poor until the early 1990s. However, patterns in survey and logbook catch rates between Top Knot and the other sites were consistent. This project demonstrated to the industry participants that harvest activities could leave symptoms of fishing on yelloweye rockfish populations. Explanations for the truncated age distribution and lower catch rates at the Top Knot site that do not require fishing pressure illustrated the possible ambiguity of results. These alternative explanations may provide impetus for future work. Indeed, fishery managers and industry agreed to close the three southernmost study sites to rockfish harvest in 1999. This intervention affords an opportunity to examine whether the signal created by the age truncation at Top Knot is a result of local recruitment or age-dependent movement of fish. If on subsequent sampling the age mode at 20 years is shifted forward an appropriate interval, one conclusion would be that the closure was effective at protecting a resident population of yelloweye rockfish. If the mode does not propagate into older ages, then

alternative explanations such as differential migration of fish by age or depth, strong incoming recruitment, or undocumented harvests are plausible. Industry collaboration in future investigations is a key to eliminating the latter explanation.

Recent support in the fisheries literature to manage rockfishes using area closures (Yoklavich 1998, Walters and Bonfil 1999, Parker et al. 2000) raises questions about the extent and distribution of closures required to ensure conservation. The requirement to monitor the effectiveness of closed areas means that performance diagnostics, including changes in age structure, growth, and maturity characteristics, are required for nearshore rockfishes since estimates of abundance are generally not available. Retrospective studies for sedentary, long-lived fishes, which contrast areas with different exploitation histories, may be a means of identifying the requisite measures. Furthermore, the involvement of industry in this type of data collection and interpretation may assist in building support for spatial management measures such as closed areas.

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Appendix 1

This appendix describes the growth model (Schnute 1981) used to compare growth curves among areas. The model involves six parameters $\Theta = (\tau_1, \tau_2, y_1, y_2, a, b)$, where τ_1 and τ_2 are two arbitrary ages in the life of a fish, such that $\tau_2 > \tau_1$. The parameter y_1 is the size of a fish at time τ_1 and y_2 is the size of a fish at time τ_2 with $y_2 > y_1 > 0$. Parameters a and b determine the shape of the growth curve by controlling the acceleration (deceleration) in growth from times τ_1 to τ_2 . The parameter a has units (time^{-1}), while b is dimensionless. Although mathematical expression of the model has four cases, these four cases actually represent the limiting forms of a single equation as a and/or b approach 0. Let $Y(t)$ be the size at time t , then:

Case 1: $a \neq 0, b \neq 0$

$$Y(t) = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b}, \quad (1)$$

Case 2: $a \neq 0, b = 0$

$$Y(t) = y_1 \exp \left[\ln(y_2/y_1) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right], \quad (2)$$

Case 3: $a = 0, b \neq 0$

$$Y(t) = \left[y_1^b + (y_2^b - y_1^b) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{1/b}, \quad (3)$$

Case 4: $a = 0, b = 0$

$$Y(t) = y_1 \exp \left[\ln(y_2/y_1) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]. \quad (4)$$

Suppose that the age and size of a sample of fish are measured to give n data points (t_j, Y_j) , $j = 1, 2, \dots, n$. If the ages are determined exactly, then additive or multiplicative errors may be specified

$$\hat{Y}_j = Y_j + \sigma \varepsilon_j; \quad j = 1, \dots, n, \quad (5)$$

$$\hat{Y}_j = Y_j e^{\varepsilon_j}; \quad j = 1, \dots, n, \quad (6)$$

where the random variables ε_j ($j = 1, \dots, n$) are assumed to be normally distributed with mean 0 and variance σ^2 .

There are compelling reasons to adopt this formulation of growth. The parameters $\Phi = (\tau_1, \tau_2, y_1, y_2, a, b)$ always exist even in cases where, for example, the most appropriate model does not include a maximum growth asymptote. Model parameters are expressed as quantities that have direct biological interpretation, and the parameterization has superior statistical properties (Ratkowsky 1986). In any case, Schnute (1981) provided transition equations to convert the parameter set Φ to those used in the various specialized growth forms.

We used likelihood ratio tests to compare growth among groups. Suppose size-at-age data are collected for $i = 1, \dots, m$ groups of data. Given that an appropriate growth formulation has been selected, there are four possible situations defined by equal or unequal variances σ^2 and independent or common parameter sets Φ (Quinn and Deriso 1999). The full model is defined by independent parameter sets and unequal variances; all other situations are obtained by reduction in the number of parameters. For example, a reduced model can be specified by assuming a common parameter set and equal variances among groups, i.e., fitting the growth model to the pooled data. Under the assumption of independent, additive normal errors, the likelihood of the data given the parameters for group i is specified by

$$L_i(\Phi_i, \sigma_i^2 | \{Y_{ij}\}) = (2\pi\sigma_i^2)^{-n_i/2} \exp\left[-\frac{1}{2\sigma_i^2} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2\right]. \quad (7)$$

In practice, parameter estimates $(\hat{\Phi}_i, \hat{\sigma}_i^2)$ are determined by minimizing the (negative) of the logarithm of the likelihood function, calculated by summation of the log-likelihood components over the m groups:

$$\ln L_F = \sum_{i=1}^m \ln L_i(\hat{\Phi}_i, \hat{\sigma}_i^2 | \{Y_{ij}\}) = \sum_{i=1}^m \left[-\frac{n_i}{2} \log(2\pi\hat{\sigma}_i^2) - \frac{1}{2\hat{\sigma}_i^2} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2 \right], \quad (8)$$

where

$$\hat{\sigma}_i^2 = \frac{1}{n_i} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2. \quad (9)$$

The likelihood ratio statistic

$$X^2 = -2(\ln L_R - \ln L_F) \quad (10)$$

can be used to test a hypothesis between a full (F) and reduced (R) model by comparing X^2 to a chi-square critical value χ^2 with degrees of freedom equal to the difference in the number of parameters between full and reduced models.

Distribution Patterns and Survey Design Considerations of Pacific Ocean Perch (*Sebastes alutus*) in the Gulf of Alaska

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Abstract

In the Gulf of Alaska, a stratified-random trawl survey has been conducted triennially since 1984 to obtain abundance estimates for major ground-fish species. There is considerable uncertainty in the survey biomass estimates for Pacific ocean perch (*Sebastes alutus*) (POP). Using a geographic information system (GIS) and log-linear analyses, survey and commercial fishery data were analyzed to determine POP distribution patterns in the Gulf of Alaska (GOA). The survey and the fishery appear to encounter POP in the same areas throughout the GOA, and POP distribution does not appear to change temporally. Analysis of CPUE data indicates POP exhibit a tightly aggregated distribution pattern which is related to habitat type. The improvement of the survey design, or relative efficiency compared to a random estimate was 65%. Altering the allocation and stratification of the current design may improve the precision of POP biomass estimates

but may be limited by the clustered distribution exhibited by POP in the GOA and the need to assess other species. Work is being conducted to evaluate the merits of adaptive cluster sampling for providing improved estimates for rockfish populations.

Introduction

Pacific ocean perch (*Sebastes alutus*) (POP) are the most abundant rockfish in the Gulf of Alaska (GOA) and are important commercially (Carlson et al. 1986). Stock assessment of POP in the GOA relies heavily on abundance data derived from triennial trawl surveys, conducted since 1984. Trawl survey estimates of POP abundance are uncertain because biomass estimates fluctuate and have high variability (Fig. 1). These fluctuations in biomass seem unlikely for a species with such longevity (>80 years), low natural mortality (~0.05) (Archibald et al. 1983), and low fishing mortality (Heifetz et al. 1995). Concern has arisen regarding the ability of the trawl survey to accurately assess the biomass of POP.

The trawl survey incorporates a stratified random sampling design and uses the area-swept methodology to estimate absolute abundance of major groundfish species (Alverson and Pereyra 1969, Stark and Clausen 1995). If survey effort is not optimally allocated or strata not defined optimally, the survey will not provide as precise an estimate as possible. Evaluation of survey designs can provide valuable information for assessing the efficiency of a particular design (Sukhatme et al. 1984, Gavaris and Smith 1987, Mohn et al. 1987). An important variable for the construction of a stratified sampling design is the frequency distribution of the variable of interest (Cochran 1977). Despite numerous studies describing POP habitat preference (Bakkala and Wakabayashi 1985, Balsiger et al. 1985, Matthews and Richards 1991, Krieger 1993, Scott 1995) little is known about the overall distribution of POP throughout the GOA. A better knowledge of the distribution of POP is needed if a more effective sampling design is to be developed.

Extensive survey and commercial fishery data exist describing the location and amount of POP catch in the GOA. The trawl survey has been conducted in the GOA since 1984. In addition to survey data, a large amount of POP catch information has been collected by fishery observers since 1989. Analysis of these data may provide insight to the spatial distribution of POP in the GOA. Until recently, large spatially distributed data sets were difficult to analyze. We used a geographic information system (GIS) (ARC/INFO 1995) to visually map the spatial distribution of POP in the GOA based on survey and commercial fishery catch data. Using log-linear modeling, we were able to study distribution patterns of POP and identify concerns for sampling POP in the GOA.

The objectives of this study were to investigate POP distribution patterns in the GOA using survey and commercial fishery data. Efficiency of the survey design for POP was evaluated and survey design considerations are discussed.

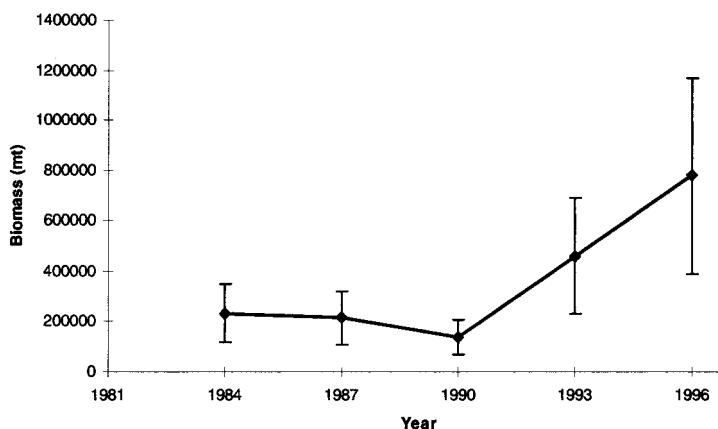


Figure 1. Biomass estimates and associated confidence intervals for Pacific ocean perch (*Sebastes alutus*) from the National Marine Fisheries Service triennial trawl surveys.

Methods

Data Sets

Data were obtained from National Marine Fisheries Service (NMFS) Gulf of Alaska triennial bottom trawl surveys conducted in 1987, 1990, and 1993. Survey catch per unit of effort (CPUE) was calculated for each tow by dividing catch weight by the area swept by the trawl:

$$\text{CPUE} = \frac{\text{catch weight (kg)}}{\text{trawl width (km)} \times \text{distance trawled (km)}}.$$

A standardized stratified-random survey design was used in all years (Brown 1986, Stark and Clausen 1995). A total of 2,269 successful tows were made at random stations throughout the GOA during the three surveys.

Since 1989, extensive records of commercial fishing activity in the GOA have been collected by observers aboard domestic trawl vessels. From 1989 through 1994, POP were caught in 7,982 observed tows throughout the GOA. Fishery CPUE was computed and expressed in kilograms of POP per kilometer fished. The fishery CPUE is nonstandardized for trawl width because this information is not collected by observers. Also, there was insufficient information to adjust effort for differences in fishing power among vessels, years, or gear.

Spatial Distribution of POP CPUE

We examined the data by North Pacific Fishery Management Council (NPFMC) management areas and NMFS survey strata. The management areas are divided into three geographic regions adopted by the NPFMC: Eastern Gulf (EG) (132°00'W to 147°00'W); Central Gulf (CG) (147°00'W to 154°00'W); and Western Gulf (WG) (154°00'W to 170°00'W) (Fig. 2). Within these regions, 49 NMFS strata have been designated for use in the stratified sampling design for surveys (Stark and Clausen 1995). Strata are categorized by bathymetry, geographical area, and statistical area boundaries. The strata were used in this analysis because they encompass both depth and habitat information and follow the management area boundaries.

Survey CPUE was divided into four quartiles by management region and survey year so temporal differences in POP distribution could be compared. Geographic units based on the three management regions were chosen since POP quotas are set for each individual region. We chose to explore within-management-area variability and did not focus on between-area comparisons. We were most interested in investigating the habitat type distribution patterns within individual management regions rather than making a gulf-wide comparison since each region is managed independently. A management area with the highest proportion or largest number of POP catches may have dominated the upper quartiles of a GOA-wide analysis. The fourth quartile represents the top 25% CPUEs and the first quartile represents the lowest 25%. Commercial CPUEs were analyzed in the same way as survey CPUEs to allow comparison between data sets. Data were analyzed by individual years from 1989 to 1994; in addition, data were analyzed from two 3-year groupings which encompassed survey years (1989-1991, 1992-1994).

POP Distribution Patterns

Log-linear analyses were used to test for differences in distribution of CPUE among the three survey years (Sokal and Rohlf 1981). Survey frequencies (f_{ijk}) were organized by quartile (k), year (i), and stratum type (j) (Table 1). The resultant 3-way tables were fit to the full model

$$\ln \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$$

where \hat{f}_{ijk} = predicted frequency, year effect = α_i , stratum type effect = β_j , and quartile effect = γ_k . The 1987, 1990, and 1993 survey data were used for the year effect (α_i), the 0 tows and four quartiles were used for quartile effect (γ_k), and strata were compiled into four types (flat, shelf, gully, slope) for stratum effect (β_j).

Three separate models were constructed to analyze survey data. One model focused on survey effort and included all five abundance levels: 0 catch and 1st, 2nd, 3rd, and 4th quartiles of CPUE catch. The second model

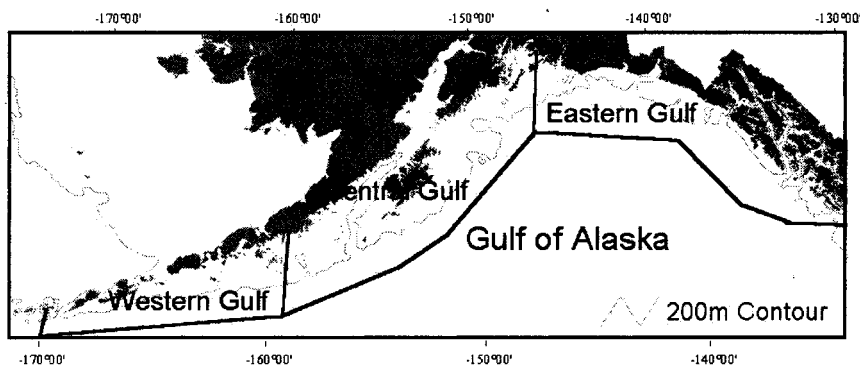


Figure 2. North Pacific Fishery Management Council management regions in the Gulf of Alaska.

considered presence and absence of POP as two levels of abundance: 0 catch and catch (1-4 quartiles combined). The third model used only the 1st, 2nd, 3rd, and 4th quartiles. A separate model was completed for each of the three management regions resulting in a total of nine models for survey data.

Log-linear analyses were further used to test for differences in distribution of CPUE by quartile (1-4) for the fishery data. A separate model and analysis were computed for each of the three management regions. A final model was constructed to compare survey and fishery data. Fishery data were grouped into two categories of 3-year intervals (1989-1991 and 1992-1994) and organized by quartile (1-4) for comparison to the 1990 and 1993 survey data. Only the four quartiles of POP CPUE were used in the quartile effect. The fishery data set from 1989-1991 was compared to the 1990 survey data set and the fishery data set from 1992-1994 to the 1993 survey data set. One additional parameter, ρ_i , was added for the data set effect.

For the log-linear analyses, a hierarchy of reduced models were fitted with some of the factors eliminated. G^2 -values for goodness-of-fit were used to test the significance of terms and presence of interaction among the three factors. The appropriate log-linear model is the most parsimonious model that is not significantly different than the full model. This was determined by comparing the difference in G^2 statistics corresponding to the full and reduced models to a chi-squared critical value with degrees of freedom equal to the difference in parameter numbers between the models (Sokal and Rohlf 1981, Agresti 1990).

Survey Design Efficiency

The sampling scheme used for the triennial trawl surveys is based on a stratified random sampling design. In stratified sampling, the population

Table 1. Survey frequencies of the quartiles by year, region, and general stratum type used in log-linear analysis.

		1987 Quartile					1990 Quartile					1993 Quartile							
		0	1	2	3	4	Total	0	1	2	3	4	Total	0	1	2	3	4	Total
Eastern Gulf																			
Gully	4		8	5	10	9	36	18	8	17	19	11	73	4	14	15	16	9	68
Shelf	55	11	10	6	6	1	83	33	22	12	7	5	79	61	10	5	3	6	85
Slope	10	1	4	3	3	9	27	5	4	4	8	12	33	4	1	4	5	10	24
Central Gulf																			
Flats	91	7	2	2	3	3	106	69	6	3	1	1	80	111	7	2	1	2	123
Gully	80	10	13	8	12	8	123	60	14	11	19	14	118	72	10	10	11	11	114
Shelf	91	19	19	19	21	20	170	85	14	20	15	13	147	64	21	25	24	18	152
Slope	12	3	5	4	4	5	29	6	2	2	3	7	20	8	1	4	5	7	25
Western Gulf																			
Flats	74	10	11	8	8	3	106	60	6	4	3	1	74	85	7	7	5	1	105
Gully	12	4	1	1	1	1	19	16	4	2	2	1	25	23	3	1	1	1	29
Shelf	12	3	5	7	7	11	38	14	1	4	2	4	25	12	1	2	4	6	25
Slope	17	1	1	1	3	4	26	8	1	2	3	5	19	5	1	1	3	5	15

is partitioned into regions or strata (h), and a sample (y_{hj}) is selected by some design within each strata (Thompson 1992). The design is called stratified random sampling if the design within each stratum is simple random sampling (SRS). The principle of stratification is to partition the population in such a way that the units within a stratum are as similar as possible since only the within-stratum variances are used (Thompson 1992).

A fundamental difference between SRS and stratified sampling is allocation of samples among strata. The NMFS trawl survey design follows an optimum allocation scheme which allocates larger sample sizes to larger or more variable strata based on population standard deviations obtained from past data. Because this is a multi-species survey, the sample size allocations were based on the variances of abundance estimates for the total groundfish complex from the 1984 triennial trawl survey.

The 1990 NMFS survey design, which was based on 49 strata, was evaluated by comparing the stratified simple random design to a totally random design. The stratified random variance of POP calculated for the NMFS survey can be expressed as

$$\hat{v}(\bar{y}_{st}) = \frac{1}{N^2} \sum_{h=1}^L N_h (N_h - n_h) \frac{s_h^2}{n_h} \quad (1)$$

where N is the total number of units, N_h is the total number of units in stratum h , n_h is the number of units in sample in stratum h , and s_h^2 is the estimated variance in stratum h . The unbiased estimator of the variance of a simple random sample from the same population, $\hat{v}(\bar{y}_{srs})$, was estimated using Cochran's (1977) equation 5A.44:

$$\hat{v}(\bar{y}_{srs}) = \frac{(N - n)}{n(N - 1)} \left[\frac{1}{N} \sum_h \frac{N_h}{n_h} \sum_j^{n_h} y_{hj}^2 - \bar{y}_{st}^2 + v(\bar{y}_{st}) \right] \quad (2)$$

According to Sukhatme et al. (1984), an estimator of the gain in efficiency due to stratification is called relative efficiency and is expressed as

$$RE = \frac{\hat{v}(\bar{y}_{srs})}{\hat{v}(\bar{y}_{st})} - 1 \quad (3)$$

Because of the additive nature of allocation and strata components in stratified sampling, each component can be extracted from the overall relative efficiency of the design (Sukhatme et al. 1984).

Results

Spatial Distribution of POP CPUE

Of the 2,269 survey hauls analyzed, 899 encountered POP. The POP hauls were distributed throughout the GOA with POP common on the continental shelf and especially along the continental shelf break (Fig. 3). In the EG survey data, CPUEs along the shelf break and in gullies were typically high (Table 1). Lower CPUEs occurred on shelf regions consistently across the three surveys. In the CG, varying levels of CPUE occurred in all types of strata. High CPUEs tended to be on the slope, in gullies, and especially along the shelf break. Many of the low CPUEs were recorded on the flats and on large shelf regions. In the WG, fewer hauls encountered POP. The slope areas and shelf break regions dominated the high CPUE areas. Low CPUEs were present in all areas.

Zero catches of POP were encountered throughout the GOA in all strata including the shelf-slope breaks and gully strata where many of the high CPUEs occurred. In the CG and WG, many zero hauls occurred in the shallow flats and gullies. Due to the allocation of sampling to depths > 100 m, few hauls were conducted in the flats of the EG but zero hauls occurred in these areas to a lesser extent. Localized areas that have no survey haul locations likely represent areas of non-trawlable substrate.

Pacific ocean perch caught in the fishery are most prevalent on the shelf break, slope, and inside major gullies and trenches running perpendicular to the shelf break (Fig. 4, Table 2). The majority of fourth quartile fishery hauls were located near the continental slope. Fishery coverage appears to be similar to survey coverage, especially when viewed on a small spatial scale.

Log-linear Models

Survey Data

The first model tested the survey frequencies of the zero catch and the catch by quartiles 1, 2, 3, and 4 by year, region, and stratum type (Table 1). For the CG and WG, the simplest model that fitted the data as well as the full model was

$$\ln \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \beta\gamma_{jk}$$

where α = year effect, β = stratum type effect, and γ = quartile effect (Table 3). This model indicates there is a strong interaction ($\beta\gamma$) between individual strata and the level of CPUE. This association, however, is not dependent or related to individual year. For the EG, only the saturated, or full, model fit the data

$$\ln \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$$

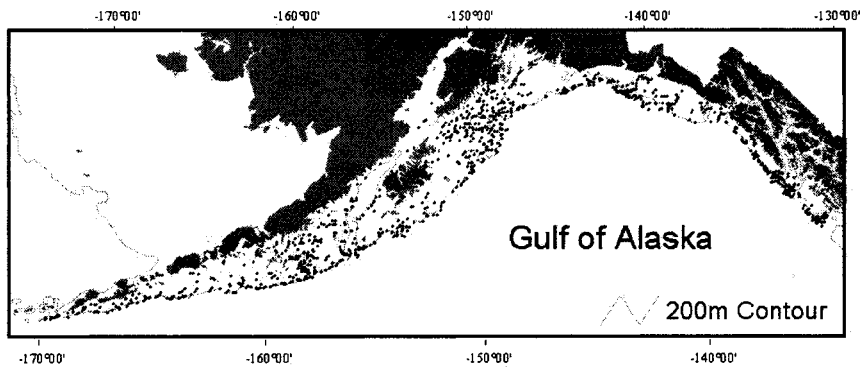


Figure 3. NMFS survey hauls in which Pacific ocean perch were caught in the 1987, 1990, and 1993 Gulf of Alaska triennial trawl groundfish surveys.

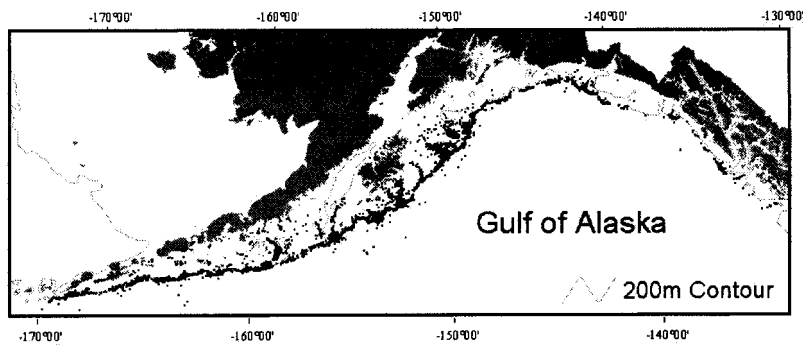


Figure 4. Commercial trawl tows in which Pacific ocean perch were caught in the Gulf of Alaska, 1990-1994.

Table 2. Commercial catch frequencies of the quartiles by year, region, and general stratum used in log-linear analysis.

	1989-1991 Quartile					1992-1994 Quartile				
	1	2	3	4	Total	1	2	3	4	Total
Eastern Gulf										
Gully	32	49	56	58	195	34	23	25	41	123
Shelf	23	19	9	3	54	31	28	27	13	99
Slope	55	42	45	49	191	15	29	28	26	98
Central Gulf										
Flats	40	19	7	1	67	28	24	21	22	95
Gully	38	20	25	13	96	64	83	59	35	241
Shelf	144	154	130	75	503	280	230	238	242	990
Slope	116	145	176	249	686	74	109	128	147	458
Western Gulf										
Flats	150	153	120	87	510	45	51	68	64	228
Gully	9	3	1	2	15	27	6	2	1	36
Shelf	40	50	77	92	259	40	56	67	88	251
Slope	21	14	22	39	96	117	116	92	76	401

Table 3. Hierarchy of log-linear models and associated statistics for comparison of survey data including the zero tows, and 1st, 2nd, 3rd, and 4th quartiles in the eastern, central, and western gulf regions.

Model	Likelihood ratio Chi-square	Degrees of freedom	P-value
Eastern Gulf Region			
$\mu + \alpha_i + \beta_j + \gamma_k$	182.7	36	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij}$	171.3	31	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik}$	169.9	28	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \beta\gamma_{jk}$	51.3	28	0.01
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik}$	158.5	24	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \beta\gamma_{jk}$	39.9	24	0.02
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk}$	38.5	20	0.01
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk}$	30.6	16	0.02
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$	0.0	0	undefined
Central Gulf Region			
$\mu + \alpha_i + \beta_j + \gamma_k$	203.7	50	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij}$	196.0	44	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik}$	202.4	42	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \beta\gamma_{jk}$	32.6	38	0.72
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik}$	194.7	36	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \beta\gamma_{jk}$	25.0	32	0.81
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk}$	31.3	30	0.40
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk}$	22.8	24	0.53
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$	0.0	0	undefined
Western Gulf Region			
$\mu + \alpha_i + \beta_j + \gamma_k$	113.1	50	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij}$	103.6	44	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik}$	107.4	42	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \beta\gamma_{jk}$	28.7	38	0.87
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik}$	97.9	36	0.00
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \beta\gamma_{jk}$	19.2	32	0.97
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk}$	23	30	0.82
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk}$	14.5	24	0.94
$\mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$	0.0	0	undefined

α = year effect, β = stratum type effect, γ = quartile effect. The p-value is associated with the hypothesis that the given model is not significantly different from the full model on the bottom row. The rows in bold type shows the most parsimonious model.

where α = year effect, β = stratum type effect, and γ = quartile effect. In this model, all two-way interactions are significant and there is a 3-variable interaction present. This is evident from the significant chi-square values for all possible models (Table 3). Since there are only three terms, the model with the 3-variable interaction has so many parameters that it forces all the expected values to exactly equal the observed values resulting in a chi-square statistic equaling zero. It should be noted the stratum-quartile interaction term ($\beta\gamma$) drastically decreased the likelihood ratio despite the failure to significantly fit.

For a better understanding of the log-linear tests, the frequencies and proportions can be compared to the model results. In the EG, the shelf stratum had significantly higher proportions of hauls that caught no POP (42-72%) in comparison to the gully stratum (13-26%) and the slope stratum (33-42%) (Table 1). The shelf stratum also had lower 3rd and 4th quartile CPUEs than the other strata. These differences were not consistent among the surveys, however, and the significance of the $\alpha\beta\gamma$ interaction indicates that at least one of these year-to-year changes in $\beta\gamma$ was different than the others.

For the CG and WG, the stratum-quartile interaction term ($\beta\gamma$) was significant. In the CG, the proportions of zero hauls in the flats stratum were significantly higher than the slope stratum, with a range of 86-90% in the three surveys, versus 30-41% in the slope stratum (Table 1). The proportions of zero hauls were intermediate in the gully and shelf strata, with a range of 42-65%. The proportion of 4th quartile hauls in the CG was 1-3% in the flats and 21-35% in the slope. This same trend of high POP CPUEs in the slope and large zero CPUEs in the flats also occurred in the WG. These differences between the strata types result in the significant $\beta\gamma$ interaction in the log-linear model for the CG and WG. Since the pattern of differences among strata are consistent over the three surveys, the $\alpha\beta\gamma$ interaction was not significant.

Analysis of only the POP catch (1-4 quartiles) yielded similar results. The simplest model that fit the data was the same for all three regions (Table 4). This is the same model chosen above for the CG and WG and indicates there is a strong interaction between individual strata and the level of CPUE ($\beta\gamma$). When presence and absence of POP in the survey hauls was tested, different models were chosen for each region (Table 4). The stratum-quartile interaction term ($\beta\gamma$) was significant in the CG and WG but in the EG the full model was chosen, indicating a three-variable interaction. In the WG, the year-quartile interaction term ($\alpha\gamma$) was significant in the presence-absence model. However, examination of the likelihood ratios and associated probabilities for this model indicates this term contributed little to the chosen model in comparison to the stratum type-quartile interaction ($\beta\gamma$) despite its statistical significance.

Table 4. Summary table of log-linear model results.

Region	Significant interactions	Likelihood ratio	Degrees of freedom	P-value
Survey data: 0, 1, 2, 3, 4 quartiles				
EG	Full model	0.0	0.0	undefined
CG	$\beta\gamma$	32.6	38	0.72
WG	$\beta\gamma$	28.7	38	0.87
Survey data: 1, 2, 3, 4 quartiles				
EG	$\beta\gamma$	20.5	22	0.55
CG	$\beta\gamma$	17.4	30	0.97
WG	$\beta\gamma$	7.2	30	1
Survey data: 0 - Catch				
EG	Full model	0.0	0.0	undefined
CG	$\beta\gamma$	23.6	14	0.05
WG	$\alpha\gamma + \beta\gamma$	19.7	12	0.07
Fishery data: 1, 2, 3, 4 quartiles				
EG	Full model	0.0	0.0	undefined
CG	Full model	0.0	0.0	undefined
WG	Full model	0.0	0.0	undefined
Survey and fishery data: 1, 2, 3, 4 quartiles				
EG	$\alpha\beta\gamma + \alpha\beta\rho + \beta\gamma\rho$	6	9	0.74
CG	$\alpha\beta\gamma + \alpha\beta\rho + \beta\gamma\rho$	7.4	12	0.83
WG	$\alpha\beta\gamma + \alpha\beta\rho + \beta\gamma\rho$	7	12	0.86

α = year effect, β = stratum type effect, γ = quartile effect.

Fishery Data

For the fishery data, there were interactions among the year effect (α_i), stratum type effect (β_j), and quartile effect (γ_k) in all three regions (Table 4). The CG had a higher proportion of large hauls in the slope stratum (Table 2). The tendency for small hauls in the flats stratum was evident in the CG but inconsistent in the WG. Gully strata were similar to the survey data, with no trend in the EG and CG and low CPUEs in the WG. Likewise, the shelf strata were similar between data sets with low CPUEs in the EG, no trend in the CG, and high CPUEs in the WG.

The distribution of POP fishery CPUE was significantly different between the two time periods (Table 2). In the EG, the tendency for low quartile hauls in the shelf stratum was much stronger in the first time period than the second. For the slope, all quartiles were nearly even for the first period but in the second period there was a low number of first quartile hauls. This pattern was similar in the CG between time periods.

Distribution of effort among strata was different between the two time periods. In the first time period, 51% of the total tows were in the slope strata but in the second time period this decreased to 26% (Table 2). In the WG, 58% percent of the total tows in the first time period were in the flats stratum but this decreased to 25% in the second time period (Table 2). Likewise, tows in the slope stratum increased from 11% to 44% between time periods.

Survey and Fishery Data

A four-way log-linear analysis was constructed to help summarize the associations among year effect (α_i), stratum type effect (β_j), quartile effect (γ_k), and data set effect (ρ_l) for survey and fishery data. For all three regions, the simplest model had three 3-way interaction terms including the year-stratum type-quartile term ($\alpha\beta\gamma$), the year-stratum type-data set term ($\alpha\beta\rho$), and the stratum type-quartile-data set term ($\beta\gamma\rho$) (Table 4).

The interesting interaction is the $\beta\gamma\rho$ term which indicates the quartile distribution by strata differs between data sets. In the EG, both data sets show a tendency for small POP CPUEs in the shelf stratum; however, in the slope stratum, survey data show a stronger tendency for large POP CPUEs than does the fishery data (Tables 1, 2). In the CG, both data sets show a tendency for hauls in the flats to be in the low quartiles and slope hauls to be in the upper quartiles (Tables 1, 2). The significant $\beta\gamma\rho$ interaction may be caused by the fishery data's higher number of low quartile CPUEs in the gully and shelf strata (Tables 1, 2). The survey data is more uniform across quartiles for these two strata types. In the WG, both data sets show trends toward low CPUEs in the gully stratum and high CPUEs in the shelf stratum (Tables 1, 2). The tendency for low flats CPUEs and high slope CPUEs seen in the CG for both data sets is seen only in the survey data in the WG, thus the significant $\beta\gamma\rho$ interaction.

Survey Design Efficiency

The stratified random variance estimate of POP biomass, $\hat{v}(\bar{y}_{st})$, from the 1990 NMFS survey was 11,495 (equation 1). An estimate of the variance of a totally random sample, $\hat{v}(\bar{y}_{srs})$, was 29,711 (equation 2). The improvement of the survey design, or relative efficiency compared to a random estimate is 62%. The distribution of sampling effort, or allocation component, accounted for 58% of the relative efficiency. The stratification component accounted for the remaining 4%.

Discussion

Using both survey and fishery data, we were able to analyze a large amount of POP catch information from throughout the GOA (Figs. 1, 2). Large catches of POP commonly occurred near the shelf break and in gullies running perpendicular to the continental shelf. Major and Shippen (1970) reported POP are common in and along gullies, canyons, and submarine depressions along the outer continental shelf and slope. A detailed description of POP habitat and maps of POP catches in the GOA can be found in Lunsford (1999).

Log-linear analysis of the survey data indicates POP distribution has not changed over time. The majority of models indicate a significant interaction occurred between stratum-type quartile ($\beta\gamma$) but not year-quartile ($\alpha\gamma$) (Table 4). The exception to this is the full model was chosen in the EG for two of the models (Table 4). Allocation of effort changed in the EG in the 1990 survey with a shift from shallow to deeper water. It is possible this shift in effort may have affected the POP catch in this survey and may explain the significant difference between years for this region. Plots of survey catch by habitat show similar trends among the surveys (Fig. 5). These observations indicate POP distribution has not changed over time.

When survey and fishery data sets were compared, the stratum-type quartile data set ($\beta\gamma$) interaction was significant, suggesting the quartile distribution by strata differs between the survey and fishery data sets. Disagreement in the spatial correspondence may be explained by the lack of survey effort in strata of high POP abundance, concentration of effort by the commercial fishery in high POP abundance areas, or the fishery data used in this study not being from POP-directed fisheries. The fishery data include non-POP-directed fisheries that may have encountered POP as bycatch. We chose to use all available data from the fishery since this provided a larger amount of information. During 1990-1994, POP quotas were reduced so there was little directed effort for POP. It would have been difficult filtering fishery data for POP-directed hauls and the majority of hauls would have been from areas of high POP abundance and would not have been representative of POP abundance throughout the GOA. Quartiles were chosen as a measure of CPUE because we wanted to compare the distribu-

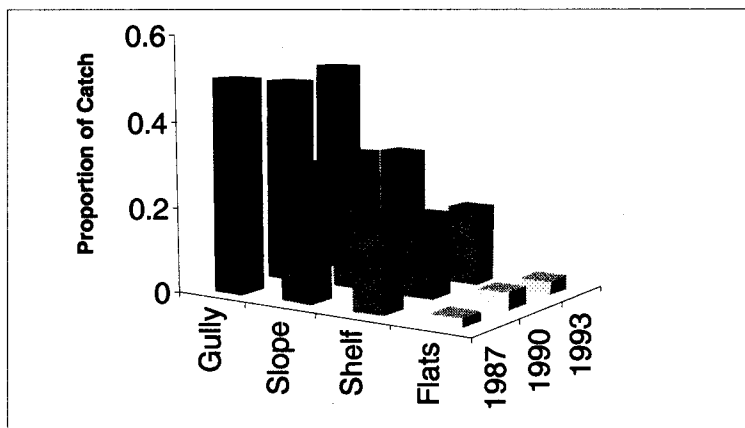


Figure 5. Proportion of POP catch by habitat type in the 1987, 1990, and 1993 Gulf of Alaska triennial trawl groundfish surveys.

tion of high versus low catches. A more exacting and rigorous approach such as linear modeling of the actual catch rates might have been chosen but the unbalanced nature of the vessel, area, habitat, and year combinations may have rendered the analysis to no more power than the simple approach chosen here. Since the data are expressed in quartiles, some of the higher CPUEs may be from areas that typically do not have high POP abundance. The full model was chosen in all three regions when only the fishery data (1-4) were analyzed, indicating that significant differences occurred in POP catch between the time periods. The large observed changes in directed effort in the fishery suggests that fishery data are influenced by other factors than the distribution of the POP population. Analysis of the fishery data for which POP was a direct target, rather than all hauls that encountered POP, may help improve this problem.

Although the stratum-type quartile data set ($\beta_{\eta\eta}$) term was significant when the survey and fishery data were compared (Table 4), the survey and commercial data show similarities. A comparison of survey and fishery catch indicates similar proportions of catch by habitat type (Tables 1, 2; Fig. 6). The GIS plots of survey catch indicate survey coverage is accurately describing POP distributions on a gulf-wide scale (Fig. 1) (Lunsford 1999). Patterns of distribution and relative abundance derived from logbook data from the U.S. West Coast groundfish fishery closely resembled those from NMFS triennial trawl research data (Fox and Starr 1996). Similar sampling designs are used in this survey and the West Coast survey (Stark and Clausen 1995, Fox and Starr 1996). This suggests survey coverage is not missing any areas of POP habitat that the commercial fishery is exploiting.

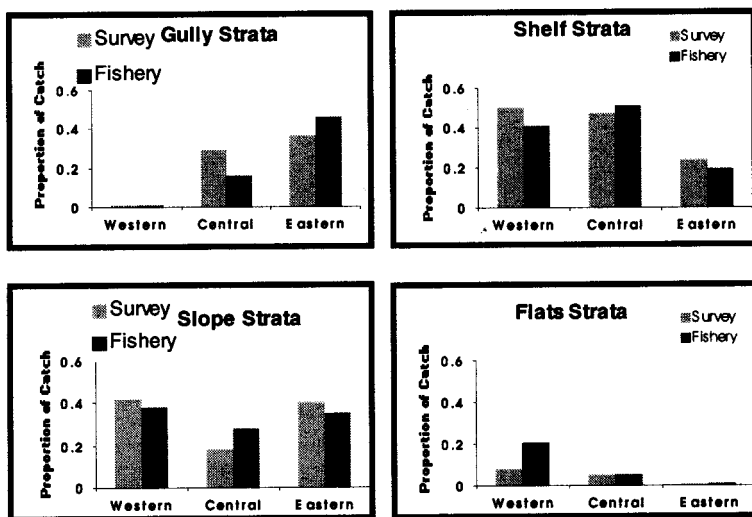


Figure 6. Proportion of POP catch by habitat and management area for the 1993 Gulf of Alaska triennial trawl groundfish survey and for the bottom trawl fishery in the Gulf of Alaska, 1993.

Survey Design Considerations

The improvement of the survey design compared to a random sampling design was 62%. The allocation component accounted for 58% of the relative efficiency while the stratification component accounted for 4%. This result indicates the stratification scheme allocates more samples into strata of high variance, but was not particularly effective in separating the sample area into strata representative of high and low POP density.

Sampling 49 different strata in a region as large as the Gulf of Alaska implies a relatively small amount of effort will be applied to at least some of the strata. If the current stratification does not reduce within-stratum variation sufficiently compared to the total variability, the loss in sample size defeats the purpose of stratifying. Gavaris and Smith (1987) found misallocation of effort in an Atlantic cod (*Gadus morhua*) survey caused losses in relative efficiency that significantly affected the precision of biomass estimates. In the EG, very few tows are allocated to the flats strata due to an allocation based on the variability of sablefish (*Anoplopoma fimbria*) abundance (Stark and Clausen 1995). The result is a focus of effort on areas that contain high amounts of POP. Analysis of the 1990 data, however, shows the EG had huge amounts of variability. Despite an increased amount of effort in strata which contained high amounts of POP, the variability did not decrease. In fact, the coefficient of variation (standard er-

ror/mean CPUE) for EG strata was 46% compared to the CG and WG which had a combined 23% coefficient of variation (Lunsford 1999).

The principle of stratification is to partition a population so units within a stratum are similar, which reduces the population to smaller independent sections representative of the population (Thompson 1992). GIS plots indicate many of the high catches occur on shelf-slope breaks and shelf-gully breaks (Lunsford 1999). These are areas where the bathymetry changes abruptly and often quickly. These breaks, or edges of the shelf, are also stratum boundaries (Fig. 7). Thus, an area of POP concentration may be split into two strata, defeating the goal of putting high catches in the same strata. Shelf strata often extend shoreward where there are few POP, again defeating the goal of putting areas of different abundance in different strata (Fig. 7). In regard to POP distribution, the 49 strata may not be optimally partitioned. However, the 49 strata are categorized by depth and geographical area which characterize habitat types and are designed to minimize variances of abundance estimates of all major groundfish species from a 1984 survey (Stark and Clausen 1995). Creating strata representative of POP density may not be beneficial to the overall objectives of the survey, which are to provide accurate estimates of all major groundfish species (Bakkala and Wakabayashi 1985). Furthermore, creating strata representative of POP density may not be possible due to the patchy distribution exhibited by POP.

The presence of high POP CPUEs in the same areas as zero catches indicates high within-stratum variability in POP distribution (Table 1). In GIS plots of survey data, a high percentage of zero catches are interspersed with differing levels of CPUE including large catches (Lunsford 1999). The same trend is seen in fishery data with low quartile CPUEs occurring close to high CPUEs (Lunsford 1999). This pattern of catch distribution indicates POP may be contagiously distributed and dispersed (Fox and Starr 1996). Kreiger (1993) found a seven-fold difference in large rockfish densities in adjacent sites. This variation may have been due to the distribution of desirable cobble habitat, which averaged 10% of the habitat at trawlable sites. A clumped distribution can be interpreted as a strong preference for a certain habitat (Krebs 1989). Habitat preference is likely on a much smaller scale than observed here. Strong frontal areas caused by local bathymetry and tidal currents (Scott 1995) or specific cobble substrate (Kreiger 1993) may be important POP habitats.

Large variances associated with survey estimates may be due to randomly sampling a species which exhibits a highly contagious distribution (Ito 1987). Everson et al. (1995) found bottom trawl surveys for mackerel icefish (*Champsocephalus gunnari*) were impractical due to the patchy distribution of the resource. Increased effort did not improve the precision of biomass estimates for yellowtail rockfish (*Sebastes flavidus*), a species which is found in small clustered schools (Weinberg et al. 1994). Increasing sampling effort or restratifying the current design to reduce sample variability would likely not be successful if POP are distributed on such a fine scale.

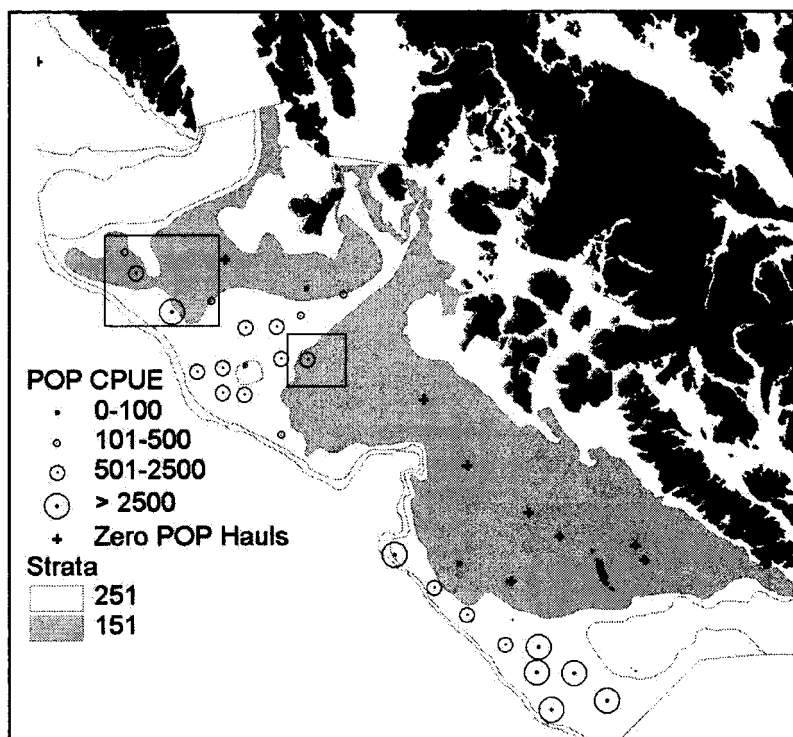


Figure 7. NMFS survey hauls from the 1993 Gulf of Alaska triennial trawl ground-fish survey. Hauls enclosed in square boxes represent large catches recorded in stratum 151 (shaded area) near stratum boundary but are more representative of catches in stratum 251. The stratum boundary represents the 200-m contour that is associated with the continental shelf break.

Alternative sampling designs exist which may be more appropriate for sampling aggregated rockfish populations. Adaptive cluster sampling, a technique not yet widely used in fisheries, can be effective for sampling species found in localized concentrations (Thompson and Seber 1996). In August 1998, an adaptive sampling experiment was conducted to test adaptive sampling for POP (Clausen et al. 1999). Results indicated the spatial distribution of POP has both fine-scale and habitat-scale patterns and modest gains in the precision of abundance estimates were observed using adaptive cluster sampling (Hanselman et al. 2000). Ongoing work is testing the feasibility of incorporating adaptive sampling as a practical survey design for sampling slope rockfish in the GOA.

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Spatial Inferences from Adaptive Cluster Sampling of Gulf of Alaska Rockfish

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Abstract

National Marine Fisheries Service trawl surveys result in more variable biomass estimates for long-lived Gulf of Alaska rockfish than researchers expect. Adaptive cluster sampling (ACS), a technique not yet widely used in fisheries studies, may provide improved estimates for aggregated rockfish populations. In August of 1998, the first of two sampling cruises tested ACS for rockfish, specifically Pacific ocean perch (POP, *Sebastes alutus*) and shortraker and rougheye rockfish (SR/RE, *Sebastes borealis*, *Sebastes aleutianus*). Two study areas east of Kodiak Island were selected for the experiment. The POP area was subdivided into four strata and the SR/RE into two strata based on habitat and geographic location. In each stratum, simple random sampling was conducted initially followed by ACS around the top one to three stations from the random sample. A stopping rule prevented the sampling from continuing indefinitely. ACS resulted in more precise estimates for POP compared to the initial random sample, but not with equal sample sizes. ACS combined with stratification provided the best estimates for POP, suggesting that the spatial distribution has both fine-scale and habitat-scale patterns. Results suggested that ACS worked better for POP than for SR/RE. Variogram analysis suggested that the distribution of POP was more aggregated than SR/RE, but not as aggregated as we expected. Both species were highly restricted to specific depths. The highest POP catches occurred during the early morning hours. While this experiment did not resolve whether ACS should be used for rockfish surveys, further investigation of this approach should continue.

Introduction

The slope rockfish assemblage in the Gulf of Alaska is a group of species including Pacific ocean perch (*Sebastes alutus*), rougheye rockfish (*Sebastes aleutianus*), shortraker rockfish (*Sebastes borealis*), and several others that are found on the slope of the continental shelf in waters deeper than 150 m (Heifetz et al. 1994). Pacific ocean perch (POP) is the dominant and most commercially important rockfish species in the Gulf of Alaska. A foreign trawl fishery on this species started in the early 1960s with a peak catch of about 350,000 t in 1965. Large catches in the 1960s led to a major stock decline that has only recently been reversed. The fishery has been a domestic fishery since 1985 and managed under conservative catch limits.

Gulf-wide triennial surveys have been conducted by NMFS since 1984 to assess groundfish stocks. Current assessment of POP in the Gulf of Alaska is controversial because of uncertainty associated with survey estimates (Table 1). A stock-synthesis model is used to assimilate this information and to provide estimates of population parameters (Heifetz et al. 1994, 1995, 1996). This model describes the population dynamics of an age-and-length-structured population (Quinn and Deriso 1999). Heifetz et al. (1994) showed that survey age composition is in accord with fishery catch-per-unit-of-effort (CPUE) data, fishery catch composition, and survey catch composition, but survey biomass is not. Survey biomass fluctuates too much over time for a long-lived species such as POP and the fluctuations are greater than can be explained by survey measurement error alone. In the stock synthesis model, survey biomass is assigned low weight in comparison to other data sources. The result is that the trend in estimated biomass approximated the trend in survey biomass, but that survey biomass in any one year can differ from estimated biomass by a significant amount.

Other concerns expressed about the trawl surveys (Rockfish Working Group 1991; ADF&G memo included in Heifetz et al. 1995) include: (1) The gulf-wide survey is designed to provide information about all groundfish species, and survey effort is fairly uniform across the gulf. Sampling effort is allocated to various depth and area strata to minimize the variance of total groundfish biomass. However, this design may not be appropriate for assessing POP and other slope rockfish, because their distributions may not be well sampled by this uniform design. (2) Unlike many species in the GOA, the distribution of POP is highly clustered, so that survey estimates of abundance are highly variable.

An alternative design that may improve the design for rockfish sampling is adaptive cluster sampling (ACS). A recent book by Thompson and Seber (1996) provides an in-depth treatment of this subject. To apply ACS to rockfish, additional samples need to be collected in areas of relatively high abundance of POP. The efficiency of ACS can often exceed that of random sampling, particularly for species found in localized concentrations.

Little work has been done on applying ACS methods to fish populations. One application is a restricted adaptive design on larval fish in

Table 1. Pacific ocean perch survey biomass estimates from 1984 to 1999 from the National Marine Fisheries Service triennial survey.

Year	Biomass (t)	95% confidence interval
1984	232,694	101,550 - 363,838
1987	214,827	125,499 - 304,155
1990	138,003	70,993 - 205,013
1993	460,755	255,253 - 665,987
1996	778,663	358,923 - 1,198,403
1999	726,785	0 - 1,156,111

California (Lo et al. 1997), which resulted in a great improvement in precision of the survey. The tradeoff is that there was an unknown amount of bias induced from the use of a stopping rule.

A field project in 1996 collected data for evaluating ACS designs for Pacific ocean perch (Clausen and Heifetz 1996). A simulated population was constructed using these data, and ACS reduced the estimated variance up to 50%, suggesting that it would be effective for rockfish populations (Quinn and Haldorson 1997).

Based on this work, we conducted an ACS experiment in 1998 in a small area of the Gulf of Alaska (Fig.1). Our main hypothesis was that ACS would be more effective in providing precise estimates of POP biomass than would a simple random survey design. A secondary hypothesis was that assessment of Pacific ocean perch abundance would benefit more from an ACS design than would shortraker and rougheye rockfish, because we believed Pacific ocean perch to be more clustered in their distribution than shortraker and rougheye rockfish. In this paper, we summarize the results from this experiment and evaluate these two hypotheses.

An important consideration of whether an ACS design is worthwhile is how the target species are distributed spatially and temporally. The design used in this study had stopping rules, set sampling distances, and depth strata imposed somewhat arbitrarily because the interaction between the spatial distributions of rockfish and ACS had not been looked at in much detail. This paper analyzes the spatial results in detail to determine if the design took advantage of the spatial distribution of POP and SR/RE and to determine appropriate methods for implementing adaptive cluster sampling on a larger scale. We also examined the diurnal pattern of survey catches to investigate if the temporal distribution could affect sampling.

Experimental Design

In the basic ACS method, one takes a simple random sample (SRS) of size n ; if y_i (weight of a particular species caught in tow i) $> c$ (a criterion value or

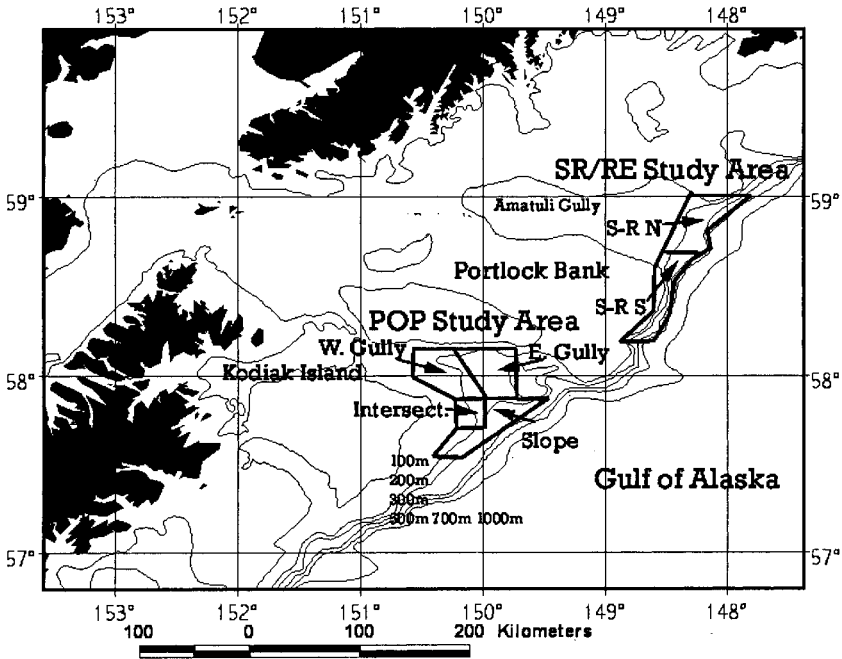


Figure 1. Map of sampling areas in the Gulf of Alaska on the Unimak Enterprise 98-01 adaptive sampling cruise.

threshold catch), then neighborhood units are added (e.g., units above, below, left, and right in a cross pattern, Fig. 2) to the sample. If any neighborhood cell has $y_i > c$, then its neighborhood is added. If the neighborhood cell has $y_i < c$, sampling stops and this cell is called an edge unit. This process continues until no units are added or until the boundary of the area is reached (Thompson and Seber 1996:93). Neighborhoods can be defined in any general way. The only condition is that if unit i is in the neighborhood of j , then unit j is in the neighborhood of i . Unbiased estimation depends on the inclusion of every unit in the neighborhood of $y_i > c$. Biased estimators result when logistics cause ACS to be curtailed before the network is complete.

If prior knowledge about the population is insufficient to select a suitable criterion value to invoke additional sampling, the criterion value can be determined with order statistics (Thompson and Seber 1996:160-175). An initial SRS of size n is taken, producing an ordered list of sample values

$$y_{(1)} \leq y_{(2)} \leq \dots \leq y_{(n-r)} \leq y_{(n-r+1)} \leq \dots \leq y_{(n)},$$

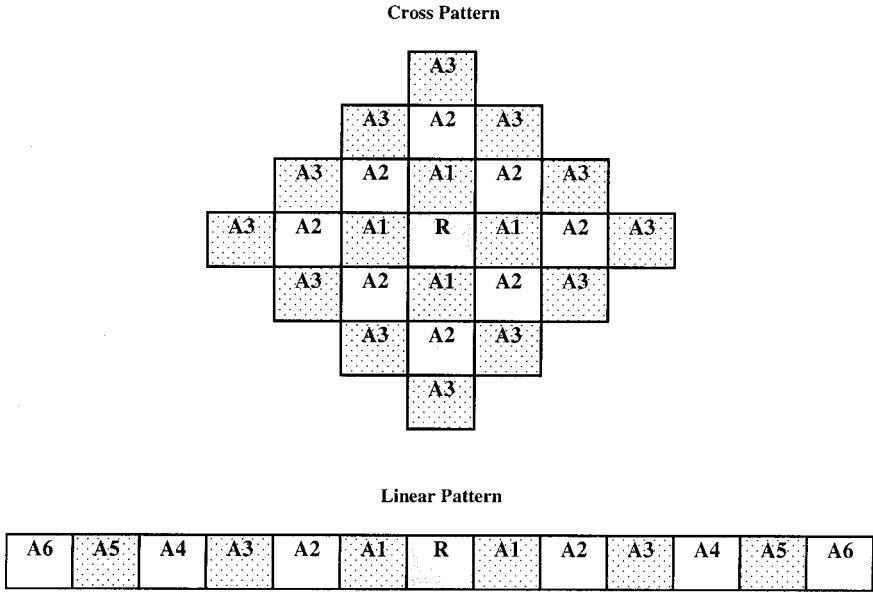


Figure 2. Maximum possible number of adaptive hauls for the cross (stopping rule of 3) and linear (stopping rule of 6) patterns with the imposition of a stopping rule. The initial random station is denoted as "R," and the adaptive stations as "A" and their respective level number.

where $y_{(1)}$ is the minimum observation and $y_{(n)}$ is the maximum observation. An adaptive sampling phase is then carried out in the neighborhoods of the top r sample units whose y -values are greater than the criterion value $c = y_{(n-r)}$. The adaptive sampling phase forms r clusters consisting of sampling units that exceed the criterion value c and boundary units called edge units that do not exceed c . A network is further defined to be a cluster with its edge units removed.

In August 1998, we carried out ACS in six strata near the Portlock Bank in the Gulf of Alaska (Fig. 1), four for POP and two for SR/RE. These strata correspond to different habitat types and presumed areas of different density. Each stratum was sampled initially with 12-15 randomly located stations (trawl hauls), in which each haul consisted of 15 minutes of towing on the bottom covering a tow length of about 1.7 km (0.9 nmi). In each stratum, after random sampling was completed, the experiment switched to an adaptive sampling phase. In this mode, a series of additional hauls in each stratum was made systematically around a selected number (r) of the random stations with the highest CPUE of the target species. For the shorttraker-rougheye study area, the target species CPUE was for shorttraker

and rougheye rockfish combined. The value of r was initially set to 3, so that the fourth largest CPUE became the criterion for adaptive sampling; this means that ACS was conducted around the three largest catches with sampling continuing as long as neighborhood catches exceeded the fourth largest catch in the initial sample. In the west gully, east gully, and intersection strata, a cross pattern of four tows around each selected high-CPUE station was used for the adaptive sampling (Fig. 2). For these strata, the bottom topography required that all tows be made in a general east-west direction. Consequently, the cross pattern consisted of adaptive tows on the eastern and western sides of each selected random tow, and tows to the north and south. In the slope and shortraker-rougheye strata, the north-south adaptive tows were omitted, resulting in a linear pattern in which adaptive tows were made only east and west of the initial random station (Fig. 2). This linear pattern was necessary because of the steeply sloping bottom in these strata. A distance of 0.17 km (0.1 nmi) was planned between all adaptive tows and the track of the initial random station to avoid depletion effects on the catches.

A major problem in applying adaptive sampling is that sampling may continue indefinitely due to a low criterion value. To limit the amount of adaptive sampling, an arbitrary stopping rule of S levels was imposed. For those strata where the cross pattern of adaptive sampling was used, the stopping rule was $S = 3$ levels, allowing for a maximum of 24 adaptive tows around each high-CPUE random station (Fig. 2). For the strata with the linear pattern of adaptive sampling, the stopping rule was $S = 6$ levels, for a maximum of 12 adaptive tows around each high-CPUE random station. In addition, no adaptive sampling extended beyond a stratum boundary. The result of adaptive sampling around each high-CPUE station was a network of tows that extended over and, in some cases, delineated the geographic boundaries of a rockfish aggregation. Specific field methods are described in detail in Clausen et al. (1999).

Statistical Methods

Adaptive Sampling

Statistical analysis of the results was based on ACS with order statistics (Thompson and Seber 1996). First, abundance for the targeted rockfish species in each stratum was estimated from the initial random stations. Then, two ACS estimators of abundance, a Hansen-Hurwitz-like estimator (HH) and a Horvitz-Thompson-like estimator (HT), were calculated. Estimates of standard errors (S.E.) and coefficients of variation of the mean ($C.V.s$, $S.E. / \hat{\mu}$) were computed for each estimator. The HH estimator essentially replaces stations around which adaptive sampling occurred with the mean of the network of adaptive tows that exceeded the criterion CPUE value. The HT estimator is based on the probability of sampling a network given the initial stations sampled and involves the number of distinct net-

works sampled (in contrast to the HH estimator based on the initial stations). The HT estimator is often more efficient than other estimators in simulation studies (Christman 1997, Brown and Manley 1998, Z. Su and T.J. Quinn II, University of Alaska Fairbanks, Juneau, Alaska, pers. comm.). Rao-Blackwell improvements of these estimators were also computed, but showed no substantial difference from the standard estimators, so they are excluded here. Because subsampling was necessary to obtain estimates of rockfish catches for each haul, the standard estimation formulae were adapted to include within-haul variation (Quinn et al. 1999).

The unbiased estimator of the mean for SRS is defined as:

$$\hat{\mu}_{\text{SRS}} = \frac{1}{n} \sum_{i=1}^n y_i, \quad (1)$$

where y_i is the CPUE value for sample unit i in the initial sample.

An unbiased estimator of the mean, the HH estimator, is defined for ACS with order statistics in Thompson and Seber (1996):

$$\hat{\mu}_{\text{HH}} = \frac{1}{n} \sum_{i=1}^n w_i = \frac{1}{n} \sum_{i=1}^n \frac{y_i^*}{x_i}, \quad (2)$$

where w_i and y_i^* are the mean and total of the x_i observations in the network that intersect sample unit i , respectively. The variance estimate used is the biased, but more practical estimator $\text{var}(\hat{\mu}_{\text{HH}})$. Thompson and Seber (1996) state this may be better because it is simpler and is invariably nonnegative.

The HT estimator of the mean (Thompson 1990) takes the form

$$\hat{\mu}_{\text{HT}} = \frac{1}{N} \sum_{k=1}^{\kappa} \frac{y_k^*}{\alpha_k}, \quad (3)$$

where y_k^* is the sum of the y -values for the k th network, κ is the number of distinct networks in a sample, and α_k is the probability that network k is included in the sample. If there are x_k units in the k th network, then

$$\alpha_k = 1 - \frac{\binom{N - x_k}{n}}{\binom{N}{n}}. \quad (4)$$

This estimator is design unbiased in ACS for a population with distinct networks defined by a constant criterion. When order statistics are used, the criterion value changes with each sample, so the estimator is biased

and is considered inappropriate (Thompson and Seber 1996) but is presented here for comparative purposes.

When a stopping rule is used, the theoretical basis for the ACS design changes. This rule may result in incomplete networks that overlap and are not fixed relative to a specified criterion. In contrast, the non-stopping-rule scheme has disjoint networks that form a unique partition of the population for a specified criterion. This partitioning is the theoretical basis for the unbiasedness of $\hat{\mu}_{HH}$. Thus with a stopping rule, not only is $\hat{\mu}_{HT}$ biased, but $\hat{\mu}_{HH}$ is too.

A recent simulation paper (Z. Su and T.J. Quinn II, University of Alaska Fairbanks, Juneau, Alaska, pers. comm.) estimated the bias induced by each of these estimators using order statistics and stopping rules. Factors examined were the initial sample size, order statistic r , and the aggregation of the population. For the HT estimator without a stopping rule under ACS, the bias is always positive but small (<10%). Applying a stopping rule of 3 to the HH estimator resulted in a maximum positive bias of 17% for a highly aggregated population but was lower for an r -value of less than 4 (as in this survey). When the stopping rule is applied to the HT estimator, its maximum bias is approximately +12% but can be slightly negative at high r -values. From these simulations, a tradeoff of relatively small bias for a gain in precision may be acceptable.

Two hypotheses were evaluated: (1) ACS would be more effective in providing precise estimates of POP biomass than would a SRS design. (2) Assessment of POP abundance would benefit more from an ACS design than would SR/RE, because POP are believed to be more clustered in their distribution than SR/RE. SRS estimates were obtained from the initial random stations and standard errors were calculated for the initial sample size (n) and for the same sample size used in the adaptive estimates (v'). These hypotheses are assessed by comparing the standard errors and coefficients of variation of ACS to SRS. Substantial reductions in these statistics using ACS compared to SRS for POP would support the first hypothesis, whereas no gains in precision using ACS compared to SRS for SR/RE would support the second hypothesis. This comparison is qualitative because relevant significance tests are unavailable and the two methods are different in terms of logistical efficiency.

Stratification

We combined the intersection and the two gully strata, all sampled with a cross pattern, into a single area, in order to explore the effects of stratification and adaptive sampling on the precision of the estimates. The analysis was also done with the slope stratum included, yielding similar results, but since the sampling pattern was different, we omitted it here. We first treated the data from the initial random stations for the combined data as a simple random sample. This is not appropriate for proper estimation, because the allocation of random samples is disproportionate to the areas of each stratum. We did so only to illustrate the changes in precision that

could occur under different designs. We then analyzed the combined area as a stratified random sample. Finally, we included the adaptive stations under both the simple and stratified designs. The combined area was analyzed as if the top five stations were sampled adaptively, with the criterion value being the sixth highest of 496 kg/km. The total number of random stations was 42, with 51 additional adaptive stations. The random combined samples are also examined at the ν' level.

Spatial Analysis

Analyzing spatial structure is often done with correlograms or variograms. Variograms are a generalized version of correlograms and are defined even when correlograms are not (Cressie 1991). Variograms were constructed as defined in Cressie and Hawkins (1980) as follows:

$$2\bar{\gamma}(h) = \left[\frac{1}{|N(h)|} \sum_{i,j \in N(h)} |Z(s_i) - Z(s_j)|^{0.5} \right]^4 / [0.457 + 0.494 / |N(h)|]$$

where $|N(h)|$ =number of distinct pairs of points $[Z(s_i), Z(s_j)]$ lagged by the distance vector h . This method was chosen because they are robust to contamination by outliers and because some of the top POP catches cause anomalous variogram behavior that can be resolved by the robust estimator. The point estimates were taken from the latitude and longitude of the halfway point of each tow and converted to kilometers apart with a Mercator conversion. The variograms were constrained for maximum distances to isolate structured variance and all bin sizes were held below 20 to smooth out the data. The fitted lines are variable span smoothers as defined by Friedman (1984). The general shape of the variogram is described by the nugget, range, and sill (Fig. 3). The nugget is the point at which the variogram is extrapolated to the y-intercept and represents the unstructured variance (variance not described by spatial scale). The sill is where the tangent crosses the smoothed line, which signifies the extent of the structured variance (the variance described by spatial scale). The range is the distance between the origin and the sill. Figure 3 shows what the variogram looks like for two simulated populations: one clustered and one unclustered. The clustered population exhibits considerable structured variance, while the unclustered population shows mainly unstructured variance.

The relationship between CPUE and depth were analyzed qualitatively for both POP and SR/RE in order to determine whether the sampling covered the likely range of these species. Adaptive samples for each species were removed to avoid clusters in a certain depth. Fourth-order polynomial functions were fitted to the data to aid this determination.

Temporal Analysis

A day versus night comparison for POP was made in order to determine if diurnal catch rates might affect adaptive sampling. The time-of-day catch

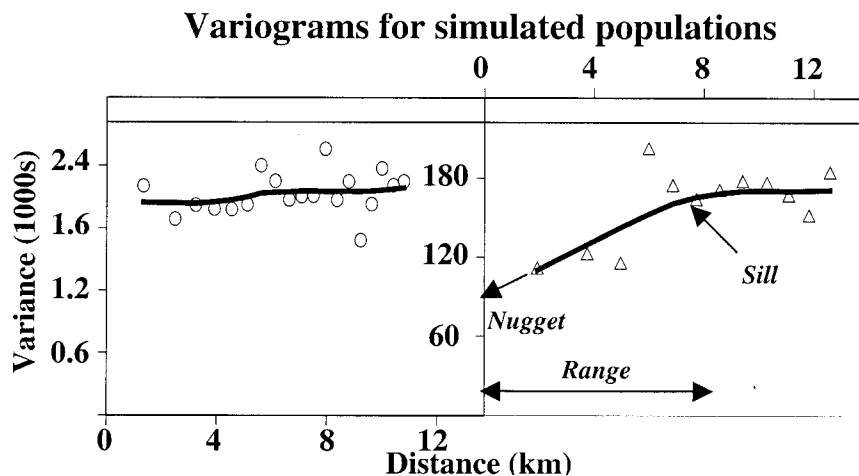


Figure 3. Variograms computed for catches from two simulated populations, one clustered, one unclustered, with the robust estimator from Cressie and Hawkins (1980) for pairwise variance compared to distance. Conditioned with an arbitrary maximum distance of 13 km.

data were standardized to values between 0 and 1 over a range of 24 hours beginning at 10 pm (corresponding to darkness for the area and time of year). Because no obvious relationship was discernable, a categorical approach with four equal time intervals was constructed. A Kruskal-Wallis rank test (Freund and Waldpole 1987) was used to compare survey catches among the four categories.

Results

Adaptive Sampling

A total of 190 hauls was completed during the cruise. Of these, four were test tows, 81 were random stations, 103 were adaptive stations, and 2 were invalid. Implementation of the ACS design was straightforward. All the random and adaptive stations were trawled successfully; no station was skipped because of untrawlable bottom. Hang-ups or net damage, however, sometimes occurred, especially in the steep topography of the shorttraker-rougheye study area.

The predominant species caught during the cruise was Pacific ocean perch. Total catches in individual hauls ranged up to 38 t. For further details about the cruise and aspects of data collection and editing and for the raw data, see Clausen et al. (1999).

Table 2. Summary information on stations fished in each stratum during the 1998 adaptive sampling experiment for rockfish.

Stratum and network	A_i	N_i	n	r	$y > c$	v	v'	Network units	Edge units
POP study area									
Intersection ^a	346	9,800	15	3	245	66	59	44	8
Adap. net. 1								17	1
Adap. net. 2								14	3
Adap. net. 3								13	4
West gully	607	17,200	15	2	214	26	16	1	10
Adap. net. 1								1	6
Adap. net. 2								0	4
East gully	648	18,400	12	1	496	24	18	6	6
Adap. net. 1									6
Slope	596	16,900	15	3	235	29	23	8	6
Adap. net. 1								3	2
Adap. net. 2								2	2
Adap. net. 3								3	2
Total	2,917	62,300	57			135	116	59	30
SR/RE Study Area									
North	180	5,100	12	2	1,146	19	17	5	2
Adap. net. 1								3	1
Adap. net. 2								2	1
South	270	7,700	12	2	479	17	13	1	4
Adap. net. 1								0	2
Adap. net. 2								1	2
Total	450	12,800	24			36	30	6	6

^a One of the initial random stations was also an edge unit. The three clusters merged to form a single network.

Notation

A_i = area of stratum (km^2).

N_i = number of possible samples.

n = number of initial random stations.

r = number of high-CPUE stations around which adaptive sampling occurred.

$y > c$ = the criterion CPUE value (kg/km) used to determine whether adaptive sampling continued beyond the first level.

v = total number of stations fished (random + adaptive).

v' = number of stations used in the computation of the adaptive estimators (random + adaptive – edge units).

Network units = number of stations in network with CPUE > criterion (excluding initial random stations meeting the criterion).

Edge units = number of adaptive stations in network with CPUE < criterion (including those that were also initial random stations).

Summary information about the random and adaptive stations in each stratum is given in Table 2. After sampling in the slope and slope-gully intersection strata was completed, time constraints caused us to reduce the sampling in the remaining strata. Specifically, the number of random stations around which adaptive sampling occurred (r) had to be lowered from three in the slope and slope-gully intersection strata to only one or two in the remaining strata. The greatest sampling effort was in the slope-gully intersection stratum, where 51 total adaptive stations were fished because large concentrations of Pacific ocean perch were encountered in that area. Criterion values of CPUE (c), for determining whether additional adaptive sampling would take place around adaptive hauls, ranged from 214 kg/km in the west gully stratum to 1,146 kg/km in the shortraker-rougheye north stratum. The stopping rule was invoked 5 of 12 times.

Statistical results of the experiment by stratum are summarized for simple random sampling and the Hansen-Hurwitz and Horvitz-Thompson adaptive estimators (Table 3). The most notable differences occurred in the intersection stratum for POP and the north stratum for SR/RE. In general, the ACS results indicate a similar or decreased standard error for POP and an increased standard error for SR/RE when compared to the initial sample size for SRS. When using the increased sample size (v') in the SRS variance estimates, the ACS standard error was substantially lower than SRS only for the HT estimator in the intersection stratum. In the remainder of the results using v' , the SRS estimates and ACS estimates shared similar precision. For a detailed presentation of the results for each stratum see Hanselman (2000).

Stratification

The intersection and gully areas were combined to produce an overall density estimate using their areas (Table 2) to weight each stratum. Stratification and ACS had a similar and synergistic effect on the precision of the estimation results (Table 4). The unstratified SRS estimator has the highest S.E., while the unstratified adaptive estimators and the area-weighted stratified estimator show similar reductions in S.E. The stratified adaptive sampling estimators showed the largest reduction in S.E. The same qualitative results occur with C.V. except the magnitude of effect is smaller. If the larger sample size (v') is used, the S.E. for stratified random sampling (66) is only slightly higher than the S.E. for the stratified adaptive HT estimate (64), which was the lowest of all estimates. A surprising result is the reduction in the point estimate with increasing stratification and/or adaptive sampling. Theoretically, all estimates should be similar (although adaptive estimators may have some small bias), and the large SEs for the estimates do indicate that the differences are not statistically significant. Stratification produced a lower estimate because the highest density stratum, the intersection, is sampled more intensively relative to its area than the other two strata. Combining all strata into one adaptive sample also reduces the

Table 3. Rockfish density estimates (kg/km) and associated statistics for each stratum in the adaptive sampling experiment conducted during F/V Unimak cruise 98-01.

Stratum	Statistic	SRS(<i>n</i>)	SRS(<i>v'</i>)	HH	HT
POP study area					
Intersection	Sample size	15	59	59	59
	Abundance	789		600	251
	S.E.	444	224	276	173
	C.V.	56.3%	28.3%	46.0%	68.8%
West gully	Sample size	15	16	16	16
	Abundance	160		157	157
	S.E.	72	70	69	69
	C.V.	44.8%	43.4%	43.8%	43.7%
East gully	Sample size	12	18	18	18
	Abundance	191		185	185
	S.E.	115	94	109	109
	C.V.	60.1%	49.2%	59.0%	58.9%
Slope	Sample size	15	23	23	23
	Abundance	228		227	227
	S.E.	90	72	80	80
	C.V.	39.4%	31.8%	35.5%	35.4%
SR/RE study area					
North	Sample size	12	17	17	17
	Abundance	743		1,017	1,018
	S.E.	158	133	320	320
	C.V.	21.3%	17.9%	31.4%	31.4%
South	Sample size	12	13	13	13
	Abundance	279		279	279
	S.E.	69	66	70	70
	C.V.	24.9%	23.8%	24.9%	24.9%

Results from three methods of estimation are shown: SRS using *n* (number of initial stations) and *v'* (equivalent number of samples used in adaptive estimates), the Hansen-Hurwitz adaptive estimator, and the Horvitz-Thompson adaptive estimator. Data are for Pacific ocean perch (POP) only in the POP study area, and for combined shorttraker rockfish (SR) and rougheye rockfish (RE) in the SR/RE study area.

Table 4. Comparison of stratified sampling versus whole area estimates of Pacific ocean perch mean density for the combined intersection and gully areas.

Whole area SRS		
$\mu = 394$		
S.E. = 167 (115)		
C.V. = 42% (29%)		
Stratified SRS	Whole area adaptive	
	$\mu(\text{HH}) = 341$	$\mu(\text{HT}) = 277$
	S.E. = 120	S.E. = 105
	C.V. = 35%	C.V. = 38%
Stratified adaptive		
$\mu(\text{HH}) = 264$		$\mu(\text{HT}) = 188$
S.E. = 79		S.E. = 64
C.V. = 30%		C.V. = 34%

The stratified estimates are weighted by area. Since the slope area was adaptively sampled linearly, it is not included. SRS values are calculated with $n = 42$. Parenthetical values are SRS estimates calculated with $v' = 93$.

mean estimate, because the adaptive networks in five of seven cases tend to average down the initial random sample. Thus, in this case both stratification and adaptive sampling act to reduce the effect of a large catch on the overall estimation.

Spatial Results

Figure 4 shows conditioned variograms with fitted lines. In the SR/RE strata, it can be seen that the variability is unrelated to distance. The north stratum has a large nugget of the order of $\sim 10^7$ (where the curve intercepts the y -axis), and little evidence of any sill. The south stratum has a much smaller nugget ($\sim 10^5$), and no apparent sill, representing unstructured variance. Unlike the SR/RE strata, the POP surveys were conducted over several different habitat types. In the slope and two gully strata, there is very little structured variance present. However, the intersection stratum shows some structure in the variance. While the unstructured variance is still large, the variogram shows increasing structured variance out to a sill at ~ 3.8 km, with an excellent fit to the data. A caveat would be that with six variograms, one might randomly show something interesting. Figure 5 shows variograms of POP and SR rockfish for the entire Gulf of Alaska, taken from NMFS triennial survey data. The SR variogram shows no structured variance while the POP variogram shows a variogram similar to the simulated clustered variogram with mainly structured variance.

The catches of both POP and SR/RE vary considerably with depth. Figure 6 shows that POP catches are maximized at a depth of ~ 200 m, exclud-

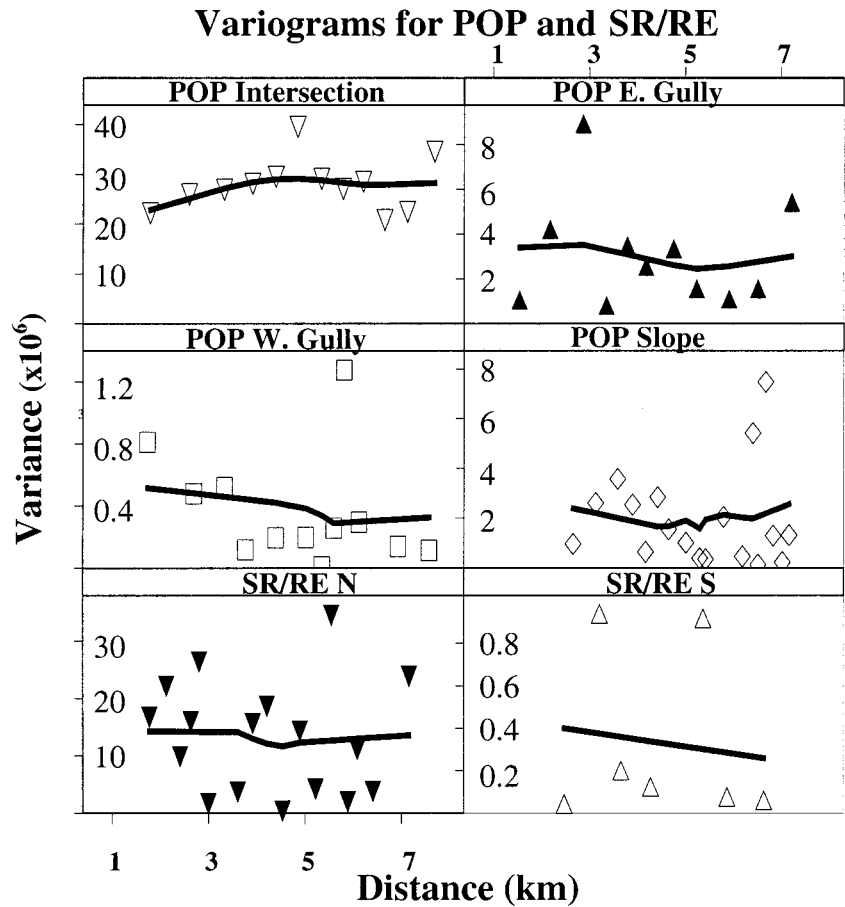


Figure 4. Variograms of 1998 POP and SR/RE strata from the Unimak Enterprise 98-01 sampling cruise computed with the robust estimator from Cressie and Hawkins (1980) for pairwise variance compared to distance. Conditioned with a maximum distance of 7 km.

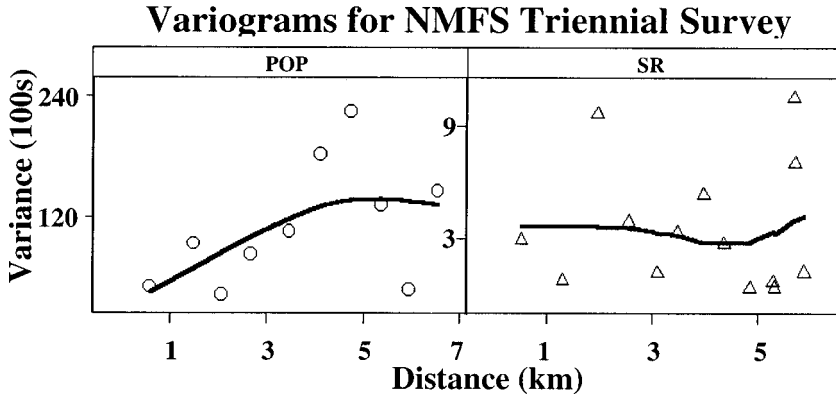


Figure 5. Variograms computed for NMFS triennial survey data for POP and SR catches with robust estimator from Cressie and Hawkins (1980) for pairwise variance compared to distance. Conditioned with a maximum distance of 7 km.

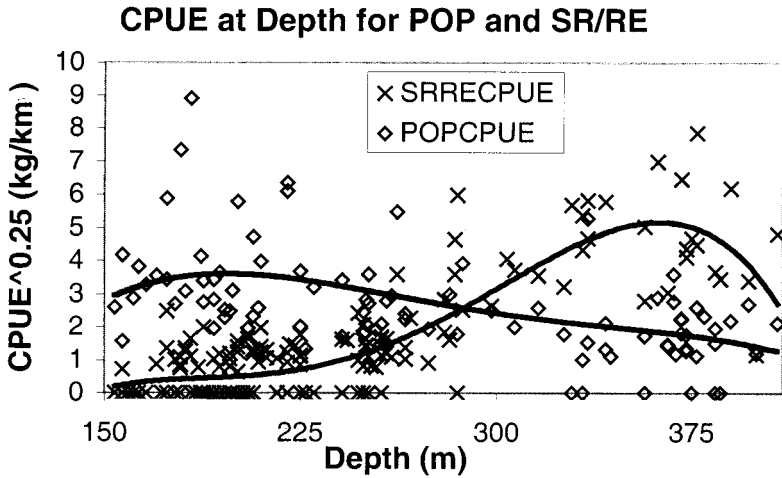


Figure 6. Catch per unit of effort $CPUE^{0.25}$ versus depth for 1998 Unimak Enterprise 98-01 POP and SR/RE stations. No tows occurred below 150 m depth or above 450 m depth. Triangles represent SR/RE and circles represent POP. Lines are fitted with fourth-order polynomials.

ing an exceptional catch of ~25,000 kg/km at 304 m (not shown on figure, to keep reasonable scale). Sizeable catches (>1,500 kg/km) are almost exclusively found between 180 and 250 m, with only three exceptions in deeper depths. SR/RE catches are more restricted to specific depths than POP. SR/RE catches maximize at a depth of ~370 m. The four largest catches are within in a tight range between 365 m and 380 m. The catch distribution drops off rapidly at less than 300 m and greater than 400 m. The polynomial fits show that POP has a larger range of habitat than the SR/RE. The shapes of the fits also suggest that both species were sampled in their primary depth intervals.

Temporal Results

Consensus among commercial fishing captains is that day catches far exceed night catches. Diel vertical migrations of POP have been documented in the past (Balsiger et al. 1985). Changes in light and feeding behavior can cause POP to ascend to 40 m off bottom (Moiseev and Paraketsov 1961). Since there was no obvious graphical relationship (Fig. 7), the data were broken up into the four time intervals based on the daylight for the area and time of year:

Time	Mean	S.E.
10pm - 4am	358.2	110.9
4am - 10am	1385.9	362.5
10am - 4pm	755.4	244.0
4pm - 10pm	836.9	172.6

The nonparametric Kruskal-Wallis test indicates that there are larger catches in the morning period ($P < 0.04$). Additionally, most of the huge catches (>2,500 kg/km) were collected during the day. This difference should have little effect on the ACS procedure because the criterion will usually be much smaller than these exceptional catches (temporal change might lower them, but they will still exceed the criterion), but could affect the estimates themselves.

Discussion

This application of ACS was straightforward, had no logistical difficulties, and allowed the survey to be changed as the cruise progressed. When compared to SRS using initial sample size, ACS increased precision in all four strata.

In order to test the first hypothesis that ACS of POP is better than SRS, some adjustment for sample size is needed. ACS, by definition, adds more samples to the initial random sample, which by design will lower the S.E. Thompson and Seber (1996) use v (the total adaptive sample size, includ-

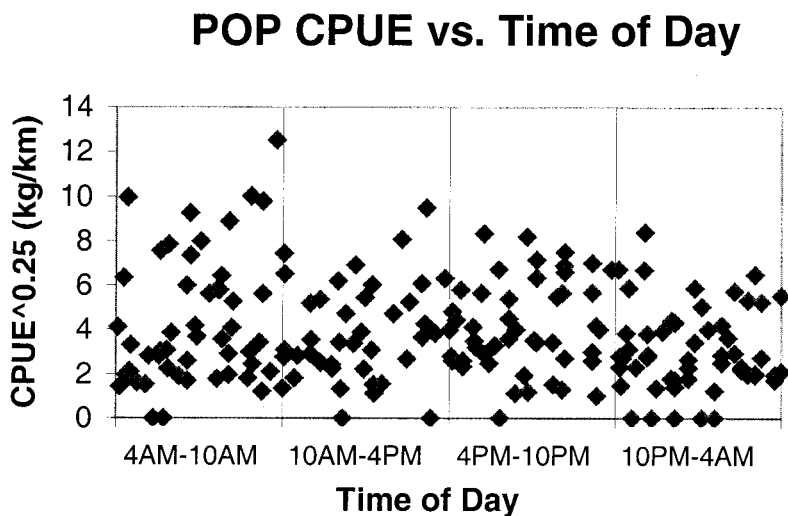


Figure 7. Unimak Enterprise cruise 98-01 Pacific ocean perch $CPUE^{0.25}$ versus time of day.

ing edge units) to compare SRS with ACS. For a fairer theoretical comparison, it is better to compare the standard errors of the estimators using the same number of samples used in the estimates (v' , edge units are not used in the estimate). In this way, we predict the SE of SRS if we had actually taken the same number of samples in a random fashion. When the SRS S.E.s are calculated using v' , they are usually similar to or lower than the ACS S.E.s (Table 3).

To fully evaluate the first hypothesis that ACS is more efficient than SRS, the issue of practical efficiency in terms of cost should be considered. Of practical interest is how precise are ACS estimates compared with a conventional SRS design for the same total cost. The expected number of stations sampled and travel time between survey stations are important factors when considering costs (Thompson and Seber 1996). With ACS, there is less travel time and, therefore, lower costs per sampling station because sampling is within a network of nearby units. ACS allowed us to devote much more time to trawling and sample more stations than had we done only SRS. We did not precisely measure cost variables in this study but intend to in the future. Therefore, the hypothesis that ACS is better than SRS for these rockfish remains unresolved by the field results.

The POP study area was divided into four strata representing different habitat types in order to see how adaptive sampling worked with different densities and clusters of fish. However, such stratification increases the sampling efficiency of simple random sampling prior to adaptive sampling,

because stratification usually improves estimation of mean density. Adaptive sampling reduces the S.E. equivalently to that of stratification of the initial samples, but stratified random sampling using the v' sample size is more effective than ACS alone (Table 4). The combination of the two methods result in a lower S.E. than ACS alone, suggesting that the adaptive sampling is accounting for small-scale variation within networks, while stratification is accounting for large-scale variation related to habitat. In addition, adaptive sampling over a broader area improves the precision of the estimate. The comparison between the stratified and unstratified estimators shows us that adaptive sampling does take advantage of small-scale spatial structure, but astute stratification—if habitat knowledge is available—can lead to more significant gains than adaptive sampling alone. This could also mean that adaptive sampling would be appropriate when little is known about habitat structure before the survey. Therefore, future experimentation would need to account for the interaction of stratification and adaptive sampling.

The intersection stratum is where clusters of fish were encountered and adaptive sampling should have worked best. Indeed, the decrease in S.E. and C.V. for the Hansen-Hurwitz estimate compared to simple random sampling was largest here. The Horvitz-Thompson estimate and its S.E. were even lower, but its C.V. was higher because of the great reduction in estimated abundance. The differences between the HH and HT estimators are mainly due to the repeated use of the merged network (Fig. 8) in the HH estimator for each initial unit intersecting this network; it is used only once in the HT estimator, because it uses only distinct networks. It is not possible to tell which estimator is better in this case, because the results from adaptive sampling were so variable and this result is one realization of a random process. All the same, the merging of networks occurred because the size of the intersection stratum was small. Further experimentation and research should investigate the effects of small areas versus large areas on adaptive sampling estimates.

Our second hypothesis was that ACS would be less beneficial in surveying abundance of SR/RE, because it is believed that they were not as clustered as POP. This hypothesis is supported by the fact that the SRS estimates for SR/RE are more precise than adaptive estimates, even using n in the SRS estimates. However, aggregations in the north stratum were found by adaptive sampling that was not found by simple random sampling and, consequently, adaptive sampling resulted in higher S.E. values and a considerable increase in abundance estimates compared with simple random sampling. The higher S.E.s for adaptive estimators in this instance may not be an indication of an inferior approach, but that the sampling happened to obtain higher CPUEs. Additional insight is gained into the population than would be with SRS alone. The contrast between this stratum and the intersection stratum show the variability of abundance estimates that occurs when adaptive sampling discovers different levels of aggregation. For the south stratum, results of random and adaptive sam-

pling were almost identical and in accord with the null hypothesis. Therefore, examining this small trial would lend support to the hypothesis, but insufficient data were collected for any significant conclusions.

The variogram analysis provides some support for the idea that adaptive cluster sampling is beneficial for POP and not for SR/RE. Since the idea behind ACS is to maximize within-network variability, ACS is more effective when there is a substantial portion of structured variance in the variogram. The intersection showed the most promise for this in the variograms, and indeed, it was the stratum that showed the most clustering. According to the range to the sill in the intersection variogram, we can expect gains in precision from adaptive sampling within 3-4 km of the initial random station. If the population sampled had produced a variogram more like the previous NMFS data indicated or like the simulated population, greater gains might have been achieved. In the SR/RE areas, the unstructured variance is too large compared to the structured variance to gain any additional information within a neighborhood. We recommend further research with a variogram as a performance indicator for when adaptive sampling is likely to be effective for a population.

The strong relationship between depth and CPUE provides further support that caution must be taken when utilizing abundance estimates from a broad range of habitat. It is evident that both species are densely clustered into a small interval of depth and this information should be incorporated into any rockfish survey design.

One definitive feature of the ACS design with order statistics we used in 1998 is that all initial random stations must be sampled prior to the adaptive phase. If adaptive sampling is to be applied to the triennial trawl survey in the Gulf of Alaska, this design may not be practical, because it could require too much travel time back to the high-density stations. This paper focuses on improving the assessment of single species or small species groups. Future research will need to be conducted to determine how to use adaptive sampling in a multi-species design. Having multiple preset criteria, where adaptive sampling is invoked when any of the species pass their specific criterion, could do this. We will be looking at alternative adaptive cluster designs in future experiments, wherein the criterion for adaptive sampling is determined before the survey or from previously sampled strata.

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Evaluating Changes in Spatial Distribution of Blue King Crab near St. Matthew Island

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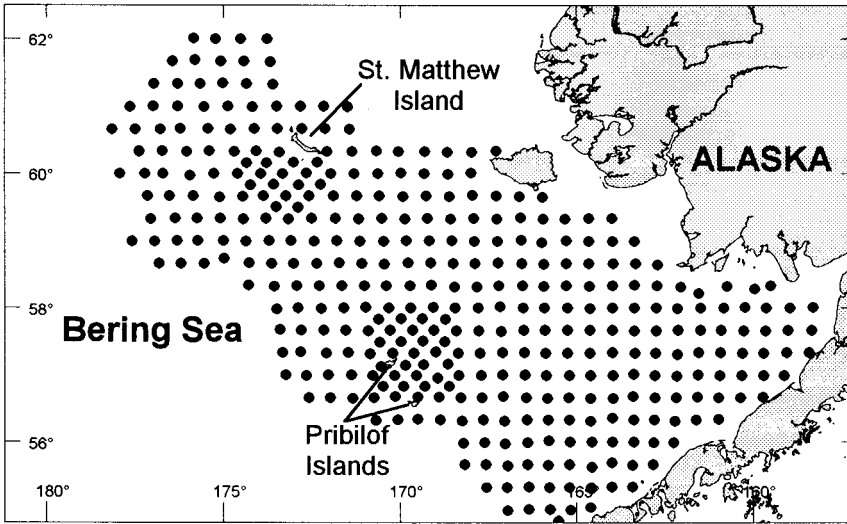
Abstract

The National Marine Fisheries Service (NMFS) performs trawl surveys in the Bering Sea each year on a 20-nautical-mile grid. Around St. Matthew Island increased tows are made to evaluate blue king crab stocks. The Alaska Department of Fish and Game (ADF&G) performed pot surveys near St. Matthew Island in 1995 and 1998, concentrating on more nearshore areas that cannot be sampled by the NMFS trawl survey. This research evaluated changes in spatial distribution of female and legal blue king crabs near St. Matthew Island from these two sources of data. Comparison of spatial distributions between the two methods was accomplished using geostatistic techniques, such as ordinary kriging. Analysis of pot and trawl surveys showed different trends in stock distribution and abundance between 1995 and 1998. The trawl survey appeared not to properly evaluate the nearshore component of the blue king crab stock, and the distance between trawl locations was too great to accurately measure spatial correlation. The NMFS trawl survey has been the only available source of data to estimate stock distribution and abundance of blue king crab in most years. The pot survey results presented here indicate that the trawl survey has not accounted for the extent of the blue king crab distribution which may lead to bias in using it to evaluate stock status.

Introduction

The National Marine Fisheries Service (NMFS) has conducted bottom trawl surveys each summer (May-August) in the eastern Bering Sea (EBS) since 1955, excluding 1962-1965 (Fig. 1a). The primary purpose of these surveys was to estimate the quantity and distribution of commercially important groundfish and crab stocks. These surveys have been the major and sometimes the only source of data when assessing the blue king crab

(a) NMFS standard trawl survey locations



(b) ADF&G pot surveys 1995 (+) and 1998 (o)

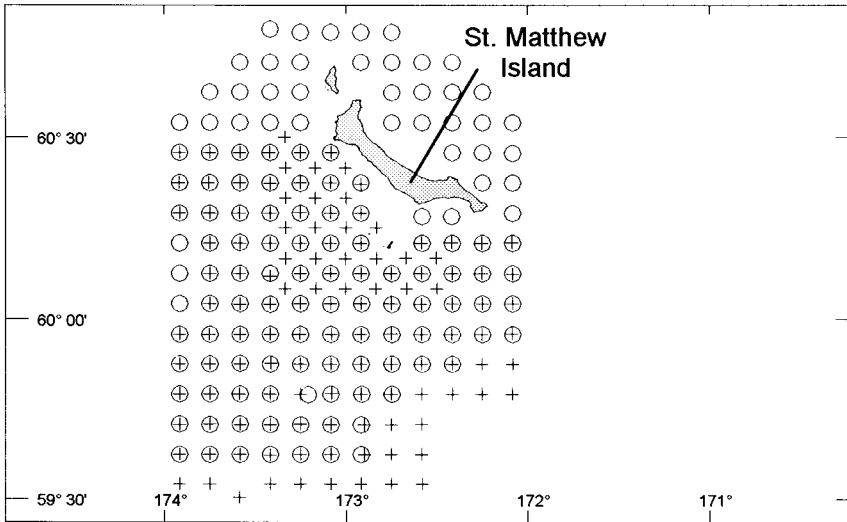


Figure 1. Location of NMFS EBS trawl survey (a), and the ADF&G port surveys (b) for 1995 (+) and 1998 (o).

(BKC) *Paralithodes platypus* stocks in the EBS, specifically near St. Matthew Island.

The Alaska Department of Fish and Game (ADF&G) conducted pot surveys in the St. Matthew Island area in August 1995 and 1998 (Fig. 1b). The purposes of these surveys were to tag BKC to determine commercial harvest rates, characterize female reproductive condition, and gather other natural history information (Blau 1996, Blau and Watson 2000). These surveys offer another source of information with which to evaluate the spatial distribution of BKC near St. Matthew Island.

Trawl locations for the NMFS survey were limited by depth and habitat, while the ADF&G pot survey could sample within a few kilometers of shore, thus providing an opportunity to evaluate St. Matthew Island BKC stocks closer to shore. This was an important function of the pot survey, because observer data from the BKC fishery suggested that a significant portion of the BKC stock inhabited nearshore areas, where the trawl survey could not sample (Doug Pengilly, pers. comm.). If this was true, then there could be serious ramifications for estimates of BKC stock abundance and distribution trends, since the trawl survey has been the major source of information for stock assessments.

Spatial statistic techniques developed in geostatistics offer a means to compare spatial distributions of BKC between different sampling designs. One such tool is ordinary kriging, a weighted linear estimator which uses distance between sample points and associated covariance between the response variable at different sample points as a function of distance to determine the weight given to each sample point for estimation at non-sampled points. Kriging was developed in geostatistics to estimate ore-grade distributions (Matheron 1963). Kriging has been employed in other fields including agriculture (Vieira et al. 1982), entomology (Kemp et al. 1989), and fisheries science (Petitgas and Poulard 1989, Simard et al. 1992, Ecker and Heltshe 1994, Maravelias et al. 1996, Vining and Watson 1996). Kriging is used here to estimate relative densities and to characterize the spatial distribution of the BKC. We compare the different spatial distributions of BKC estimated from the trawl and pot surveys, and discuss the consequences of changes in the spatial distribution from 1995 to 1998.

Methods

Data Collection, Standardization, and Conversion

Only the distribution of female and legal BKC are analyzed in this paper due to time and space considerations. The term "legal" BKC refers to those which can be retained in the St. Matthew Island BKC fishery, namely male BKC with carapace width (CW) ≥ 139.7 mm (Alaska Department of Fish and Game 1998). The NMFS trawl survey measures only carapace length (CL) for BKC and considers male BKC with CL > 119 mm as "legal" (Stevens et al. 1996, 1998). In this report, the term "legal" BKC refers to male BKC with

CL > 119 mm, to maintain consistency between surveys (pot surveys measured both CL and CW).

Trawl survey data used in this study were collected by NMFS during annual EBS systematic trawl surveys in July of 1995 and 1998. The trawl surveys generally consist of one tow in the middle of a 37.04×37.04 km (20×20 nmi) grid (Wakabayashi et al. 1985). Survey strata with higher densities of tows have been established near St. Matthew and the Pribilof Islands, to better assess the BKC stocks (Fig. 1a). Information collected by the trawl surveys used in this study included: trawl location, area trawled, and number of female and legal BKC caught. The estimated area fished by the trawl, recorded in square nautical miles (nmi²), was calculated by multiplying the distance towed by the width of the net opening. The number of female or legal BKC caught was then divided by the area fished. This calculation was used as the catch per unit of effort (CPUE) for the tow, in number of crab per square nautical mile.

Pot survey data were collected by ADF&G during the St. Matthew pot surveys, in August 1995 and 1998. The pot surveys had stations on a 9.26×9.26 km (5×5 nmi) grid, with additional pots fished nearshore in 1995 and on the northeast side of St. Matthew Island in 1998 (Fig. 1b). Data collected by the pot surveys used in this study included: station location, number of pots fished, and the number of female and legal BKC captured per station. The number of female or legal BKC caught was then divided by the number of pots retrieved. This calculation was used as the CPUE for the pot string, in number of crab per pot. No correction for soak time was used because all deployments had similar (30-40 hours) soak times (Blau 1996, Blau and Watson 1999).

It is difficult to compare trawl CPUE (crabs per nautical mile) with pot CPUE (number of crab per pot), so CPUE for both the trawl and pot survey data were standardized for comparison purposes. The maximum CPUE of each gear type was determined for female and legal BKC, with both years combined. All values for the given category were then divided by the maximum value. The maximum was derived from combined years to provide more information regarding relative magnitude within a gear type.

Tow and pot string locations were recorded in decimal degrees longitude and latitude and converted to a Cartesian coordinate system, with measurement between points in kilometers. This was done because distance between locations, as well as actual location, were needed for the geostatistical analysis. A projection equation developed by Snyder (1983) was used to make the conversion.

Statistical Analysis

Four major steps of the geostatistical process were: evaluation of stationarity, estimation of an experimental variogram, fitting a variogram model, and estimate points and their standard error using kriging (Isaaks and Srivastava 1989, Cressie 1994). Under the spatial stationarity assump-

tion, variability between points are a function of distance, not location. Spatial stationarity was investigated by constructing plots of CPUE by location for each year, gear type, and crab group. Departures from spatial stationarity can lead to bias in standard error calculations of the point estimates and to a lesser extent, in the point estimates themselves (Myers 1989).

An experimental variogram was calculated for each year, gear type, and crab group to visualize and estimate the spatial autocorrelation. Experimental variograms were estimated using standard methodology (Matheron 1963, Journel and Huijbregts 1978, Isaaks and Srivastava 1989, Cressie 1994). Each experimental variogram was fit to a model variogram using the weighted least squares method (Cressie 1994). The variogram model was used to estimate covariance between different points. A model of the spatial variability was used to ensure that the covariance matrix used during kriging was positive-definite which guarantees a unique solution for each estimate.

The three components of a variogram model are the nugget, sill, and range. The nugget or nugget effect refers to the difference between the intercept and the origin on the y-axis of the variogram plot and is assumed to represent small scale white noise. A large nugget indicates high variability between points near each other. The sill is the asymptotic upper limit of the exponential variogram model, with a higher sill indicating greater variability (i.e., higher variance). The range is the distance beyond which there is little or no spatial autocorrelation (Isaaks and Srivastava 1989). The range is reached at approximately 90% of the sill value for exponential variogram models. The kriging procedure used here was "ordinary kriging" (Journel and Huijbregts 1978, Isaaks and Srivastava 1989, Cressie 1994). Relative densities were estimated for a specific set of points for each year and gear type. A search radius of 1.5 times the range was used during kriging, but only the closest 15 sample locations were used when ranges were high.

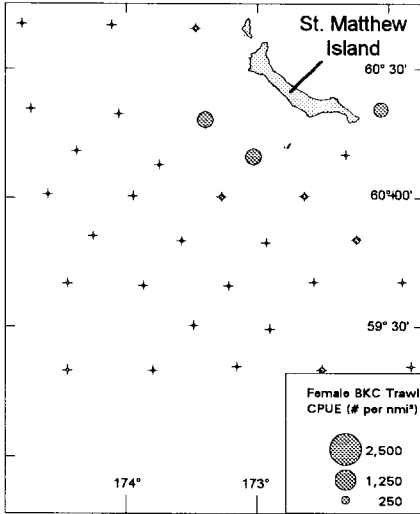
All statistical analyses were performed using functions written in S-PLUS (MathSoft 1999), and maps were constructed using MapInfo (MapInfo 1994).

Results

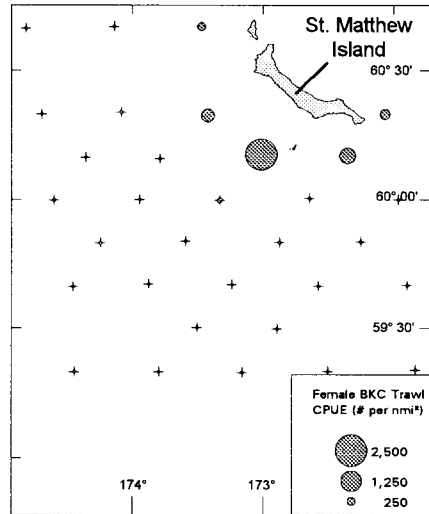
Data

Trawl locations were nearly the same for both years and were located south and west of St. Matthew Island within 50 km of the 1995 pot survey area (Fig. 2). Blue king crab had been caught in these locations in the past. The CPUE by station for female BKC from the trawl survey was similar between years, with one station in 1998 catching more than the other stations (Figs. 2a and 2b). The CPUE by station of legal BKC from the trawl survey was also similar between years, with two stations having higher CPUE than the others (Figs. 2c and 2d).

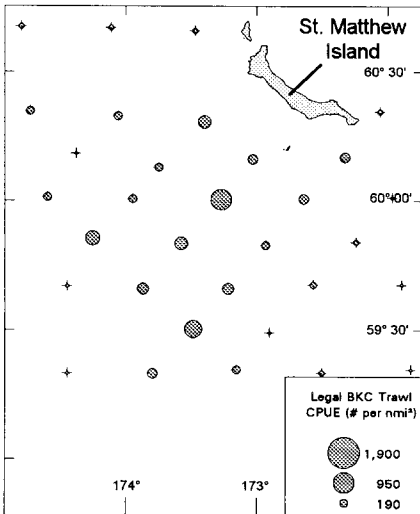
(a) 1995 trawl survey female BKC CPUE



(b) 1998 trawl survey female BKC CPUE



(c) 1995 trawl survey legal BKC CPUE



(d) 1998 trawl survey legal BKC CPUE

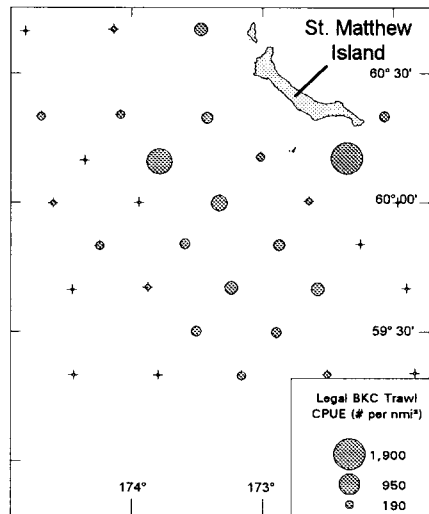


Figure 2. NMFS trawl survey BKC CPUE by trawl station for female 1995 (a) and 1998 (b), and for legal 1995 (c) and 1998 (d).

The pot surveys had different sampling designs from 1995 to 1998 (Fig. 1b). Sampling intensity was high off the southwest shore of St. Matthew Island in 1995, while the 1998 survey covered around the entire circumference of island (Fig. 1b). Higher densities of female and legal BKC were evident close (<20 km) to St. Matthew Island in 1995 (Figs. 3a and 3c). The concentration of female and legal BKC close to St. Matthew Island seemed to have decreased by the time of the 1998 pot survey (Figs. 3b and 3d). However, the exact same areas were not surveyed in both years so a direct comparison was difficult. Due to time and depth constraints, the area near (<32 km) St. Matthew Island was not surveyed by the trawl survey.

Data from all pot locations from the 1995 pot survey and data from all the pot locations south and west of St. Matthew Island from the 1998 pot survey were used in the analysis (Fig. 4b). Data collected from pots to the north of St. Matthew Island were not used (Fig. 4b). The conversion from longitude and latitude in decimal degrees to relative longitude and latitude in kilometers changed the relative view of the survey locations (Fig. 4). The area where the kriging estimates were calculated combines the pot locations used in this study (Fig. 4b). Trawl locations outside the kriging area were used to estimate the variogram and kriged points because too few trawl locations occurred within the kriging area.

Spatial Stationarity

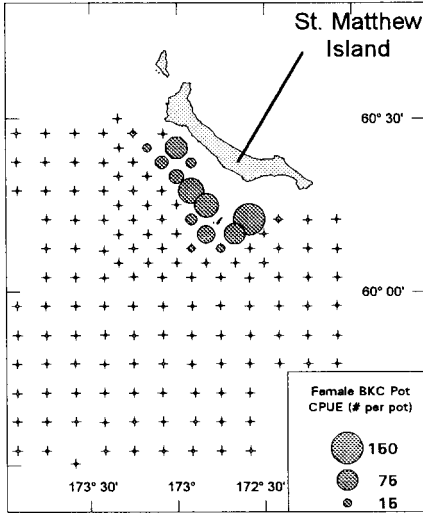
It was difficult to ascertain whether there was spatial stationarity for the trawl surveys for female or legal BKC, due to few sample points (Fig. 2). The pot survey showed greater variability near St. Matthew Island than farther offshore for female BKC in 1995 and 1998, and for legal BKC in 1995 (Fig. 3). Due to this difference in variability between these two areas, and because more stations were sampled near-island in 1995 than in 1998, the area was split into near-island and off-island components for analysis of the pot survey legal and female CPUE of 1995 and female CPUE of 1998. For the remainder of the paper, near-island will refer to the area with high sampling intensity during the 1995 pot survey, and off-island will refer to stations outside this area. This division removed an obvious lack of stationarity. No further de-trending was performed, and stationarity was assumed within the near and off-island components.

Variogram Calculations

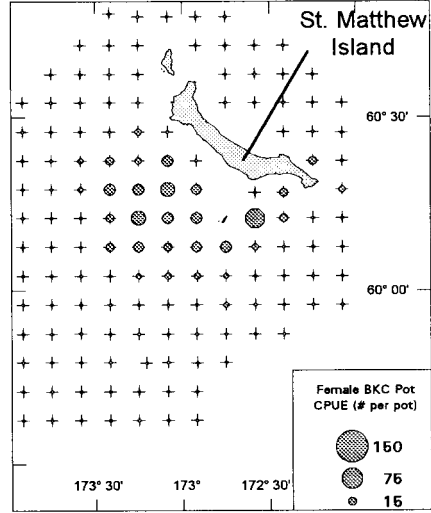
The shapes of the experimental variograms seemed to be best represented by either an exponential or a spherical model (Cressie 1994); however, only the exponential variogram model was chosen because use of the spherical model has been discouraged due to irregular behavior in the likelihood (Zimmerman and Zimmerman 1991, Stein 1999).

All exponential variogram models were fit assuming isotropy (difference in spatial variability depending on distance only and not direction). The 1995 near-island pot survey data were initially fit to include

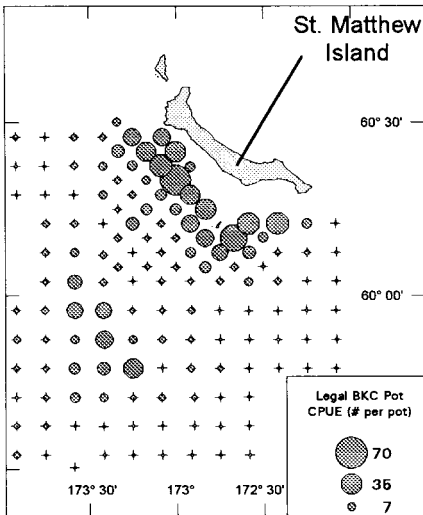
(a) 1995 pot survey female BKC CPUE



(b) 1998 pot survey female BKC CPUE



(c) 1995 pot survey legal BKC CPUE



(d) 1998 pot survey legal BKC CPUE

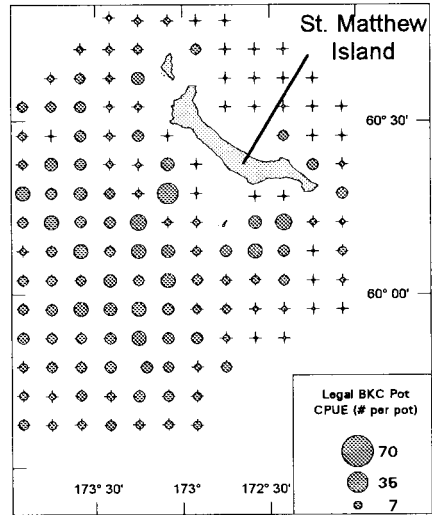


Figure 3. ADF&G pot survey BKC CPUE by pot station for female 1995 (a) and 1998 (b), and for legal 1995 (c) and 1998 (d).

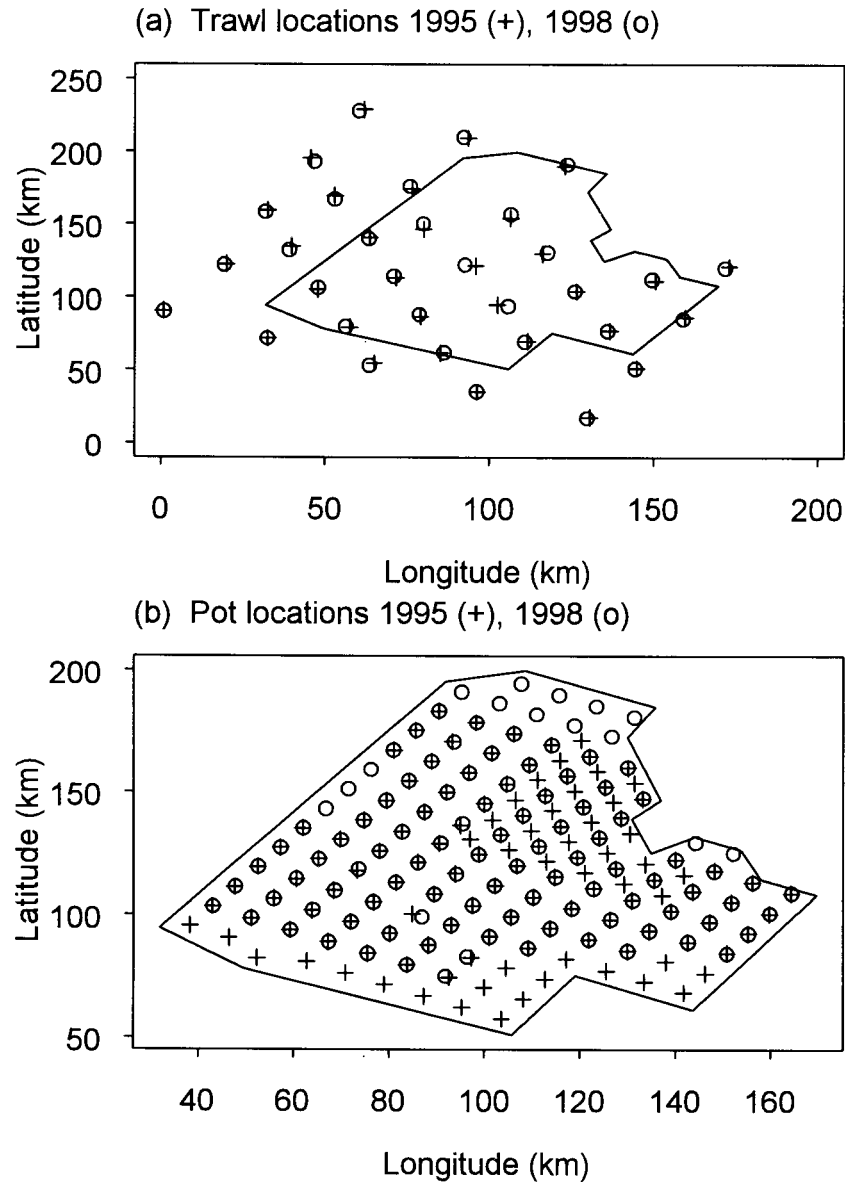


Figure 4. Location of survey points, converted from longitude and latitude in decimal degrees to longitude and latitude in kilometers for the trawl (a) surveys in 1995 (+) and 1998 (o), and pot surveys (b) in 1995 (+) and 1998 (o). The boundary where the 5 by 5 km grid was to be grided is indicated.

anisotropy (difference in spatial variability depending on distance and direction), but both the female and legal pot survey experimental variograms provided better fits to variogram models when isotropy was assumed.

Variogram models fit to experimental variograms of trawl survey female BKC had relatively similar ranges and nuggets but different sills, with the 1998 sill being greater (Table 1, Figs. 5a and 5b). Similarly, the near-island pot survey models for female BKC had similar nuggets and ranges, with different sills. However, in the near-island pot survey the 1995 sill was greater (Table 1, Figs. 5c and 5d). The sill estimated for the 1995 near-island pot survey was nearly the same as the 1998 trawl survey sill estimate; and the sill estimated for the 1998 near-island pot survey was nearly the same as the 1995 trawl survey sill. Experimental variograms and variogram models for the off-island pot survey were very different from the other experimental and model variograms, with very little variability, although a spatial component was evident in both 1995 and 1998 (Table 1 and Figs. 5e and 5f).

Variogram models fit to experimental variograms of the trawl survey legal BKC were much different than those for female BKC variograms. Variogram models for the two trawl survey legal BKC had different nuggets, ranges, and sills (Table 1, Figs. 6a and 6b), and the 1998 trawl survey model exhibited virtually no spatial correlation, as seen by the high nugget and a sill slightly higher than the nugget (Table 1, Fig. 6b). The 1995 trawl survey variogram model indicated weak spatial correlation, although not as weak as for the 1998 data. Experimental variograms and variogram models for both the near-island and off-island 1995 pot survey legal BKC indicated fairly strong spatial correlation. Similar nuggets and ranges were found in the variogram models for the near-island and off-island pot survey legal BKC, indicating similar spatial correlation, with the near-island area having greater variability (Table 1, and Figs. 6c and 6d). The 1998 pot survey legal BKC experimental variogram and variogram models had the least amount of spatial correlation of any of the pot surveys, as indicated by the nugget and sill being relatively close (Table 1 and Fig. 6e).

Kriging

Points for the kriging estimates were located on a regular 5 km grid within the boundary as shown on Fig. 4. This grid was used to analyze females and legal, by gear type and year.

Kriging estimates of female BKC (Fig. 7) show similar relationships between the 1995 trawl survey and the 1998 pot survey, and between the 1998 pot survey and the 1995 trawl survey. The 1998 trawl survey and the 1995 pot survey showed relatively high densities of female BKC, near St. Matthew Island. The 1995 trawl survey and the 1998 pot survey also showed more females near shore, although in lower densities. The trawl survey kriged data were smoother than the pot survey due to larger variogram ranges estimated for the trawl surveys.

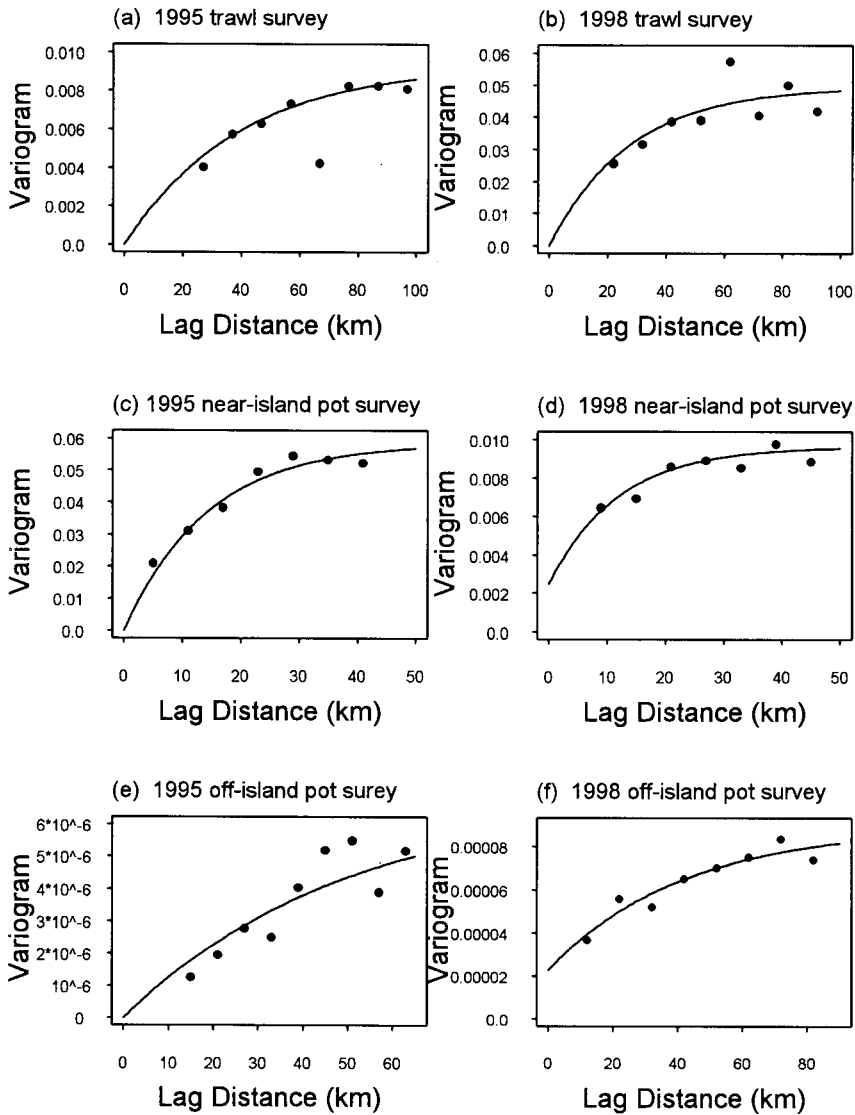


Figure 5. Sample and fitted exponential model variogram for female BKC from the trawl survey 1995 (a) and 1998 (b), and from the pot survey near-island 1995 (c) and 1998 (d), and off-island 1995 (e) and 1998 (f).

Table 1. Parameters from the semi-variogram model, as fitted to the sample semi-variogram, for females and legal BKC, by year, and near-shore and off-shore for the pot survey in 1995, and females only in 1998.

BKC group (Female/ legal)	Gear type (Trawl /pot)	Year (1995/ 1998)	Shore distance (Near/off)	Nugget	Sill	Range (km)
Female	Trawl	1995	N/A	0.00	9.35×10^{-3}	39.716
Female	Trawl	1998	N/A	0.00	4.96×10^{-2}	27.475
Legal	Trawl	1995	N/A	5.07×10^{-3}	2.12×10^{-2}	199.342
Legal	Trawl	1998	N/A	2.77×10^{-2}	5.17×10^{-2}	67.018
Female	Pot	1995	Near	0.00	5.86×10^{-2}	14.308
Female	Pot	1995	Off	0.00	6.89×10^{-6}	50.088
Female	Pot	1998	Near	2.48×10^{-3}	9.63×10^{-3}	11.789
Female	Pot	1998	Off	2.28×10^{-5}	8.92×10^{-5}	41.742
Legal	Pot	1995	Near	8.29×10^{-3}	7.02×10^{-2}	18.830
Legal	Pot	1995	Off	0.00	9.71×10^{-3}	14.295
Legal	Pot	1998	N/A	3.46×10^{-3}	9.05×10^{-3}	40.177

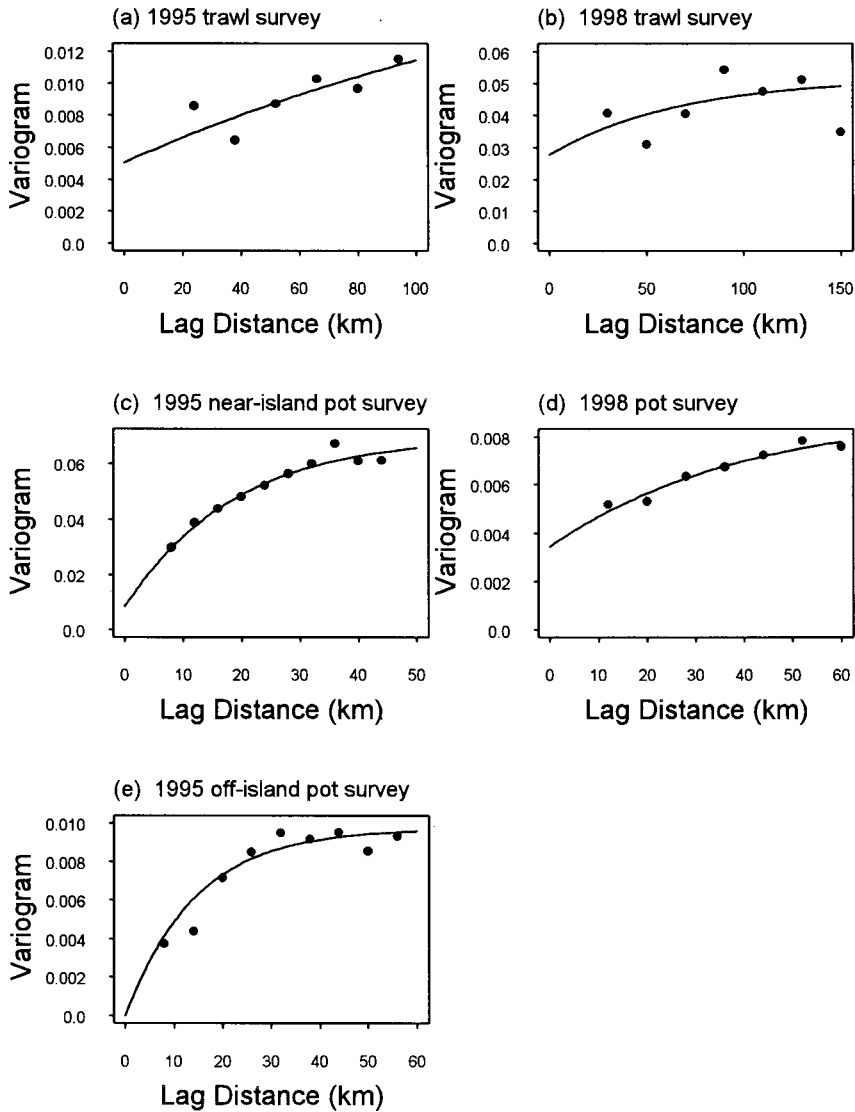
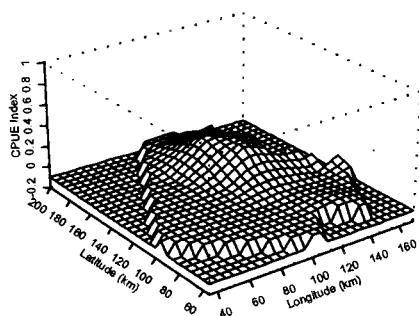
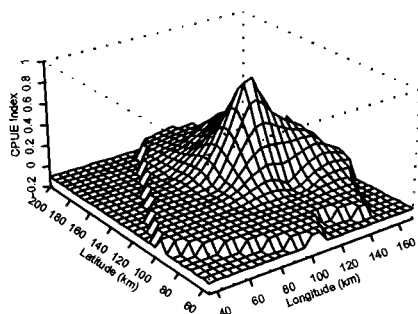


Figure 6. Sample and fitted exponential model variogram for legal BKC from the trawl survey 1995 (a) and 1998 (b); and from the pot survey near-island 1995 (c), and off-island 1995 (d) and from the pot survey 1998 (e).

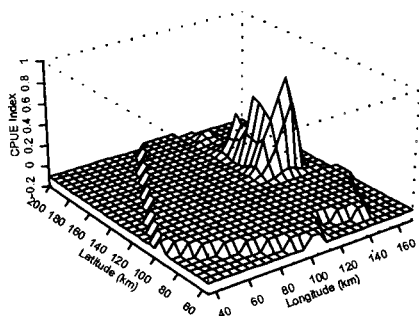
(a) 1995 trawl survey



(b) 1998 trawl survey



(c) 1995 pot survey



(d) 1998 pot survey

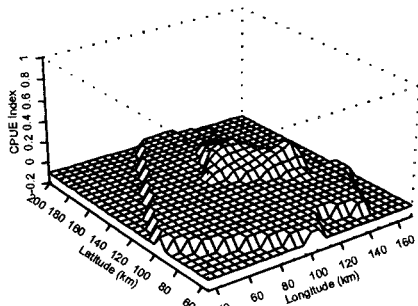


Figure 7. Kriged point estimates on a 5 km grid near St. Matthew Island for female BKC from the trawl survey 1995 (a) and 1998 (b), and from the pot survey 1995 (c) and 1998 (d).

Standard errors of the kriged estimates for the female BKC trawl survey were similar, though at a different scale; this again is due to the ranges being relatively large (Fig. 8). Standard errors for the female BKC pot surveys showed distinct demarcation of the near-island and off-island analysis, with the off-island standard errors being much smaller than the near-island values. The difference in these standard errors was due to the low sill of the off-island variogram, compared to the near-island (Table 1). The 1995 pot survey near-island female BKC standard errors have a peak in the northwest corner due to a relatively short range of the variogram model and few data points available to estimate points in this area.

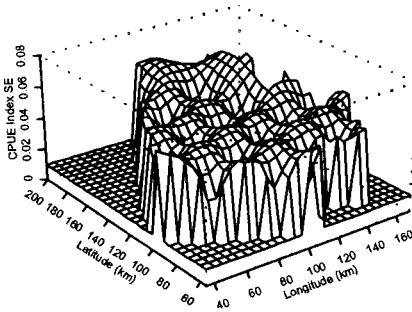
For both 1995 and 1998, the kriged estimates for legal BKC from the trawl survey were very smooth due to the lack of spatial correlation (Figs. 9a and 9b). Due to the similar spatial correlation between locations, the weights used in kriging are very similar, and because the variogram ranges are relatively large, a large proportion of the data set was used to estimate each kriged point. In essence, it is similar to averaging the data and using the average to estimate each of the points. The 1998 pot survey provided similar results for the legal BKC as the trawl surveys, for similar reasons (Fig. 9d). Only the kriged estimates of legal BKC from the 1995 pot survey have enough spatial correlation to give a clear picture of the legal BKC distribution (Fig. 9c).

Standard errors of the different kriged estimates of legal BKC were similar to the results observed in the female standard errors (Fig. 10). For the 1995 pot survey, which had strong spatial correlation and low variogram ranges, standard errors were highly variable (Fig. 10c). Standard errors were much smoother for systems with weak spatial correlation and with high variogram ranges (Figs. 10a, 10b, and 10d).

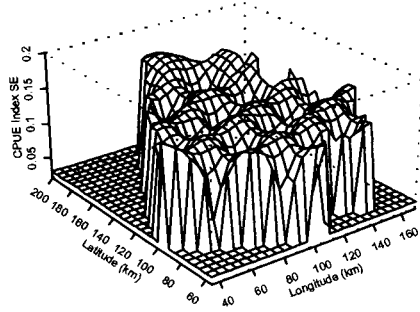
Discussion

It is difficult to ascertain whether the trawl or pot survey more accurately predicted the female BKC distribution and trend. Both trawl and pot surveys showed the highest densities of BKC females near shore (Figs. 2a, 2b, 8b, and 8c). Both survey types showed similar sill values between the high-density years (trawl 1998 and pot 1995) and between the low-density years (trawl 1995 and pot 1998; Table 1, Fig. 5). The survey types were different in that the trawl survey indicated an increase in female BKC density from 1995 to 1998, while the pot survey showed a decline. The pot survey sampled at locations nearer shore, where both survey types showed the greatest density of female BKC. Also, the pot survey near-island variogram showed strong spatial correlation at distances shorter than the average distance between trawl tows, indicating that spacing of the trawl survey stations was too great to assess spatial correlation (Table 1, Fig. 5c). Furthermore, the pot survey showed greater density of BKC further off-island from 1995 to 1998. The spatial distribution of the 1998 pot and trawl kriged estimates were similar, though the 1998 trawl survey was smoother and

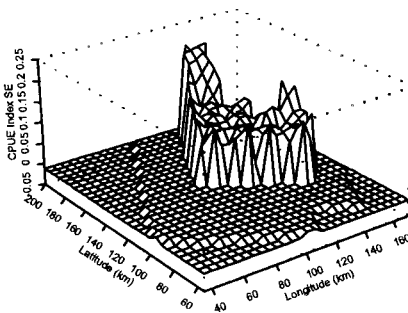
(a) 1995 trawl survey



(b) 1998 trawl survey



(c) 1995 pot survey



(d) 1998 pot survey

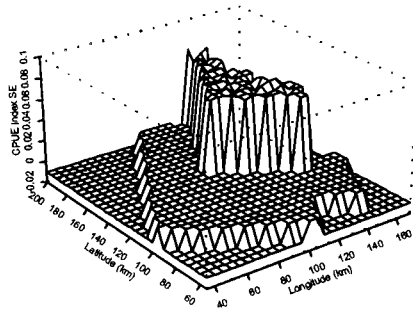
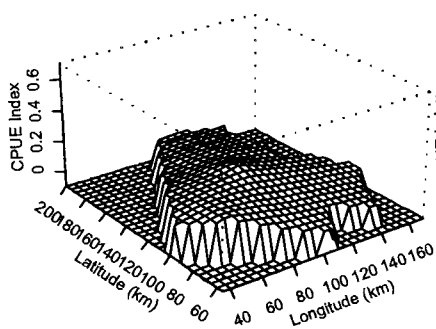
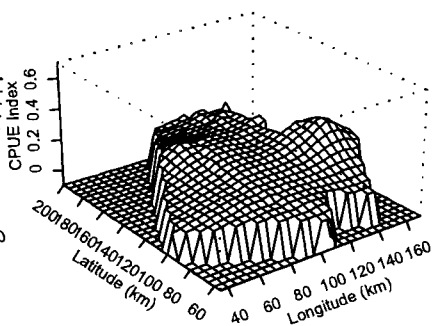


Figure 8. Standard errors for the kriged estimates on the 5 km grid near St. Matthew Island for female BKC from the trawl survey 1995 (a) and 1998 (b), and from the pot survey 1995 (c) and 1998 (d).

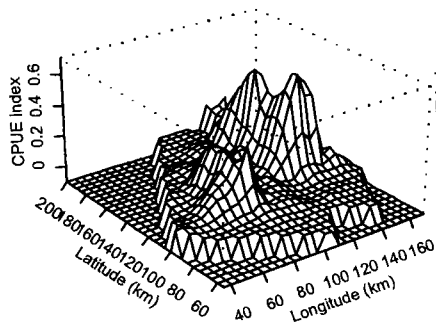
(a) 1995 trawl survey



(b) 1998 trawl survey



(c) 1995 pot survey



(d) 1998 pot survey

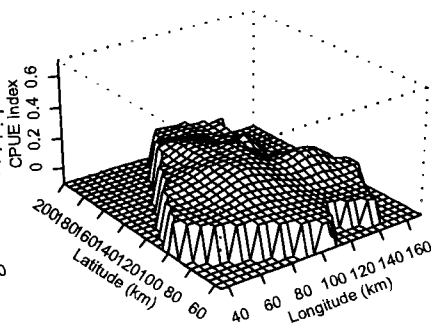
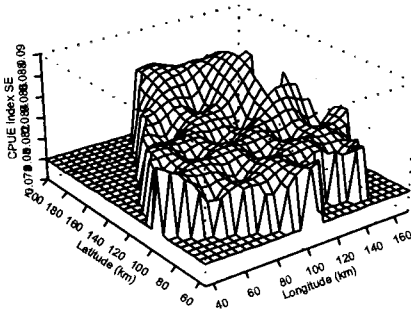
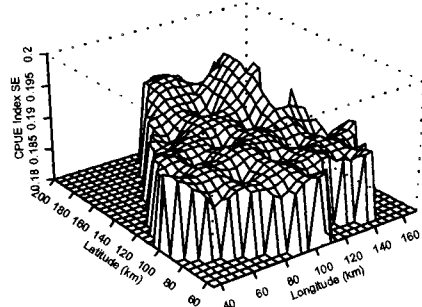


Figure 9. Kriged point estimates on a 5 km grid near St. Matthew Island for legal BKC from the trawl survey 1995 (a) and 1998 (b), and from the pot survey 1995 (c) and 1998 (d).

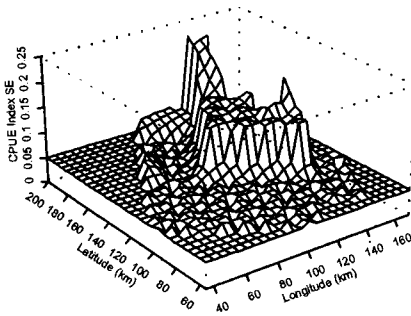
(a) 1995 trawl survey



(b) 1998 trawl survey



(c) 1995 pot survey



(d) 1998 pot survey

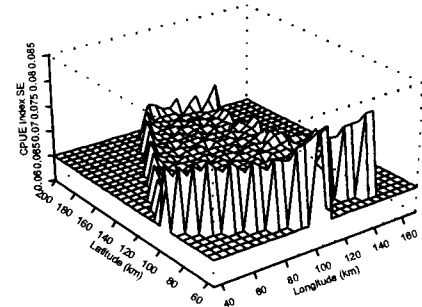


Figure 10. Standard errors for the kriged point estimates on the 5 km grid near St. Matthew Island for legal BKC from the trawl survey 1995 (a) and 1998 (b), and from the pot survey 1995 (c) and 1998 (d).

the pot survey showed greater density near shore in the southeast area near St. Matthew Island.

Information from other sources provides insight into St. Matthew Island BKC population dynamics. The BKC fishery typically produces a high bycatch of female BKC (Tracy 1995), but there was a reduction in female bycatch during 1998 season (Rance Morrison, ADF&G, Dutch Harbor, AK, pers. comm.). In addition, the 1999 NMFS trawl survey indicated that BKC abundance near St. Matthew Island declined markedly from 1998 (Bob Otto, NMFS, Kodiak, AK, pers. comm.).

Overall, the pot survey was better at measuring the spatial distribution of female BKC near St. Matthew Island than the trawl survey. Female BKC seemed to have been more dispersed in 1998 and density declined as well.

The 1995 pot survey was the only survey considered in this study that showed strong spatial correlation of legal BKC density (Table 1 and Fig. 9c). The 1998 pot survey indicated some spatial correlation, but both trawl surveys showed little. The difference between the trawl and pot survey in 1995 may be due, in part, to the greatest density of legal BKC occurring in the 1995 pot survey near (<15 km) St. Matthew Island and female BKC density decreasing considerably before the nearest trawl location (>20 km). However, both the 1995 trawl and pot survey showed higher density of legal BKC near the middle of the boundary area. The range for the pot survey's BKC variogram, for both the near-island and off-island areas was considerably less than the distance between trawl locations.

The 1998 pot survey does show a similar spatial distribution to the 1998 trawl survey. There is a peak density of legal BKC near the southeast corner of St. Matthew Island as well as increases in legal BKC density near the center and west of the island. Both 1998 surveys also showed weak spatial correlation for legal BKC as observed by their variograms (Figs. 6b and 6d). However, as with the 1995 pot survey, the 1998 pot survey seems to provide a better measure of spatial distribution.

Harvest information from the fishery also provides insight into changes in BKC spatial distribution from 1995 to 1998. The 1995 BKC guideline harvest level (GHL, the estimated biomass allowed to be taken in the fishery) for the St. Matthew Island area, was 1.09 million kg (2.4 million lb). The 1995 fishery produced 1.45 million kg (3.2 million lb) in 5 days and averaged 14 legal BKC per pot (Morrison et al. 1999). On the other hand, the 1998 BKC GHL was 1.82 million kg (4.0 million lb) and the fishery could only catch 1.32 million kg (2.9 million lb) in 11 days and averaged only 7 legal BKC per pot (Morrison et al. 1999). Observer reports indicated that the BKC fleet tended to fish near St. Matthew Island (Larry Byrne, ADF&G, Kodiak, AK, pers. comm.) However, in 1998 the fleet fished in a broader area (Morrison et al. 1999). Information from the fishing fleet indicated that either the BKC were not on the "normal" fishing grounds, that the stock had decreased, or both.

The pot survey provided a better picture of the spatial distributions of legal and female BKC. The trawl survey, however, is the only source of data

used in most years for BKC stock assessment. The difference in the spatial distribution of legal BKC between the 1995 and 1998 pot surveys is probably due to a phenomenon similar to that discussed for the female BKC, namely that legal BKC were more dispersed and not located in traditional areas. Furthermore, a decline in overall abundance may explain overall decline in density between 1995 and 1998 as estimated by the pot survey and BKC fishery.

Overall, the pot survey did a better job estimating spatial distribution of BKC than the trawl survey. The main reasons are: (1) the pot surveys could be performed near St. Matthew Island (where a large portion of the BKC population was often found); and (2) the pot survey fished more intensively (pots closer together) than the trawl survey (with the pot survey indicating the strongest spatial correlation occurring at distances less than the distance between trawl stations). The trawl surveys captured only the basic spatial distribution of the BKC, although it should be noted that this could be improved by increasing sampling intensity (see Vining and Watson 1996). In other studies using geostatistics the importance of having a wider range of distances between sample locations has been noted (Kemp et al. 1989, Petitgas and Poulard 1989, and Maravelias et al. 1996).

Further studies on the spatial distribution of this and other crab stocks, using pot and trawl surveys, will provide useful information on stock trends and health.

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Density-Dependent Ocean Growth of Some Bristol Bay Sockeye Salmon Stocks

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Abstract

The sockeye salmon runs to the Kvichak River in Bristol Bay undergo cyclic changes in abundance and average length or weight of each age class. One initial interpretation could be that the Kvichak sockeye salmon are segregated while feeding in the ocean. However, sockeye salmon in adjacent streams, like the Egegik and Ugashik rivers, also undergo cyclic density-dependent ocean growth, caused by competition with the dominant Kvichak runs in peak years. The average length of sockeye salmon can be used to define the carrying capacity of the feeding grounds in the ocean, used by these stocks.

Introduction

The largest single stock of sockeye salmon (*Oncorhynchus nerka*) in the world is found in the Kvichak River (Fig. 1). It undergoes cyclic changes in abundance as well as changes in average lengths or weights. The motivation for this study was an observation made by members of the canning industry. They noticed that the number of salmon needed to produce one case, with 48 one-pound cans, increased in peak years of the Kvichak cycle. It was tacitly assumed that weight and length in peak years was a result of density-dependent growth in the ocean. Most of the other Bristol Bay sockeye salmon runs were at that time rather small, usually totaling 2-3 million fish, and no changes in size were recorded (Fig. 2).

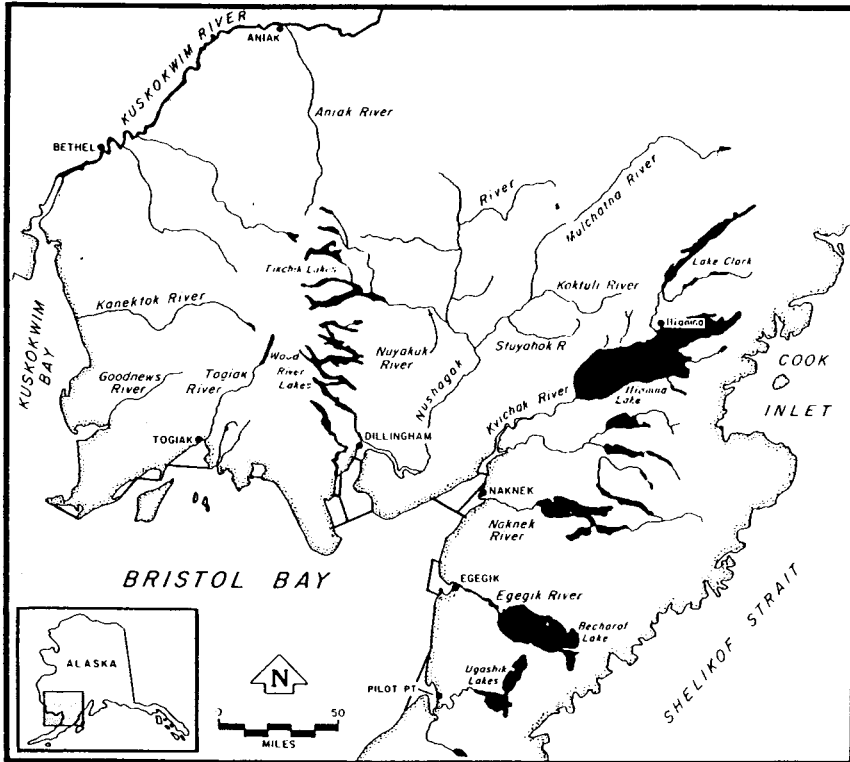


Figure 1. Map of Bristol Bay, Alaska.

Today, with the availability of consistent length measurements and good abundance estimates of the escapements to the various trunk streams, the cyclic nature of the runs can be investigated in depth. Using escapement data circumvents the problem of dealing with mixed stocks in the commercial catches. If salmon runs to other streams do not display cyclic changes in length or weight, it would be a strong indication that the Kvichak sockeye salmon in the ocean feed segregated from the other Bristol Bay stocks. On the other hand, if the smaller stock units also display cyclic changes in length that follow the Kvichak changes, the conclusion must be that the oceanic distribution of some stocks of the Bristol Bay sockeye salmon overlap in peak cycle years. The mixing of stocks in the ocean is supported by some tagging experiments. One-time tagging at a single location has yielded tag recoveries in widely separated streams (Neave 1964).

Some papers by Peterman (1983) and Rogers and Ruggerone (1993) dealt with ocean growth of sockeye salmon from Bristol Bay as a unit. Pyper et al. (1999) examined the covariation in length and age at maturity of

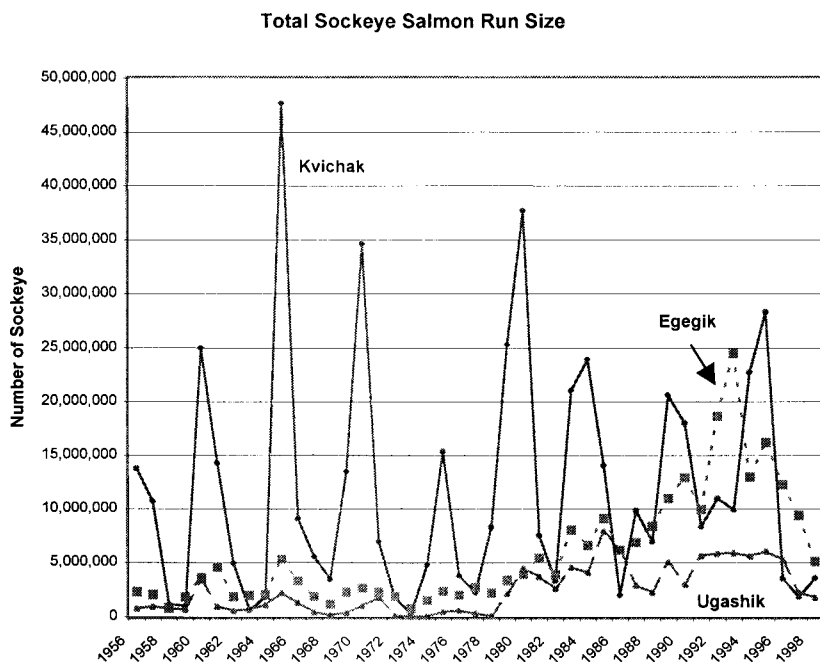


Figure 2. Total run size (total catch plus escapement) of sockeye salmon to the Kvichak, Egegik, and Ugashik systems.

sockeye salmon from British Columbia and Alaska and concluded that the distribution of stocks either overlapped or large-scale environmental processes influenced the stocks. Recently, Isakov (1998) examined ocean growth of Kvichak sockeye salmon, based on historical scale collections. However, all failed to consider the cyclic nature of the Kvichak sockeye salmon, and the changing biomass of feeding salmon.

Material and Methods

The area of investigation included the streams on the east side of Bristol Bay (Fig. 1). Five major trunk streams drain into the bay. Because of its proximity to the Kvichak River, we eliminated the Naknek River in this analysis.

Abundance, age, and length data for the sockeye catch and escapement are compiled annually by the Alaska Department of Fish and Game (ADF&G) and published in Technical Data Reports for the years 1957 through 1983, after which they were called Technical Fishery Reports covering 1984 through 1997. In this analysis we use total run (catch plus escapement) for

the abundance estimates and escapement data for the length and sex information for the years 1957-1997. Size of salmon in the catch might be biased due to gear selectivity.

ADF&G staff estimate the escapements to the Bristol Bay systems based on intermittent counts, usually 10 minutes per hour throughout the 24-hour day, from towers erected on each bank near the outlet of the nursery lakes. This estimation process was developed initially by members of the Fisheries Research Institute, University of Washington, and it has provided a solid basis for the sockeye management system in Bristol Bay since 1956. In addition, ADF&G takes regular samples from the escapement for sex, length, and age composition. Usually this is accomplished by nonselective seine hauls along the riverbanks. The total sample size varied each year, but seldom was less than 1,000 individuals. When separated into age groups, the sample sizes were smaller and varied depending upon the number of ages represented in the sample.

Salmon length is measured from the middle of the eye to the fork of the tail, and expressed in millimeters. Age determination was based on readings from the impression of scales transferred to plastic scale cards under pressure and heat, and analyzed using well-established methods of age readings. Age designation follows that published by Koo (1962). It consists of two numbers separated by a period, $x.y$. Here x denotes the number of freshwater annuli and y gives the number of years spent in the sea.

Annual salmon returns include fish that have spent 0, 1, 2, or 3 years in the nursery lakes and that have stayed from 1, 2, 3, or 4 years in the sea. Theoretically, this produces 16 different age groups. In practice, however, there are only four dominant age groups, 1.2, 1.3, 2.2, and 2.3, which account for about 90% of the returns and of which the age 2.2 group, or 5-year-old fish, is the most important one. Consequently, only these age groups have been considered. Six-year-old salmon (age group 2.3) have always been a small group in the run. Sockeye salmon migrating to sea in their second year can return after 2 or 3 years in the ocean, respectively, as 1.2- or 1.3-age salmon. Normally they represent minor groups in relation to the dominant age 2.2 group. In some years one of these two age groups becomes more numerous in relation to their average values. Our knowledge of the factors that trigger the return migration is very incomplete today. With four age groups and two sexes we have eight groups for analysis from each of the three trunk streams, the Kvichak, the Egegik, and the Ugashik rivers. This results in a total of 24 age/sex/area groups, and for each there is a time series of average length covering the period 1957-1997.

Coherence between two time series was measured using the Pearson correlation coefficient. Difference in mean length between two time series was tested using the paired sample t -test.

As it is conceivable that length of smolts will influence the final size of adults, the correlation between smolt and adult size was also estimated. The average length of smolts from the three systems was provided by Crawford and Cross (1999).

Results

Comparisons of Length Measurements in the Escapements

Coherence of Annual Changes

It has been assumed that males and females of the same age group are most likely to travel and feed together. Therefore, year-to-year changes in length should track each other. The observed time series of length data for Kvichak males and females for both age 2.2 and 2.3 track each other very closely, especially the age 2.2 fish (Fig. 3). The same pattern was seen for sockeye salmon from the other two systems. Coherence is verified by the high correlation coefficients for all four age groups in all three systems (Table 1).

The correlation coefficient is highest for age 2.2 fish; and it is expected that this age group would have the highest degree of coherence since this age group is more abundant than the age 1.2 group and has larger sample sizes and the age group has had less time in the ocean than the age 2.3 group. The age 2.2 and 2.3 groups should not be compared directly, since the age 2.3 fish represent sockeye that entered the ocean 1 year earlier and the two groups are not expected to be coexisting spatially to the same degree as salmon migrating to sea in the same year. The generally smaller correlation coefficients for .3 fish (compared to the age .2 of the same freshwater age) might indicate a wider spatial distribution of the older fish.

Effect of Smolt Size on Final Length

Among the three systems, the Egegik smolts are the largest in all age classes, while the Kvichak smolts are the smallest every year. Ugashik smolts fall between the two extremes (Fig. 4). In the case of the Kvichak smolts, there are annual differences in the mean length of age I smolts; but these are more synchronized with the total biomass of juveniles from the preceeding group of spawners, represented by age II juveniles in the Iliamna Lake nursery area. The age II smolts display a cyclic pattern in length distribution with differences between high and low values reaching 25 mm. Therefore, it becomes important to establish if the final size of the Kvichak adults is related to the size of the smolts and, especially, the size of age II smolts.

The range of sizes for each age group and each system over the 1957-1997 period overlaps considerably, but the average size shows a trend of increased size of males over females, age 2.2 over age 1.2, and age 2.3 over 1.3, and of age .3 over .2 no matter what the freshwater age (Fig. 5). While there are relatively large increases in length between ocean age .2 and .3 fish in every district, the increase in size of age 1. and 2. (freshwater years) fish within the same ocean age category were small. This has been examined further in Table 2, which compares the length of age 1. and 2. fish. In every case there is shown a significant difference between the final length of age .2 or .3 fish, except for two cases, age .3 Kvichak fish and age .3

Table 1. Correlation in length of male versus female sockeye salmon from the Kvichak, Egegik, and Ugashik escapements during the period 1957-1997. The Pearson correlation coefficient is used.

Age	Kvichak	Egegik	Ugashik
1.2	0.75	0.79	0.83
1.3	0.71	0.76	0.75
2.2	0.95	0.93	0.87
2.3	0.59	0.87	0.63

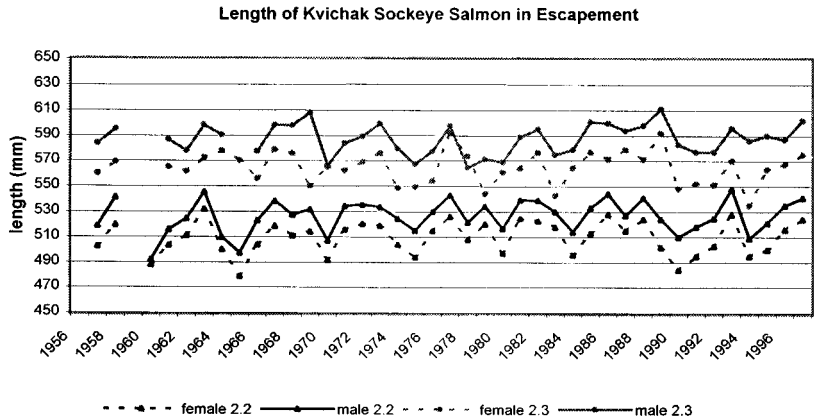


Figure 3. Length of age 2.2 and 2.3 Kvichak female and male sockeye salmon in the escapements from 1957 to 1997.

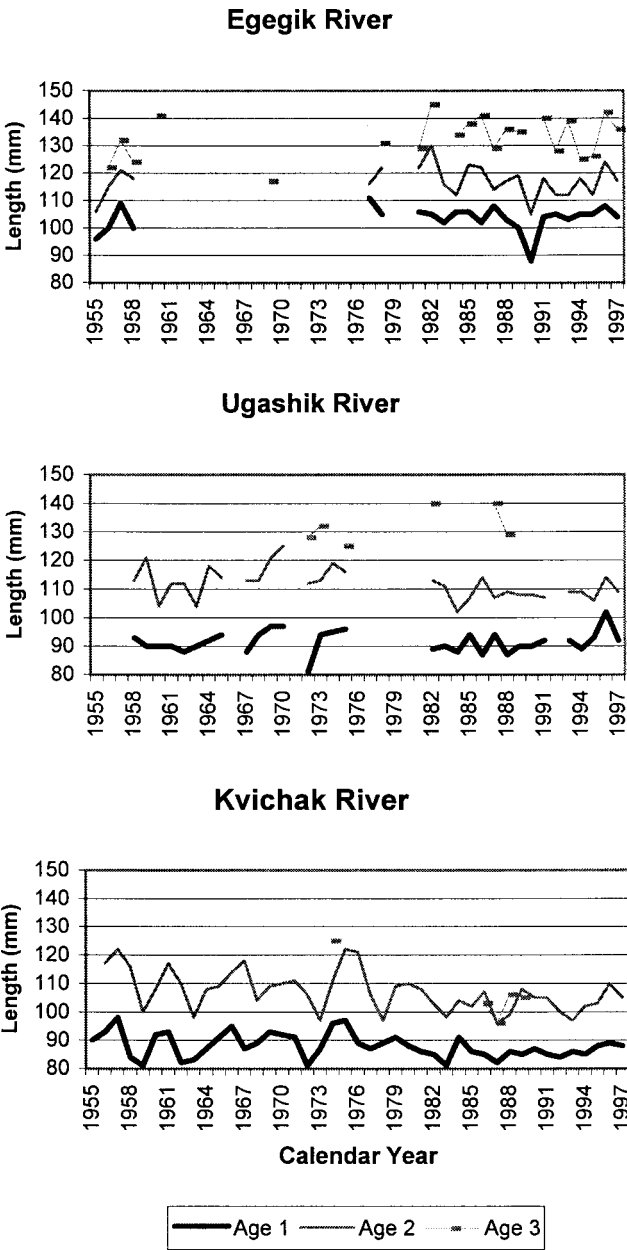


Figure 4. Average length (tip of snout to tail fork) of Kvichak, Egegik, and Ugashik smolts, 1955-1997.

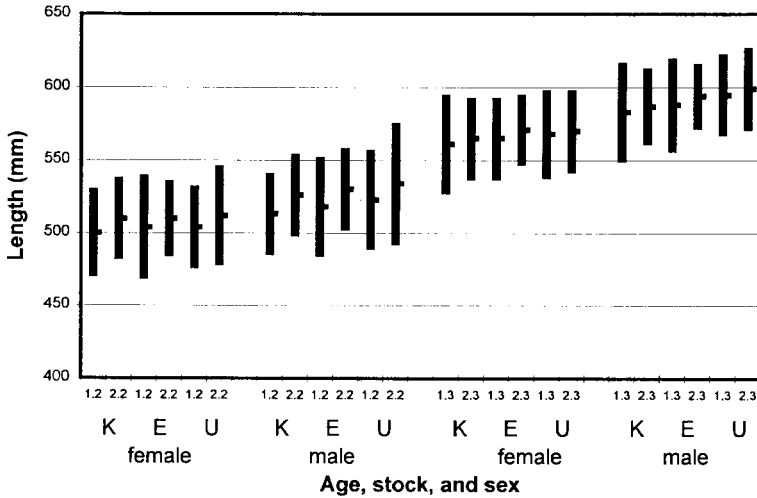


Figure 5. Average length of Kvichak (K), Egegik (E), and Ugashik (U) sockeye salmon in the 1957-1997 escapements by age class and sex. The upper and lower 95% confidence limits are given as bars around the average length. The four groups of bars represent, in order, female marine age 2, male marine age 2, female marine age 3, and male marine age 3 fish. Within each group the Kvichak freshwater age 1 and 2 are given first, then Egegik, and finally Ugashik sockeye.

Ugashik fish. Because of the large number of samples, the one-tailed paired mean test is very powerful even though the actual differences are small.

Comparisons of Time Series of Average Length of Adults

Next we compared changes in mean length between Kvichak fish and both Egegik and Ugashik fish. Such comparisons must be made within the same age/sex classification and is shown for female age 2.2 and 2.3 fish in Fig. 6. There are common features in the cycles among the three systems. The middle part of the time series is less coherent than during the later years. The middle period took place at a time when the Egegik and Ugashik runs were small (Fig. 2). In later years with strong development of the Egegik runs, the coherence becomes strong between the three districts. Additionally, there is a downward tendency in the mean length of the fish. Other age groups, like 1.2 and 1.3, have been examined with similar results.

The correlation coefficients between the time series of mean annual length of Kvichak salmon and those from the Egegik and Ugashik districts were calculated and are given in Table 3. In all cases, the correlation coefficients were higher for age 2.2 fish than age 2.3, but were below that calculated for Kvichak age 2.2 male versus female fish (Table 1), which is

Table 2. Comparison of the length of freshwater age 1. and 2. sockeye salmon for the two major marine ages in each system for the years 1957-1997. The Pearson correlation coefficient, mean difference in length (mm), and the one-tailed paired-mean *t*-test probability are given.

Marine age	Female		Male	
	.2	.3	.2	.3
Kvichak				
Pearson correlation	0.55	0.31	0.64	0.45
Mean difference	9	3	14	5
Probability	<0.001	0.13*	<0.001	0.03
Egegik				
Pearson correlation	0.78	0.82	0.78	0.75
Mean difference	6	6	12	6
Probability	<0.001	<0.001	<0.001	<0.001
Ugashik				
Pearson correlation	0.79	0.59	0.81	0.49
Mean difference	7	1	10	4
Probability	<0.001	0.22*	<0.001	0.02

* There is no measurable difference in size between female sockeye salmon age 1.3 and 2.3 for either the Kvichak or the Ugashik system.

the reference we are using for fish that are assumed to school together in the ocean.

Discussion

Spatial Segregation in the Ocean

The original hypothesis postulated that the pattern of cyclic changes in length of Kvichak sockeye salmon is specific for this stock and, therefore, an indication of spatial segregation in the ocean of this stock from other stocks. This hypothesis cannot be sustained. However, the smolts from any river system enter the marine environment as a group and they return from the sea as a group. It could be considered that the fish maintain their own density centers during the intervening time, but overlapping occurs when abundance increases and feeding areas expand laterally in every direction. This does not preclude that Bristol Bay sockeye salmon can operate as a group, partially segregated from other major sockeye salmon groups.

Origin of the Kvichak Cycle

There is a linkage from a peak escapement in a given year to reduced length of resulting age II smolts and finally to reduced average length of the return

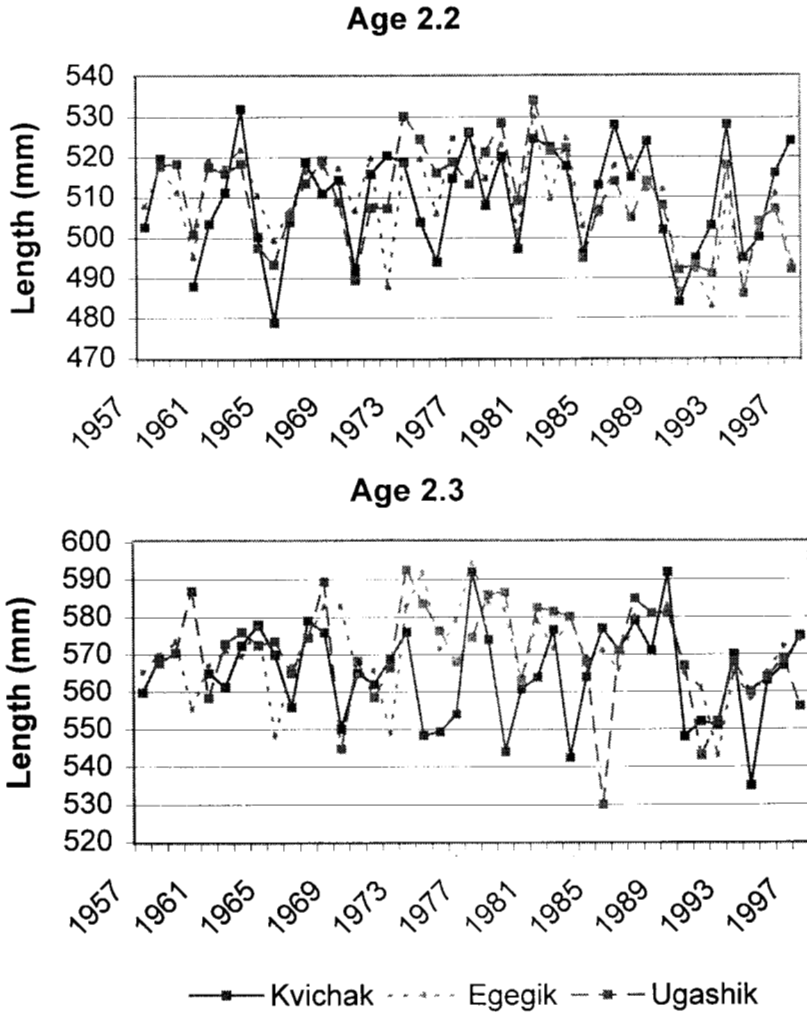


Figure 6. Average annual length of female sockeye salmon from Kvichak, Egegik, and Ugashik escapements from 1957 to 1997. Upper graph is age 2.2 and lower graph is age 2.3 sockeye salmon.

Table 3. Correlation coefficients of sockeye salmon lengths between districts by age and sex.

	Age 2.2		Age 2.3	
	Male	Female	Male	Female
Kvichak-Egegik	0.45	0.57	0.30	0.27
Kvichak-Ugashik	0.58	0.61	0.07	0.23

of age 2.2 spawners (Fig. 7). It is recognized that there are deviations from this general scheme; but age 2.2 fish is the most common element both in escapement and subsequent returns from a peak year escapement. The important conclusion is that the factors contributing to the Kvichak cycle abundance begin in the nursery lakes with smolt growth and continue in the ocean environment with competition and availability of food affecting growth.

One might rightfully ask why the Egegik or Ugashik stocks of sockeye salmon do not develop a 5-year cycle. One answer could be that the present management process does not allow large escapements, which could initiate a cycle, as with the Kvichak stock. In 1993 the total Egegik run amounted to 24 million fish with an escapement of 2.0 million spawners, i.e., a fishing mortality of about 90%.

Cyclic Manifestations in the Egegik and Ugashik Runs

The dominant peak years in the Kvichak cycle tend to reduce the length of Egegik and Ugashik fish feeding in the same areas, so in the end, all salmon of east-side Bristol Bay origin undergo cyclic changes in their yearly average length for each age group as can be seen in Fig. 7. Regular measurements of smolts, although not as extensive as adult measurements, exist from both the Egegik and the Ugashik rivers since 1978 and 1980, respectively. Although there are year-to-year fluctuations in the length of age II smolts, they are independent of the cyclic changes in Kvichak smolts (Fig. 7). In conclusion, the cyclic changes in the final lengths of sockeye salmon from Egegik and Ugashik are therefore acquired on the marine feeding grounds where they compete for food with the Kvichak salmon.

Carrying Capacity

Historically, peak years of Kvichak River sockeye have been composed largely of 2.2 fish, thus the ocean population of sockeye salmon has a high component of age 2.2 fish during periods of high ocean abundance of sockeye salmon. Age 2.2 returns to the Egegik and Ugashik river systems and probably to other systems in Bristol Bay would have periods of ocean residence coincident with age 2.2 to Kvichak River. Under the hypothesis of limited ocean carrying capacity (i.e., limitations reflected in density-dependent growth) and similar ocean distribution, one might expect length

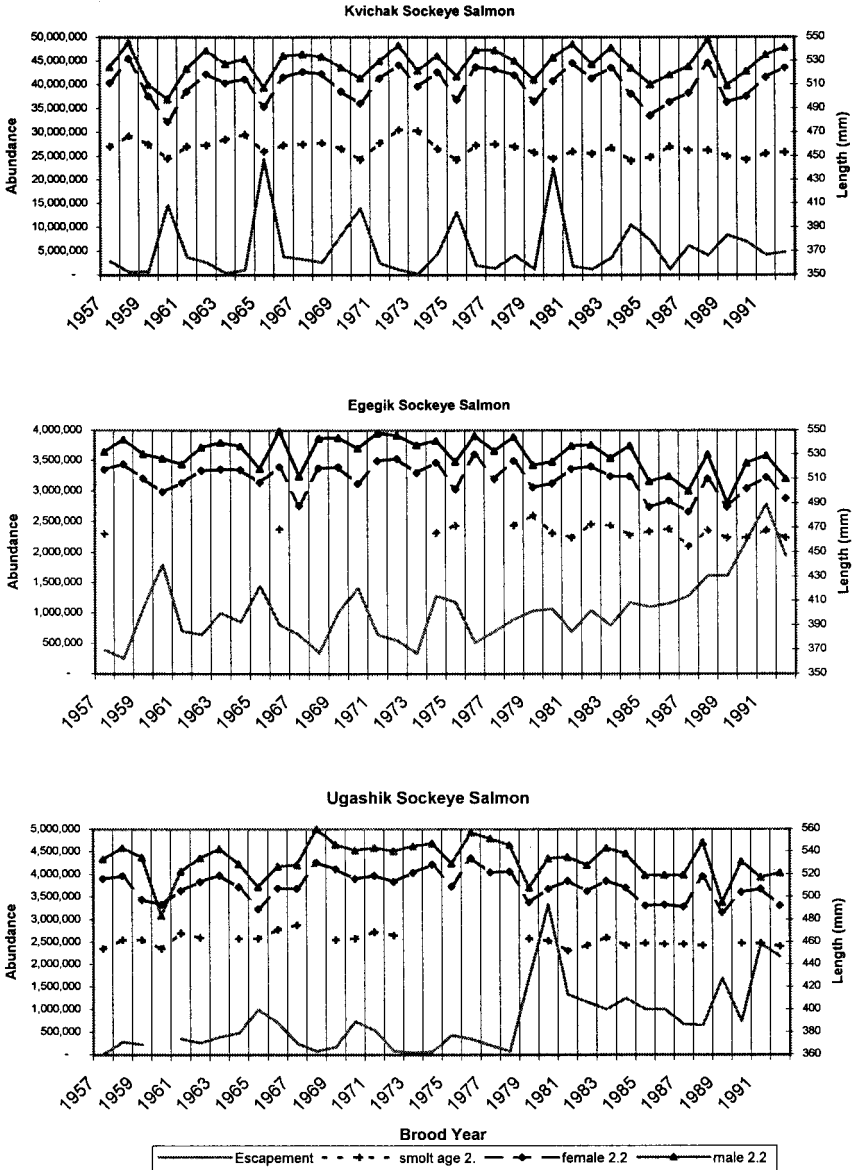


Figure 7. A comparison of the size of escapement (abundance) with the size of resulting age 2. outmigrating smolts (3 years later) and the size of age 2.2 returns (5 years later) for sockeye salmon from three Bristol Bay systems. Top: Kvichak; middle: Ugashik; bottom: Egegik. Note: Subtract 350 mm for smolt length.

at return for age 2.2 fish to be highly correlated among the three stocks examined and probably most of the stocks in Bristol Bay.

The described reduction in size of the eastside stocks of sockeye salmon can only mean a temporal taxing of the carrying capacity. This does not imply the whole North Pacific Ocean, but only selected ocean areas where the Bristol Bay salmon feed. The reduction in length becomes more impressive if length is converted to weight. According to Ricker (1976) the relationship is given by:

$$\log \text{ weight} = -2.27 + 3.27 \log \text{ length.}$$

A maximum difference in length of 3 cm between peak and off-peak years (Fig. 3), equates to a weight difference of 0.309 kg for males and 0.259 kg for females. Assuming a sex ratio of 1:1, the average weight loss is 284 g per fish. In 1995 the returns of Kvichak, Egegik, and Ugashik fish amounted to 50 million or a weight difference of 14,200 metric tons or 31,305,666 pounds. Assuming a price of \$1 per pound and a catch of 33 million pounds, this represents a loss to the fishermen of \$33 million. Since fecundity is a function of length, this also represents reduced potential egg deposition on the spawning grounds. Managers could theoretically optimize this weight loss due to size reduction and increased returns by controlling the size of the Kvichak peak escapements.

In the years since 1992-1993 there appears a general decline in length of both age 2.2 and 2.3 salmon from the Egegik and Ugashik Districts and age 2.3 spawners from Kvichak (Fig. 6). This decline could be due to recent increases in biomass of feeding salmon from all sources, both wild and enhanced stocks; but it could also be interpreted as a lowering of the general productivity in the North Pacific Ocean. We hope that continued monitoring will eventually answer this question.

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Evidence of Biophysical Coupling from Shifts in Abundance of Natural Stable Carbon and Nitrogen Isotopes in Prince William Sound, Alaska

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Abstract

Carbon and nitrogen natural stable isotope abundance was used to define signatures of food sources for juvenile herring in Prince William Sound, Alaska (PWS). Terminal feeding stage *Neocalanus* copepods collected each year at the time of peak abundance in PWS were used as a proxy for pelagic organic carbon sources. PWS copepods had relatively consistent $^{13}\text{C}/^{12}\text{C}$ content and were always statistically different from Gulf of Alaska (GOA) copepods. The inferred $^{13}\text{C}/^{12}\text{C}$ signature of GOA carbon shifted up to 5.5‰ among years whereas PWS varied < 1‰ (relative to the international stable isotope standard). The $^{13}\text{C}/^{12}\text{C}$ content of juvenile herring collected from PWS reflected changes in the isotopic signature of GOA carbon shifting seasonally and from year to year up to 3‰. GOA production thus provided an important subsidy for PWS herring. *Neocalanus cristatus* in diapause within PWS were identified as originating from the GOA by their $^{13}\text{C}/^{12}\text{C}$ signature. Each year a portion, from about half to nearly all, of diapausing copepods were of GOA origin. Physical processes such as advection by Ekman transport or deepwater exchange are postulated to transfer GOA carbon in the form of zooplankton forage into PWS. The latter mechanism explains how GOA-origin copepods would be diapausing at > 400 m within PWS.

Introduction

Productivity in marine ecosystems is not uniformly distributed. For example, large latitudinal gradients in annual productivity that are driven by the solar cycle exist at the planetary scale (Sverdrup et al. 1942). Fishery

productivity in the northeast Pacific was classified by Ware and McFarlane (1989) into large-scale domains. They classified the northern Gulf of Alaska as a Coastal Downwelling Domain. Within this domain, productivity patterns also occur at the mesoscale, ca. 100 km (Kline 1999). Since many fishes have the capability of moving across distances > 100 km, they have the opportunity to utilize different food sources occurring within a mesoscale productivity gradient. For example, amphidromous fishes living in the coastal region of Arctic Alaska make annual migrations to the more productive marine waters but overwinter in fresh water (Craig 1989). The proportion of carbon derived from marine feeding was reflected by their stable isotope composition (Kline et al. 1998). Plankton form the base for pelagic productivity and are subject to advective processes. Potentially, advection could transport pelagic production across productivity gradients. Planktivorous fishes living in less productive waters would thus be subsidized by forage advected from adjacent waters. When there is a coexisting stable isotope gradient, stable isotope ratio analysis can reveal the relative contribution of these alternate production sources for consumers such as fishes (Gearing 1988).

The stable isotopes used as natural tracers involve differing ratios of two types of carbon (^{13}C and ^{12}C) and two types of nitrogen (^{15}N and ^{14}N) that are distinguished by their number of neutrons. In biological material, approximately 1.1% and 0.4%, respectively, of the carbon and nitrogen consists of the heavy isotopes, ^{13}C and ^{15}N (Wada et al. 1991). The amount of ^{13}C and ^{15}N varies slightly due to isotopic fractionation occurring in biochemical reactions. The heavy isotope of nitrogen, ^{15}N , is enriched by 3.4% (relative to the natural abundance) with each feeding process, allowing one to use $^{15}\text{N}/^{14}\text{N}$ data to measure the trophic level of species within an ecosystem (Minagawa and Wada 1984, Cabana and Rasmussen 1994). Stable carbon isotope data can be used to trace carbon sources in food webs by exploiting natural ^{13}C gradients while using C/N ratio and stable nitrogen isotope data to correct $^{13}\text{C}/^{12}\text{C}$ values for lipid storage and trophic-level isotope effects, respectively (Fry and Sherr 1984, Kline 1997, Kline et al. 1998).

A previous report (Kline 1999), which was limited to isotopic analysis of juvenile herring and pollock and copepods, from two years, 1994 and 1995, showed that the $^{13}\text{C}/^{12}\text{C}$ content of pelagic organic carbon from PWS and the GOA was statistically dichotomous. Carbon with low ^{13}C content was diagnostic for the GOA. The PWS-GOA region has a spring zooplankton bloom that is dominated by large herbivorous copepods of the genus *Neocalanus* (Cooney 1988). These copepods are called interzonal since they spend the part of their life history actively feeding in the upper water column but also migrate to depths greater than 400 m to undergo diapause during fall and winter at penultimate life history stages (Miller et al. 1984). Their life histories are timed such that feeding stages coincide with the spring phytoplankton bloom. At other times, they are rare in the upper water column. The large size of *Neocalanus cristatus* enabled isotopic mea-

surements of individuals of late life history stages (Kline 1999). Because of their particular life history, *Neocalanus* from a given year class were sampled at two distinctive copepodite V (CV) stages by habitat: terminal feeding CV near the surface and later CV while undergoing diapause at depth (Kline 1999). Much of PWS is > 400 m deep and thus contained populations of diapausing CV *Neocalanus*. There was a regional ca. 100 km scale, i.e., mesoscale, isotope gradient in samples of feeding CV *Neocalanus* as well as bulk (species and life history stage aggregate) zooplankton samples. These data were used to characterize carbon isotope signatures for PWS and GOA. The $^{13}\text{C}/^{12}\text{C}$ signatures of diapausing CV *Neocalanus* suggested origin from the GOA as well as PWS (Kline 1999). While about half the CV *Neocalanus* from the 1994 year class that were diapausing within PWS had a PWS $^{13}\text{C}/^{12}\text{C}$ signature, fewer than 10% of those diapausing in the fall of 1995 did (Kline 1999). In 1995, juvenile herring and pollock and *Neocalanus* copepods in diapause all shifted to a low mean $^{13}\text{C}/^{12}\text{C}$ value compared to 1994. These concomitant shifts were interpreted to correspond to increased advection of GOA carbon into PWS during 1995, compared to 1994 (Kline 1999).

The purpose of this paper is to evaluate the results of Kline (1999) by examining new isotopic data collected over the 1994-1998 period as part of the Sound Ecosystem Assessment (SEA) project (see Kline [1999] for details and references); that is, to investigate if the $^{13}\text{C}/^{12}\text{C}$ temporal shifts and inferred shifts in dependency of the PWS pelagic ecosystem upon GOA carbon observed from 1994 to 1995 occurred in the 4-year time series as well. Kline (1999) could only compare $^{13}\text{C}/^{12}\text{C}$ values in herring from 1994 to the fall of 1995. Herring were sampled systematically throughout the year from four PWS sites during 1996-1998 under the SEA program (Stokesbury et al. 1999, 2000), providing more data for comparison. Kline (1999) could only infer that a large influx of GOA carbon affecting juvenile fishes occurred sometime between 1994 and the fall of 1995. Samples from the spring of 1995 are analyzed here to further elucidate timing by when the isotope shift occurred in herring.

Materials and Methods

Samples were collected as part of a large multi-investigator project called Sound Ecosystem Assessment (SEA) using a variety of vessels, nets, and research teams (Kline 1999). SEA project zooplankton and herring sampling sites were established by Cooney (1997) and Stokesbury et al. (1999), respectively, and were shown collectively in Kline (1999). Sample processing and isotopic methods were given in detail by Kline (1997, 1999) and Kline et al. (1998), but are briefly summarized here. Individual *Neocalanus cristatus* at terminal feeding stages were collected from plankton hauls made in the upper 50 m of the water column during the spring bloom period (they occur within the upper 50 m) at 20 PWS and GOA hydrographic stations. Individual diapausing *N. cristatus* were collected from plankton

nets hauled from ca. 20 m off the bottom to the surface during fall and winter at PWS hydrographic stations that had maximum depths ranging from 400 to 700 m (the nets effectively sampled the lower portion of the water column since *Neocalanus* occur during this period below 400 m; Miller et al. 1984). Juvenile herring < 15 cm in standard length were collected as part of PWS surveys in October–November 1995 and March 1996 (Stokesbury et al. 1999) and opportunistically for 1994 and early 1995 samples. Commencing in May 1996, herring were collected as part of a 2-year four-bay study (Stokesbury et al. 1999, 2000). The approximate 2-month interval of these latter samples provided better temporal coverage whereas the two PWS surveys provided better spatial coverage (all of PWS). Copepod and fish samples were frozen (-20°C) in the field and stored frozen until freeze-dried.

From each bay ca. 25 juvenile herring were systematically subsampled from 100 that were randomly sampled (see Kline 1999). Samples were freeze-dried and then ground to a fine powder. Powdered samples were analyzed for natural stable isotope abundance at the University of Alaska Fairbanks Stable Isotope Facility. Quality assurance and quality control was as described by Kline (1999).

Raw $^{13}\text{C}/^{12}\text{C}$ data were normalized for lipid content using the method of McConnaughey and McRoy (1979) which was rationalized and tested for application in PWS (Kline 1997, 1999). Herring $^{13}\text{C}/^{12}\text{C}$ data were also normalized to the trophic level of *Neocalanus* based on their $^{15}\text{N}/^{14}\text{N}$ content (Kline and Pauly 1998, Kline et al. 1998, Kline 1999). The resultant data, $\delta^{13}\text{C}'$ of copepods and $\delta^{13}\text{C}'_{\text{TL}}$ of herring, using modified conventional delta notation in ‰ units, could be compared directly and with greater accuracy than without these normalization procedures (Kline 1997, Kline et al. 1998). The $^{15}\text{N}/^{14}\text{N}$ content data were generated simultaneously with $^{13}\text{C}/^{12}\text{C}$ (Kline 1999). These nitrogen data were used for trophic level normalization and are reported here without any modification using conventional delta notation. Isotopic values are discussed in terms of relative enrichment or depletion of the minor isotope, ^{13}C or ^{15}N , thus ^{13}C -enriched means that the carbon pool contained relatively more ^{13}C . Statistical analyses, including assessment of standard deviation, *t*-tests, and ANOVA, were performed on the data using Statview on an Apple Macintosh 8500 computer. ANOVA post-hoc tests included Fisher's PLSD, Scheffe, and Bonferroni/Dunn (Abacus Concepts 1996). Statistical significance was determined by the computer program at $P = 0.05$ (Abacus Concepts 1996).

Results

Copepods at Terminal Feeding Stage

A consistency for carbon generated in PWS and to some extent, GOA, was suggested by $\delta^{13}\text{C}'$. *Neocalanus cristatus* at terminal feeding stages in PWS consistently had mean $\delta^{13}\text{C}'$ values ca. -19.5 while GOA stations had mean $\delta^{13}\text{C}'$ values that ranged from ca. -23 to ca. -17.7 (Fig. 1). ANOVA suggested

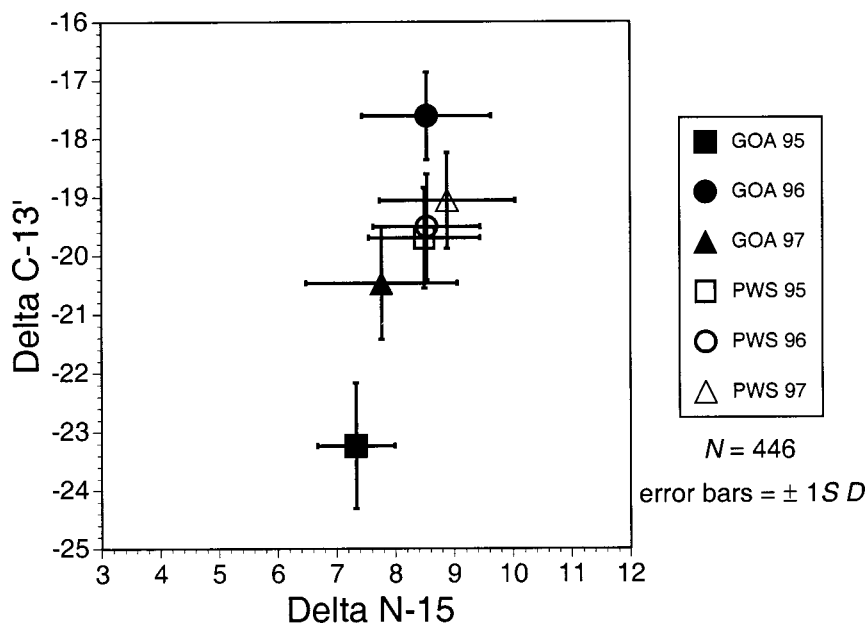


Figure 1. The carbon and nitrogen stable isotope composition of *Neocalanus cristatus* at terminal feeding stages. Note that the axes were scaled to allow including the majority of points for Fig. 2 to enable side-by-side comparisons of the figures.

that there were significant area (PWS vs. GOA), year (1995 vs. 1996 vs. 1997), and area-year interaction effects for $\delta^{13}\text{C}'$. All post-hoc tests for area and year effects were statistically significant. Because of the interaction effects, each area and each year was also tested independently using ANOVA or *t*-tests. Within GOA, year was a significant factor, and each year was significantly different from the others in post-hoc tests. Within PWS, year was a significant factor, but post-hoc comparisons were inconsistent. For all post-hoc tests, however, 1995 vs. 1997 and 1996 vs. 1997 were significantly different. Post-hoc tests for 1995 vs. 1996 had $P > 0.7$. In 1997, PWS carbon was ^{13}C enriched by 0.6‰ compared to the previous 2 years. This range in mean $\delta^{13}\text{C}'$ for PWS carbon was, however, relatively narrow compared to the differences between GOA and PWS carbon each year. A carbon isotope signature of -19.5 (S.D. = 0.9) for PWS was thus suggested from the $\delta^{13}\text{C}'$ values of *Neocalanus* at terminal feeding stages during 1995-1997. In contrast to the 0.6‰ range for PWS carbon, similarly spring-measured GOA carbon isotope signatures ranged 5.5‰ in value among years. Within-year *t*-tests suggested that GOA and PWS *Neocalanus* $\delta^{13}\text{C}'$ signatures were al-

ways statistically significant with differences in value ranging from 1.4 to 3.5‰.

Copepods at Diapause Stage

Neocalanus diapausing within the deep areas of PWS each year had a gamut of $\delta^{13}\text{C}'$ values that ranged from at least -17.0 to -24.0 (Fig. 2). These values were characteristic for both PWS and GOA carbon. Source signatures are indicated by symbols to right in Fig. 2. The $\delta^{13}\text{C}'$ values adjacent to P, G, and G* in Fig. 2 reflect the observed spring carbon isotope signatures for PWS during 1995-1997, the GOA in 1995, and the GOA in 1996, respectively. There was, however, a preponderance ($> 50\%$ of all the $\delta^{13}\text{C}'$ data) of diapausing *N. cristatus* with $\delta^{13}\text{C}'$ values lower than the P signature in Fig. 2; i.e., they had values more like those of terminal feeding stages from GOA in 1995 than any from PWS.

In the 1996 year class, diapausing copepods exhibited values similar to those observed during the spring in both GOA and PWS, as well as values unlike any observed when that year class was feeding, but similar to a previously observed GOA carbon isotope signature. Many of the diapausing copepods from the 1996 year class were more depleted in ^{13}C as well as ^{15}N compared to the generally enriched values observed over the entire study area in May and June 1996 (solid circles in Fig. 2). For example, there were no observed terminal feeding stage copepods with $\delta^{13}\text{C}'$ values < -21.0 , yet many in diapause ranged between -21.0 and -25.0 (Fig. 2). Furthermore, there were 1996 year-class copepods in diapause with ^{13}C -enriched values similar to those observed feeding in the GOA in 1996; i.e., a portion of the values were within 0.2‰ (S.E. multiplied by 2) of signature G* in Fig. 2.

Carbon Isotope Shifts in Juvenile Herring

Juvenile herring underwent large (2-3‰) shifts in their mean $\delta^{13}\text{C}'_{\text{TL}}$ values while ranging 2-3‰ at any one time (Fig. 3). While their mean $\delta^{13}\text{C}'_{\text{TL}}$ value during fall 1995 was a ^{13}C -depleted $\delta^{13}\text{C}'_{\text{TL}}$ value of -22.8 , they ranged as high as -20.0 . Given that differences in mean $\delta^{13}\text{C}'_{\text{TL}}$ were 0.6‰ or less in comparisons of site-pairs from among the 10 sites sampled (Kline 1999), a scatterplot was the only effective way for showing the value range. Furthermore, the fall 1995 data and some of the summer data, especially those from 1996, appear either skewed or bimodal. The complex, non-normally distributed nature of $\delta^{13}\text{C}'_{\text{TL}}$ data for herring was thus not unlike the nature of $\delta^{13}\text{C}'$ values observed for diapausing copepods.

The largest observed isotopic shift during 1994-1998 occurred in 1995 between the spring and fall (the solid line with negative slope shown in Fig. 3). The low fall 1995 values for herring paralleled the observed values for 1995 diapausing copepods. Low fall 1995 herring $\delta^{13}\text{C}'_{\text{TL}}$ values rebounded to higher values through the winter (shown as a dashed line in Fig. 3) and then increased sharply during the spring of 1996 (shown as a solid line

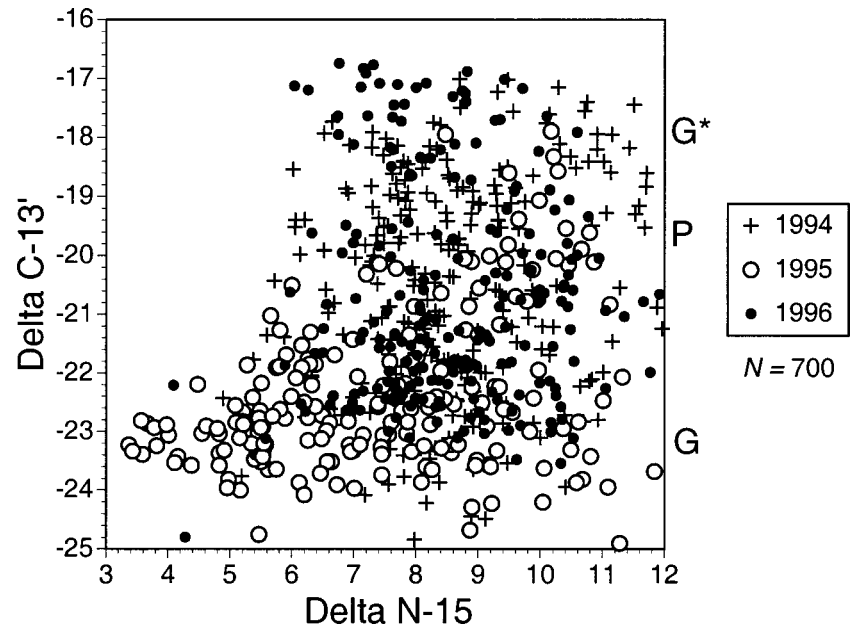


Figure 2. The carbon and nitrogen stable isotope composition of *Neocalanus cristatus* from three year classes (corresponding to the spring when they were feeding) in diapause within PWS and their correspondence to major carbon sources based upon terminal feeding stage carbon isotope values. Isotope signatures of the major carbon sources are shown as letters: G and G* correspond to mean $\delta^{13}\text{C}'$ GOA values of -23.2 and -17.7 for 1995 and 1996, respectively; and P is the overall (1995-1997) mean PWS $\delta^{13}\text{C}'$ value of -19.5. Data for copepods with $\delta^{15}\text{N} > 12.0$ ($N = 25$) are not shown.

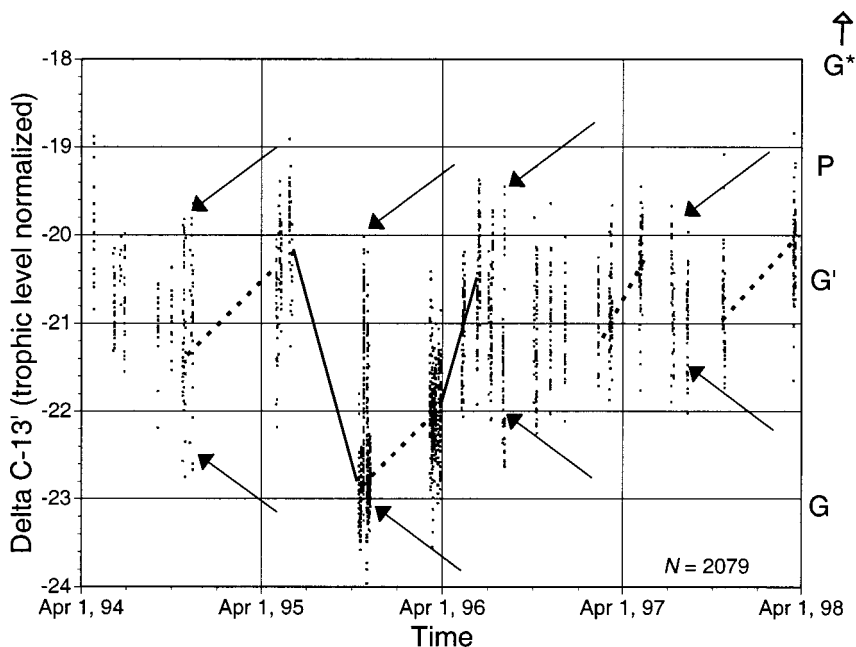


Figure 3. Shifts in carbon source dependency for juvenile herring, 1994-1998, in PWS inferred from $\delta^{13}C'$ signatures following trophic level normalization. Major features are indicated by annotations: (1) arrows indicate divergence in feeding during the growth period; (2) broken lines indicate consistent shift to more positive values during the winter; and (3) solid lines indicate a large, rapid isotopic shift leading to ^{13}C -depleted carbon during 1995 and a shift to positive values in spring 1996 when regional pelagic carbon was highly ^{13}C -enriched (carbon source signatures are annotated like Fig. 2 with the addition of G' which corresponds to the $\delta^{13}C' = -20.5$ of spring 1997 GOA carbon).

with positive slope in Fig. 3). The sharp herring spring 1996 shift thus corresponded to the ^{13}C -enriched carbon observed in the copepods in spring 1996. The most depleted herring $\delta^{13}\text{C}'_{\text{TL}}$ values observed during a given year tended to occur during the summer (see upward-pointing arrows in Fig. 3). ^{13}C -enriched carbon was apparent during the summers as well (see downward arrows in Fig. 3). During all four winters, there was a shift to more ^{13}C -enriched values (note the positive slope of the dashed lines shown in Fig. 3).

Discussion

The results of this study can be summarized as follows: (1) ^{13}C content of PWS was less variable than that in GOA; (2) the presence of low ^{13}C content carbon associated with GOA sources in herring and diapausing copepods each year suggest a recurrent isotopic gradient in the PWS-GOA region and a recurrent GOA carbon flux into PWS; (3) the influx of carbon from the GOA into PWS varied from year to year; and (4) there were seasonal shifts in dependency on GOA carbon by PWS biota. These observations and the underlying physical processes postulated to drive them are discussed below.

Neocalanus copepods feed within PWS in a relatively narrow time frame; e.g., their biomass in surface waters (upper 50 m) peaked during May (1994-1996) and they were virtually absent after early June (Willette et al. 1999). Their limited occurrence in time and space facilitated collecting representative PWS *Neocalanus* samples (Kline 1999). PWS *Neocalanus* sampled during the course of this study fell within a narrow $\delta^{13}\text{C}'$ range. Therefore, *Neocalanus* with values outside this range had to have come from the only alternate source, the GOA. Those *Neocalanus* observed in diapause during 1996 containing ^{13}C -depleted carbon thus had to have come from the GOA even when none of those from the GOA collected earlier that year during May and June cruises were ^{13}C -depleted. Only a small portion of the GOA adjacent to PWS could be physically sampled during spring cruises (e.g., 1-4 stations per cruise, see Kline [1999]; there were 4 GOA stations during May 1996). Those copepods observed in diapause with $\delta^{13}\text{C}'$ values out of the isotopic range of those observed during the spring of 1996 thus came either from farther away in the GOA or from later in the year such as early summer. The latter is suggested by recent observations of *Neocalanus* late feeding stages persisting near the continental shelf break until mid-July, but virtually absent in the upper 100 m of PWS at the same time (Ken Coyle, University of Alaska, Fairbanks, unpubl. data). SEA sampling in 1996 did not include the continental shelf break area in July.

There were three isotopic signatures for pelagic organic carbon sources in 1996: (1) a GOA carbon signature that was very ^{13}C -enriched; (2) a PWS carbon signature that was ^{13}C -enriched but not to the same extent as spring GOA carbon (1996 PWS carbon ^{13}C content was also not unlike PWS carbon of other years); and (3) a ^{13}C -depleted signature that was not sampled in spring 1996, but similar to the GOA signature of spring 1995. Since cope-

pods containing the third, ^{13}C -depleted signature were not sampled in spatial isolation (when at terminal feeding stages in the spring), statistical tests could not be performed. Nevertheless, since their range in $\delta^{13}\text{C}'$ values was several standard deviations from the enriched spring GOA or PWS values, they could be inferred to have been statistically unique. Following the spring of 1996, some of the herring shifted to $\delta^{13}\text{C}'$ values more ^{13}C -depleted carbon than the PWS signature, a recurrent summer pattern for herring. All the evidence points to low ^{13}C as being from the GOA. Therefore, during this study, with the sole exception of the spring of 1996 ^{13}C anomaly, there was a recurrent $\delta^{13}\text{C}'$ gradient between PWS and the adjacent GOA with more depleted organic carbon derived from GOA. The $\delta^{13}\text{C}'$ gradient between PWS and the adjacent GOA reflected similar patterns seen in the Bering Sea (Schell et al. 1998) and in the northeast Pacific Ocean west of Vancouver Island (Perry et al. 1999). While Schell (2000) suggested that decadal shifts in the ^{13}C content of organic carbon reflected changes in system carrying capacity, there was also interannual variability in the ^{13}C -content of whale baleen that was similar to the range observed here for spring GOA copepods. Therefore one needs to consider ^{13}C variability causation.

The ^{13}C content of pelagic biota reflects how well phytoplankton isotopically fractionate the inorganic carbon pool which is strongly dependent upon physical and chemical water column processes (Laws et al. 1995, Bidigare et al. 1997, Schell et al. 1998). Variations in phytoplankton ^{13}C content are propagated into the food chain to zooplankton and fishes (Fry and Sherr 1984). The exceptionally calm (and sunny) conditions that prevailed during the spring 1996 cruises may explain the ^{13}C anomaly that year. Furthermore, Willette et al. (1999) reported that PWS winds from late April through early May 1996 were < 3 m per second, much less than the same period for the previous 2 years when winds were only occasionally < 5 m per second and once exceeded 15 m per second. Primary production modeling suggested that calm conditions initiate a spring bloom and, if maintained, result in an intensive short-duration productivity spike, while continuous but intermittent wind events maintain a protracted but less intensive (with minor productivity spikes) period of increased productivity that when integrated over time yields more carbon per unit area (Eslinger et al. 2002). The increased phytoplankton growth rate occurring during a productivity spike is expected to decrease isotopic discrimination (Bidigare et al. 1997). The isotope observations thus corroborate the modeling implications since the proportion of carbon derived from calm conditions (^{13}C -enriched carbon) although pervasive in copepods during the spring cruise, was short-lived in effect upon herring and contributed to only a minor portion of diapausing copepods.

The consistency in ^{13}C content of the pelagic organic carbon pool generated within PWS suggests little year-to-year change in the mechanisms controlling isotopic fractionation within PWS. There was, however, year-to-year variation in the ^{13}C content of GOA carbon from near PWS. Neverthe-

less, each year a portion of diapausing copepods had $\delta^{13}\text{C}'$ values < -21.5 , lower than ever observed for copepods feeding within PWS. The recurrence of carbon more ^{13}C -depleted than -21.5‰ , ascribed to the GOA, in herring provides further evidence for the importance of productivity derived from phytoplankton that had more effectively isotopically fractionated the inorganic carbon pool (i.e., productivity resulting from slower instantaneous growth due to wind-mixing but generating more organic carbon over time within a season).

Natural stable isotope abundance demonstrates that productivity derived from the GOA can subsidize and therefore be important for biological production in adjacent coastal waters such as PWS. The flux of GOA zooplankton into Prince William Sound appears to fluctuate from year to year. This carbon flux was likely due to oceanic zooplankton species (which are dominated by *Neocalanus* spp.) that are advected by Ekman transport onto the continental shelf (Cooney and Coyle 1982; Cooney 1988, 1993). Furthermore, a "ring of zooplankton" occurring near the Gulf of Alaska continental shelf break fluctuates in size on inter-decadal time scales (Brodeur and Ware 1992). If these zooplankters are the source of the ^{13}C -depleted copepods in diapause, then their relative proportion as well as absolute abundance is predicted to fluctuate on similar time scales though modulated by the inter-annual influx variability. Carbon flux across the continental shelf is a potential mechanism to explain how climate change effected ecological regime shifts simultaneously throughout the coastal GOA area (Anderson and Piatt 1999).

It is difficult to directly observe advection of zooplankton across a continental shelf. Furthermore, the flow of water into PWS was shown by an acoustic Doppler current profiler (ADCP) mooring and ship-mounted ADCP transects to be spatially and temporally complex (Vaughan et al. 1998). This complexity coupled with the lack of precisely (e.g., 1-m scale) coupled (by species and life history stage) zooplankton distribution data, temporally and spatially, precludes assessing effects of advection upon the biota when integrated to the seasonal level. Stable isotope data provide a means of inferring the effects of advection.

High-latitude systems such as PWS are driven by the seasonal solar cycle. Seasonal patterns occur not only in the generation of organic carbon by primary producers, but also in water column physics and circulation patterns. During the summer, the regional downwelling pattern subsides and upwelling prevails (Royer 1985). It is during this period that exchange of deep PWS water with the GOA is thought to take place (Niebauer et al. 1994). Deep water exchange may explain how diapausing copepods and other zooplankton from the GOA entered PWS. During the prolonged high-latitude winter, resident consumers such as herring must subsist on the existing organic carbon pool. Their shift to more positive $\delta^{13}\text{C}'_{\text{TL}}$ values are consistent with feeding on ^{13}C -enriched carbon such as PWS pelagic carbon or littoral carbon, which is also ^{13}C -enriched (Kline 1999). The interplay of alternate organic carbon sources over longer time scales is uncertain. Sea-

sonal fluctuation in $^{13}\text{C}/^{12}\text{C}$ content of the available carbon pool, however, is likely to vary in amplitude according to the amount of GOA carbon present or according to shifts in the isotopic signature of GOA carbon, since the main source of isotopic variability found here was in the GOA while PWS was relatively constant.

Isotopic data provided evidence that oceanographic processes can vary the supply of the macrozooplankton forage base of PWS fish populations. The isotopic data from 1994 to 1998 had large year-to-year fluctuations. These may, in part, have been due to atypical climatic variability concurrent to SEA, including very large positive temperature anomalies in Alaskan coastal waters (Royer 1998). A longer time series is needed to show how changes in carbon flow may be related to changes occurring on long time scales (e.g., Schell 2000).

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Classification of Marine Habitats Using Submersible and Acoustic Seabed Techniques

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Abstract

Seabed habitats were defined based on submersible observations in coastal Newfoundland. Habitats included mud, gravel, cobble, rock, boulder, and bedrock. When macroalgae occurred it was classified into different density classes: sparse, moderate, and dense. Identification of these marine seabed habitats from a submersible was used to develop a set of calibration sites for a QTC VIEW digital acoustic classification system. Following calibration of the acoustic system in Placentia Bay, Newfoundland, seabed classification was carried out within Bonavista Bay, Newfoundland. A single submersible dive consisting of two transects over a distance of approximately 1.5 km within the classified area was carried out to independently validate the acoustic seabed classification. There was a close association between marine habitats observed from the submersible compared to seabed classification by the acoustic system. Overall, hard bottom habitats represented 88% and 83% of all submersible and acoustic classifications, respectively. Gravel habitats accounted for 12% of the submersible habitats and 10% of the acoustic classifications. Macroalgae accounted for 5% of the acoustic classifications, where these would be associated with hard bottoms. Dense macroalgae occurred for 8% of all submersible classifications. Small- and large-scale variability in seabed habitats occurred for both classification systems. Habitat spatial scales occurred mostly at distances <40 m, while the largest scales were on the order of 140-170 m. Habitat mapping in coastal Newfoundland will need to reflect the small-scale structure of the different habitats.

Introduction

Conservation management of coastal resources requires explicit knowledge of marine habitats and their associated communities (Sotheran et al.

1997). Such knowledge will permit more comprehensive stratification of resource surveys (Greenstreet et al. 1997) and should lead to the rational development and management of marine reserves. Developing remote sensing techniques to rapidly and non-invasively measure and map marine landscapes will be necessary to significantly improve our knowledge of marine habitats and species use of these habitats.

Juvenile Atlantic cod (*Gadus morhua*) are dependent on preferred demersal habitats and this dependency changes with age and density. Historically, juvenile cod varied their range in the waters off Newfoundland, expanding at high abundance and contracting at low abundance (Anderson and Gregory 2000). At higher abundance and broader distribution, juvenile cod experienced increased rates of cannibalism (Anderson and Gregory 2000). Experimental studies have demonstrated habitat dependence in ages 0 and 1 cod that varies with predation risk (Gotceitas and Brown 1993, Gotceitas et al. 1995, Fraser et al. 1996). In the field, settling juvenile cod exhibited strong association with different substrate habitats that were related to growth and survival (Tupper and Boutilier 1995a,b). Juvenile cod have been observed to use a variety of substrate habitats and predator avoidance behaviors that affect distributions at various spatial scales (Keats et al. 1987, Lough et al. 1989, Gregory and Anderson 1997).

Several years ago we began a research program to develop a digital acoustic seabed classification system for the coastal waters of Newfoundland (Collins et al. 1996, Gregory et al. 1997). This work began in association with a submersible-based research program to define marine habitats important to juvenile cod in the same region (Gregory and Anderson 1997). The purpose of the present study was to calibrate and validate a QTC VIEW (Quester Tangent Corporation, Marine Technology Centre, 99-9865 West Saanich Road, Sideny, BC, Canada V8L 5Y8) digital acoustic seabed classification system based on a set of habitat types that we had identified from submersible observations. While calibration of the acoustic system implies that the known seabed types would be classified correctly, we wanted to independently validate the acoustic classification system. Classification of seabed habitats was carried out at a location separate from the original calibration sites and validation was carried out using a separate submersible dive. In this study, we compared the seabed habitats classified independently by acoustic and submersible observation techniques within Bonavista Bay, Newfoundland.

Methods

Study Sites

Different areas were used for calibration versus classification with the acoustic system. Initially, submersible dives were made in April and October 1995 in Placentia Bay, Newfoundland (Fig. 1). The Placentia Bay study area was chosen to represent a wide range of habitats over a 15-km² area, in-

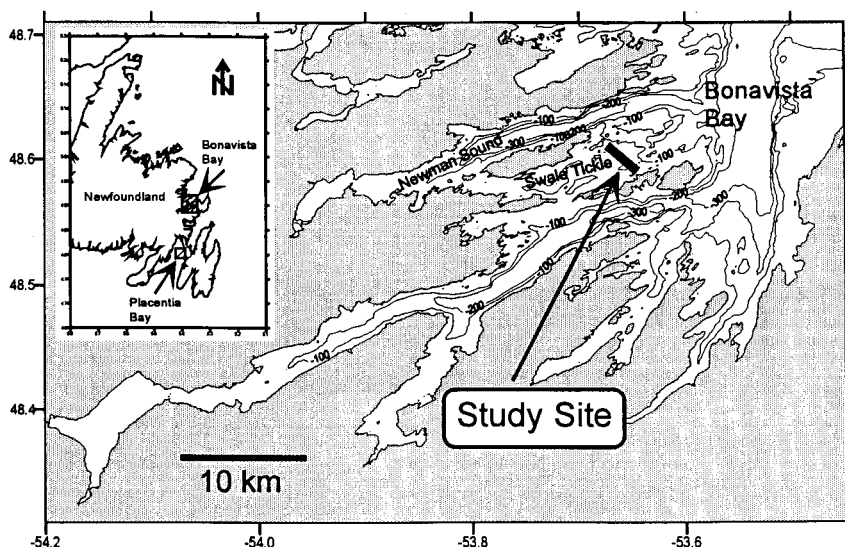


Figure 1. Southern Bonavista Bay, Newfoundland, indicating the study site where submersible and acoustic sampling was carried out. The Placentia Bay and Bonavista Bay study sites are referenced within the coastal areas of Newfoundland (inset). Depth contours are in meters from the surface.

cluding shoreline, a shallow fishing bank reaching a depth of 18 m, and a deep ocean trench that exceeded 300 m in depth (Gregory et al. 1997). Observations made during these dives were used to develop a set of seabed habitat classifications that could be reliably estimated using the submersibles and, in particular, that related to simultaneous observations of habitat use by juvenile cod (Gregory and Anderson 1997).

A second study area was chosen in Bonavista Bay, Newfoundland, for classification of seabed using the QTC VIEW system. The area was chosen for its wide range of habitat types within the coastal area of Newfoundland and its historical importance for Atlantic cod. The area being studied at present includes all of Newman Sound and Swale Tickle (Fig. 1). In this paper, we report on results from a small area in Swale Tickle that was sampled by the submersible in October 1996 and by the QTC VIEW acoustic system in October 1997.

Submersibles

Two submersibles were used during this research project, PISCES IV and SDL-1, which are free-diving and capable of operating at depths of 2,000 m and 610 m, respectively. During our studies, dives were made from depths of approximately 15 m to 300 m for durations up to 6 hours. The

submersibles were piloted near the sea floor, maintaining a constant distance as much as possible and an operating speed of 0.5 m per second. During our study, PISCES IV carried a crew of three, one pilot and two scientific observers, while SDL-1 carried a crew of four, two pilots and two scientific observers. Both submersibles were equipped with externally mounted video cameras (VHS) that were fixed in position prior to each dive, aimed forward and down to provide a continuous video record of the seabed. Visual observations were made through three small windows in the PISCES IV and through a large (ca. 1 m diameter), forward-facing window in the SDL-1. All observations made in this study used artificial light. External lighting was provided by two 1,000-W and two 500-W quartz lights (PISCES IV) and by three 1,000-W and two 250-W quartz lights (SDL-1). The submersibles were maintained aboard the Canadian Navy ship HMCS *Cormorant*.

Location of the submersibles near the seabed was determined by cross-referencing transponder signals, using a Honeywell 906 tracking system in 1995 and a TrackPoint II system in 1996. The position of the HMCS *Cormorant* was obtained using GPS (global positioning system). During each dive, a systematic record of depth was kept while underway and during periodic stops to fix the submersible position. Cross-referencing the submersible position and depth with high resolution maps of bathymetry within the dive sites, as obtained from the Canadian Hydrographic Service, resulted in a positioning accuracy of 16 m or less. In addition to the continuous video record of the seabed, we maintained a constant audio record of observations of both seabed type and the presence of Atlantic cod, and other species. The audio record was recorded to both the video tape and a separate cassette tape recorder with a continual time stamp. Finally, a written record summarizing operational aspects of each dive was maintained.

The seabed was classified into six different categories: mud; gravel (0.1-2.0 cm); cobble (2.0-25 cm); rock (26-100 cm); boulder (>1 m); and bedrock (Gregory and Anderson 1997). The mud category was soft sediment that could easily be cored, using the submersible articulating arm and sediment sampler. Gravel was a harder substrate that sometimes was covered with crinoids, starfish, and other biological life. Both of these substrate types were associated with low-relief topography. The cobble and rock substrates consisted primarily of aggregations of broken rock, typically overlying bedrock or gravel substrates. Boulders were defined as the presence of one or more large stand-alone rocks. Bedrock was a broad classification that included exposed rock, sometimes relatively smooth but more often broken rock with crevices and edges. Macroalgae in Bonavista Bay consisted primarily of Irish moss (*Chondris* sp.) and small (*Agarum* sp.) and large (*Laminaria* sp.) kelp. For our purpose here, algae was simply classified according to percent cover as sparse (1-5%), moderate (6-25%), and dense (>25%) (Gregory and Anderson 1997). Sometimes it was not possible to classify the degree of macroalgae occurrence based on the video and audio records.

Calibration

A total of 15 submersible dives were conducted in April and October 1995 in Placentia Bay, Newfoundland. Seven dives were made using SDL-1 and eight using PISCES IV, where duration ranged from 0.8 to 5.2 hours. Seabed habitats identified and mapped during these submersible dives were used to develop a set of representative habitat types for the calibration of the acoustic system. These calibration sites included mud (2 sites), gravel (3 sites), rock (2 sites), macroalgae on rock (2 sites), and were selected from areas large enough for calibration data to be collected while the ship lay idle for 5 or more minutes. The calibration sites ranged in depth from 18 m to approximately 300 m and consisted of low relief (7 sites) and high relief (2 sites).

During June 1997, QTC VIEW calibration files were collected at each of the nine sites in Placentia Bay, following standard operating procedures for the system. The quality of each calibration file, consisting of approximately 50 records, was examined in three-dimensional feature vector space (Q-space). A tight association of values from each calibration file and a broad separation of values among different seabed types were criteria for accepting high quality calibration data. From the total set of calibration files collected, we selected six files representing four of the six different habitat types identified using the submersibles for the creation of a calibration catalogue: mud (2 sites); gravel (2 sites); rock; and macroalgae (Fig. 2).

Digital Acoustic Seabed Classification

The QTC VIEW seabed classification system is an integrated acoustic signal processing system which analyzes and classifies the first return echo from a ship's echo sounder. Five acoustic echoes are normalized into a single return signal for classification. Each return signal is digitally transformed and analyzed to provide 166 discrete parameters which collectively characterize signal shape and strength. These parameters are then reduced to three feature vectors (Q-values) using principal component analysis (PCA). The feature vectors, or eigenvalues, are then compared to a calibration catalogue of known seabed types using cluster analysis. The calibration catalogue consists of a series of hyper-ellipsoids representing each calibration file in three-dimensional feature vector space (Q-space). Each return echo is classified into one of the calibration seabed types based on its closeness of association in Q-space. A measure of association is also calculated, where close association of each classified signal with one of the calibration types results in a high measure of "confidence." The QTC VIEW system used in this study was connected to a 38-kHz Simrad EQ100 echo sounder hull-mounted in the 23-m research ship *Shamook*. The echo sounder has a 10-degree beam angle, and was operated at 1 ping per second, a range of 150 m at one-tenth power, and a bandwidth of 0.3 ms. Position data were collected using differential GPS.

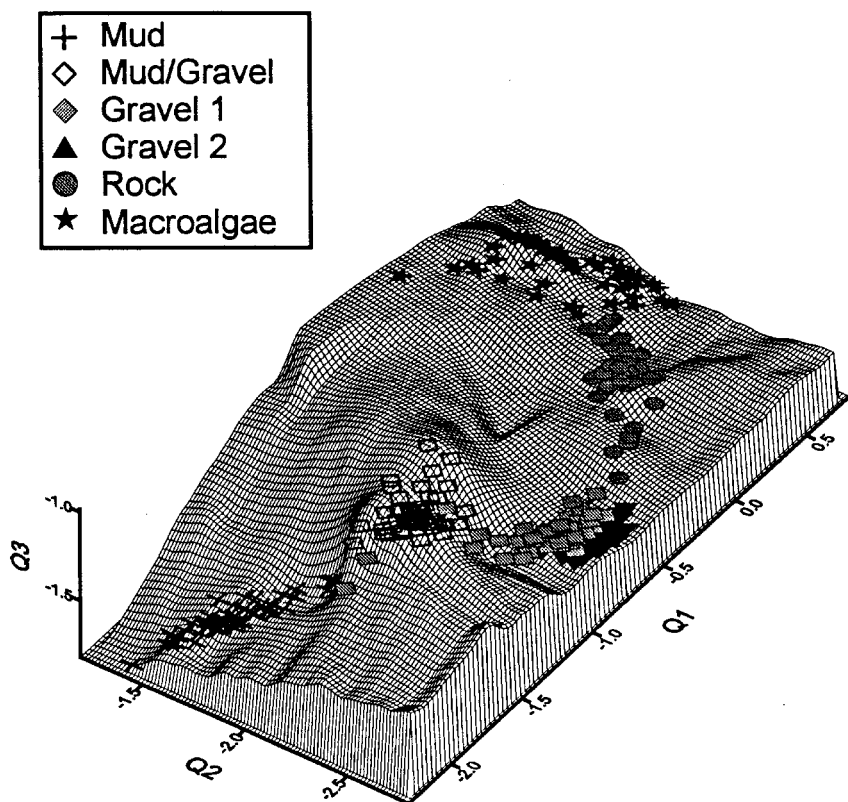


Figure 2. Calibration data collected at six different sites in Placentia Bay, Newfoundland, and plotted on a three-dimensional surface of Q -space.

Validation

A single submersible dive using SDL-1 was conducted in October 1996 within Swale Tickle, Bonavista Bay (Fig. 1). This dive consisted of two transects, one during daylight and a second at night. The dive commenced at 1422 hours and ended at 2048 hours local time. The dive track began in 70 m of water and crossed two submarine ridges which reached depths of approximately 20 m before descending to 102 m. The night transect retraced the day transect, although it was shorter in duration due to time constraints (Fig. 3).

Acoustic seabed classification surveys were carried out in Bonavista Bay, Newfoundland, during October 1997. Two acoustic transects selected in the vicinity of the submersible dive passed on either side of the submersible transects and actually crossed at one end (Fig. 3). These transects

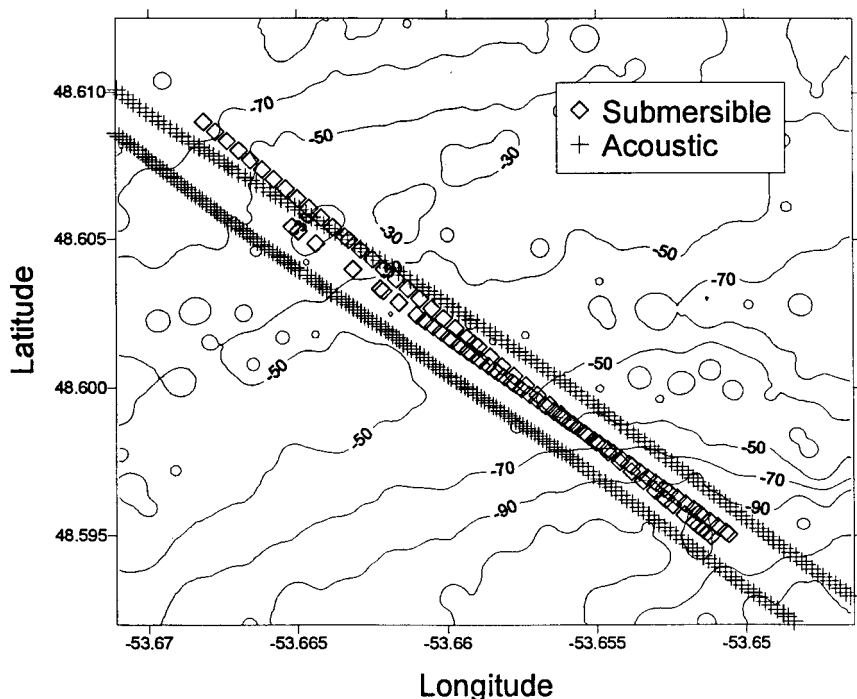


Figure 3. Submersible and acoustic sampling transects sampled in Swale Tickle, Bonavista Bay. Each symbol represents an observation where the seabed habitat was classified. Depth contours are in meters from the surface.

were selected because of their close proximity to the submersible dive. However, they are part of a much larger data set collected in June and October 1997 throughout Swale Tickle and Newman Sound.

The QTC VIEW seabed classification system classifies each normalized return signal with respect to the set of bottom types in the calibration catalogue. Classification results from the bottom type that the acoustic signal is most closely associated with in Q-space, whether that seabed type is in the catalogue or not. For example, our calibration catalogue did not include an explicit "cobble" bottom type even though this was known to be an important seabed type. Therefore, it will be necessary to carry out some degree of postclassification analysis when the calibration catalogue is incomplete compared to all possible seabed habitats that might be sampled during classification surveys.

We carried out a comprehensive postclassification analysis of the QTC VIEW data collected in Bonavista Bay. This analysis was done primarily by comparing the data in Q-space simultaneously with its position within the

bottom topographic landscape. We developed a high-resolution map of the topography based on bathymetric data recently collected by the Canadian Hydrographic Service which could be purchased from Nautical Data International Ltd., St. John's, Newfoundland. We used kriging techniques to create a smooth high-resolution bottom from the discrete depth data. Secondly, we used biological observations from the submersible dives to further refine our postclassification procedures. For example, we knew that macroalgae did not occur deeper than approximately 50 m within the study area. Therefore, any classification data that indicated "macroalgae" which occurred deeper than 50 m was postclassified into a new category. The postclassification analysis is both extensive and ongoing (Anderson et al. 1998). Our analysis resulted in the creation of three new seabed categories: cobble or sparse algae, cobble and steep relief, and other. In addition, we refined the boundaries among the original four seabed types used for the calibration catalogue.

Results

Submersible Dive

Bedrock was the dominant substrate type, representing approximately 78% of the bottom type observed during both transects (Table 1). Gravel habitat ranked second at 12%, cobble was 9%, and rock habitat was <1%. Macroalgae occurred predominantly on bedrock and was observed over 18% of the area surveyed. Within the macroalgae, sparse cover accounted for approximately 11% of all macroalgae habitat, moderate cover for 45%, and dense cover for 44%.

Spatially, gravel and cobble substrates tended to occur at the bottom of bedrock slopes (Fig. 4). Bedrock habitat was extensive, ranging from distances of approximately 10 m to greater than 100 m while traversing the submarine ridges. Macroalgae occurred at <50 m of water depth in all but one instance. During the night transect, one low-relief area was encountered at a depth of approximately 60 m, consisting of a gravel bottom but covered by free-floating Irish moss, suspended immediately above the seabed (Fig. 4). On the two ridges there was no consistent pattern to the occurrence of dense algae. On the day transect, dense algae was observed on the approaching (west) side of the first ridge encountered, with moderate algae on the descending side with very little algae on the second ridge (arrow, Fig. 4). On the night transect, dense algae was observed on the ascending slope of the first ridge encountered (i.e., the second ridge encountered in the day dive) and primarily moderate algae was encountered on the second ridge encountered (i.e., first ridge day dive). To some degree this demonstrates the variability in observations over small spatial scales orthogonal to the dive transects.

Table 1. Summary of substrate habitats and macroalgae cover observed during two submersible transects in Swale Tickle, Bonavista Bay, Newfoundland.

Substrate type	Night dive observations	Night dive proportion (%)	Day dive observations	Day dive proportion (%)
Seabed				
Bedrock	175	79.2	103	76.3
Rock (26-100 cm)	3	1.4	0	0.0
Cobble (5-25 cm)	19	8.6	14	10.4
Gravel	24	10.9	18	13.3
Mud	0	0	0	0
Macroalgae				
Sparse (1-5%)	6	14.3	2	8.3
Moderate (6-25%)	15	35.7	13	54.2
Dense (>25%)	21	50.0	9	37.5
Total area	42	19.0	24	17.8

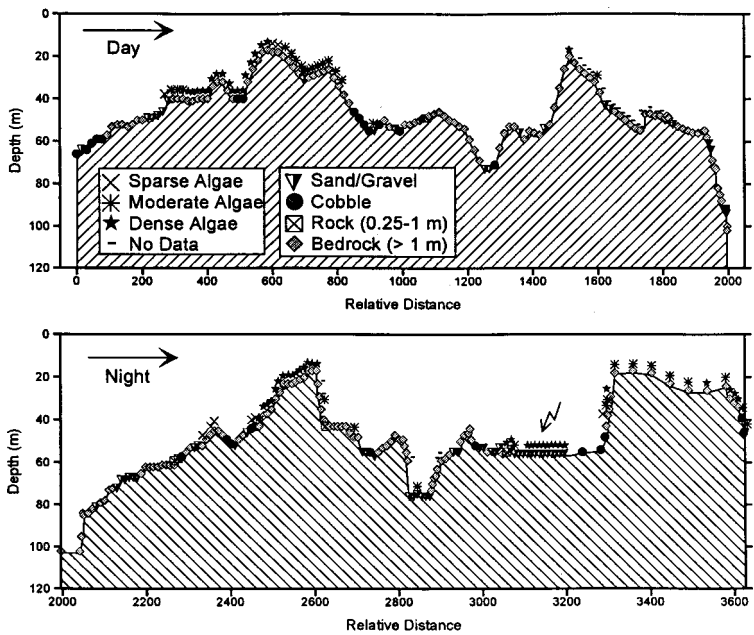


Figure 4. Submersible observations of seabed substrate and macroalgae cover along the day and night transects, Swale Tickle, Bonavista Bay. The jagged arrow indicates the area of free-floating Irish moss.

Acoustic Classification

A total of 864 classifications were included in the acoustic data set, classified into seven different seabed types (Table 2). Rock and cobble/sparse algae were the dominant seabed types classified by the QTC VIEW system, accounting for 61.4% of all seabed classifications. Steep cobble/rock type and gravel accounted for a further 32.5% of the acoustic seabed classifications. Macroalgae classification accounted for 4.5% of the bottom types while mud only occurred in a single classification. Thirteen acoustic classifications, 1.5% of the total, were classified as "other." This classification type was spaced sporadically along the acoustic transects, usually associated with a transition between habitat classifications.

Combining rock with steep cobble/rock seabed types accounted for 54.9% of the total classifications. These seabed classifications primarily differ by the degree of bottom relief, as both were essentially hard rocky bottom types. Macroalgae is mostly associated with hard substrate, to which it is attached. If the macroalgae and cobble/sparse algae classification types are combined with rock and steep cobble/rock then we estimate that 82.7% of the seabed within the acoustic surveyed area was some form of hard rock bottom.

Spatially, macroalgae was primarily associated with the shallow ridges that occurred within each transect (Fig. 5). Acoustic signals classified as macroalgae typically occurred in association with the cobble/sparse algae signal. While we cannot distinguish this signal between "cobble" versus "sparse algae" in Q-space, the occurrence of this classification type in shallow waters associated with the macroalgae classification indicates that the cobble/algae signal was probably sparsely occurring macroalgae on a rock substrate. This was confirmed by comparison with the submersible data where moderate and dense algae occurred in these areas. However, the cobble/algae classification also occurred at depths greater than macroalgae was observed to grow within the study site, indicating that a similar acoustic classification signal occurred for a hard and uneven surface that was similar in classification to a sparse macroalgae signal on a hard bottom.

A single macroalgae classification was observed on transect 2 at the bottom of a steep slope at approximately 65 m, preceded by a cobble/algae classification and followed by a bedrock classification. This single classification may be an artifact or may be associated with free-floating macroalgae, as was observed during the submersible dive.

Bedrock classification occurred throughout both transects, usually as a continuous classification at the scale of meters, but sometimes as an individual classification associated with other seabed types. The gravel classification usually occurred as a continuous signal in low-relief areas but also occurred as single classifications among other seabed types. The small-scale variability (i.e., single classifications) in the occurrence of bedrock and gravel is consistent with small-scale variability of seabed habitats observed from the submersible.

Table 2. Summary of seabed types classified by the digital acoustic seabed system for two transects sampled within the submersible dive site.

Type	Proportion (%)	Acoustic observations
Rock	38.1	329
Steep cobble/rock	16.8	145
Cobble or sparse algae	23.3	201
Macroalgae	4.5	39
Gravel	15.7	136
Mud	0.1	1
Other	1.5	13

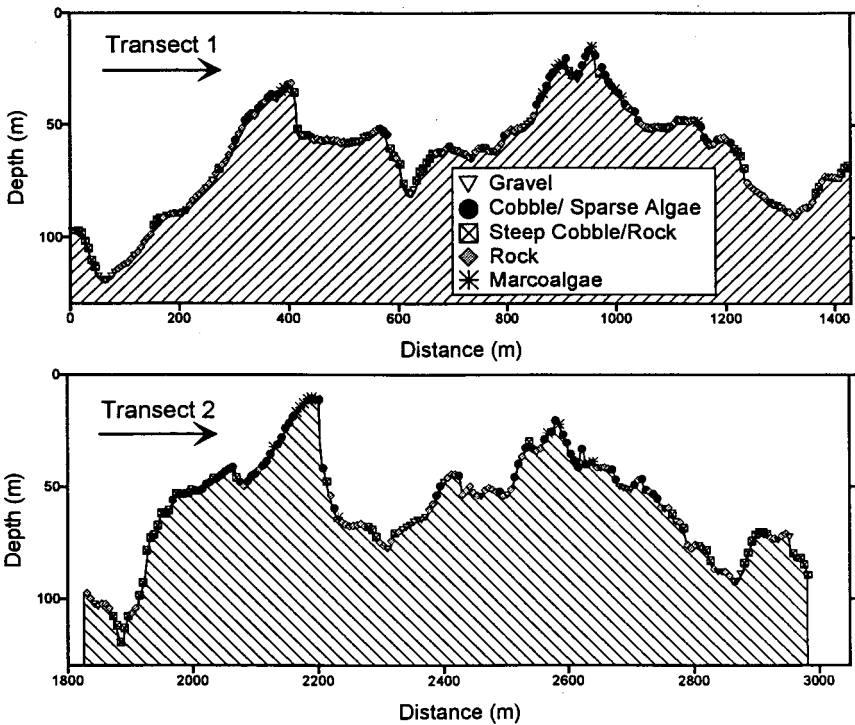


Figure 5. Digital acoustic classification of seabed types along two transects in the vicinity of the submersible transects, Swale Tickle, Bonavista Bay.

The scale of spatial variation in habitats was similar for the submersible and acoustic methods. Both methods demonstrated that small-scale variation at distances <50 m predominated while common habitats >100 m were rare (Fig. 6). At large scales, both methods classified several continuous habitats >100 m in length. The submersible data measured three areas 160-170 m in extent, while the acoustic method measured a maximum extent of 140 m. Finally, comparison of habitat classification distances between transects indicates that the acoustic method was less variable.

Discussion

Comparison of seabed classification between the two methods was reasonably good. For example, from the submersible data we classified gravel habitat to occur over 12.1% of the area compared to 15.7% for the gravel classification by the acoustic system (Fig. 7). Hard bottom types (bedrock, rock, and cobble) accounted for 88% of the seabed surveyed by submersible compared to the total hard bottom types classified by the acoustic system of 82.7%. Finally, from the submersible, dense macroalgae occurred over 7.9% of the total area surveyed compared with the macroalgae signal from the acoustic signal over 4.5%. This close comparison of the acoustic system to habitats classified using submersibles indicates that the acoustic classification system can realistically sample habitats at scales that are relevant to biological study. Further, the ability of the acoustic system to distinguish both small- and large-scale habitats will be important in mapping seabeds. The scale of spatial variability along the transects demonstrated that small scales of 10-20 m distance were a predominant feature of the seabed habitats. The largest-scale features were on the order of 140-170 m. In coastal Newfoundland, it will be necessary to develop habitat maps that reflect this small-scale structure, in order to quantify suitable habitats and to realistically define borders between different habitats.

Seabed classification by submersible and by acoustic signal interpretation are fundamentally different observational systems. The submersible observations rely on visual interpretations of the seabed and are intentionally biased to represent our best interpretation of fish habitats. Therefore, our classifications of rock (25-100 cm) and cobble (5-25 cm) represented bottom habitats that we could identify but are also important refugia for juvenile cod (Fraser et al. 1996, Gregory and Anderson 1997). In contrast, soft smooth bottoms seldom, if ever, were associated with cod. However, we occasionally discovered such bottoms may have consisted of a relatively thin layer of silt, only a few centimeters thick, overlying a very hard bottom. Visually, we would not classify these bottoms differently. However, the acoustic system would classify these differently, one as soft and smooth and the second as hard and smooth.

In our comparison of the submersible and acoustic seabed classification data, we have tried to categorize the acoustic data to resemble the submersible data as much as possible. However, much more information is

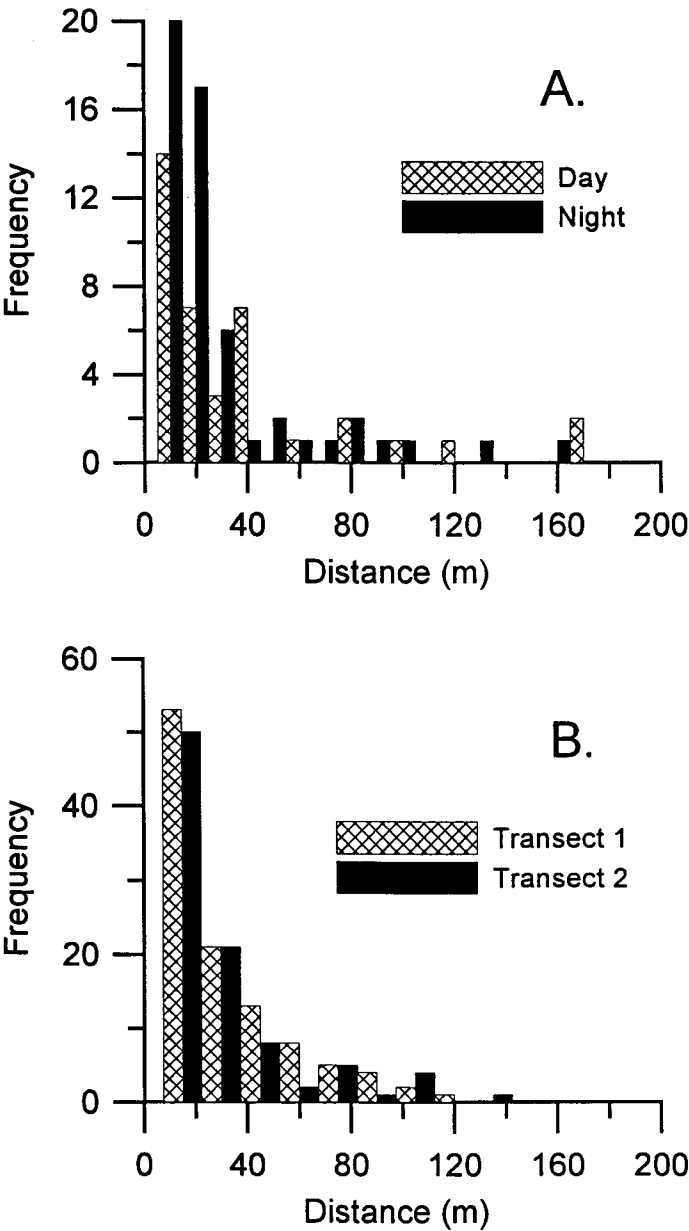


Figure 6. Frequency of occurrence of continuous habitat classifications using (A) submersible and (B) acoustic methods. Distance was measured as the sum of individual habitat observations that did not change along a transect.

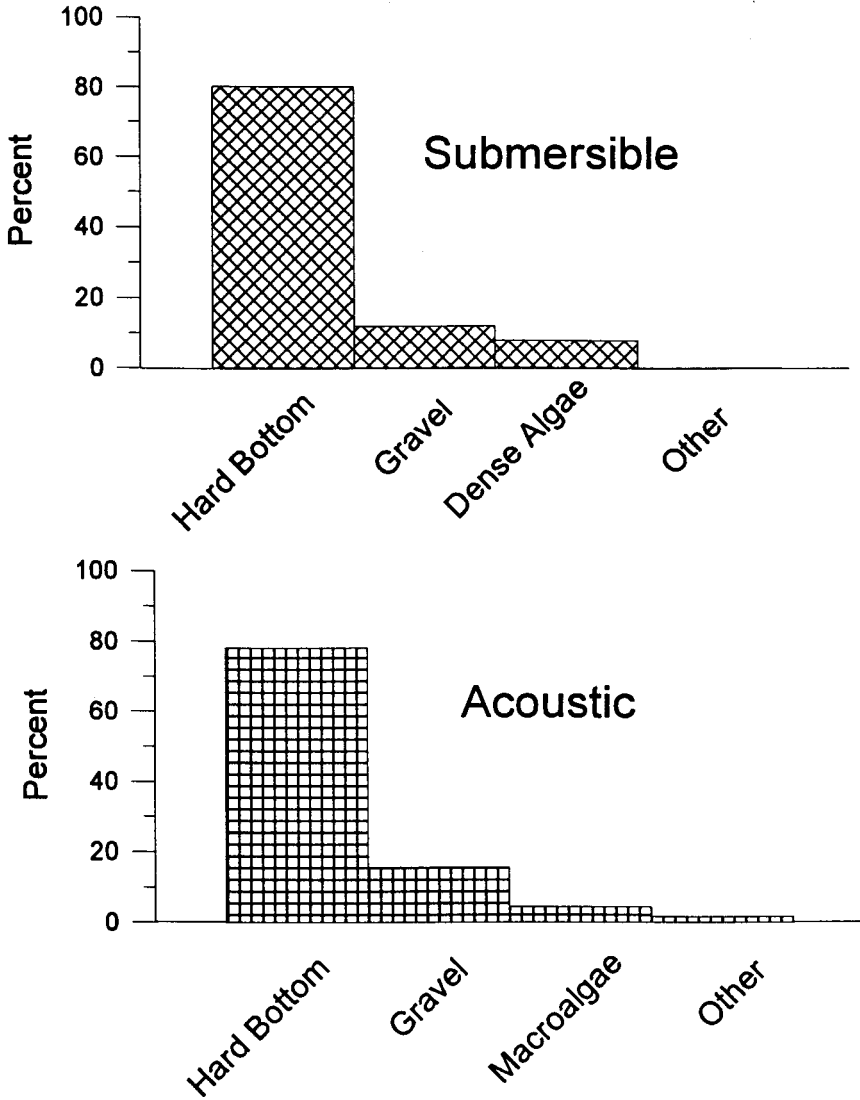


Figure 7. Frequency of occurrence of seabed habitats classified by submersible and acoustic techniques summarized into four broad categories. Hard bottom represents a composite of different habitats classified by each method. Gravel, dense algae, and macroalgae are original classification categories. Other represents habitats such as mud and transitional bottom types that were not common within the study area.

available from the acoustic system. For example, we believe the steep cobble/rock classification is an unique combination of high relief with hard bottom that was associated with rough cobble at the bottom. The submersible data did not have any comparable category. The steep cobble/rock classification typically occurred in association with high-relief bottoms, such as cliffs which were >10 m in height. Side-shadowing of an acoustic signal is associated with backscatter from high-relief bottoms. This occurs when part of the acoustic signal is returned from a steeply sloping bottom ahead of the remaining signal that has not yet come into contact with the bottom. In addition, we know from our submersible observations that a rough cobble bottom often occurs at the bottom of steep cliffs. Therefore, we should expect that such habitat would produce a unique acoustic signal. We also know from our submersible observations that juvenile cod are often associated with such areas. Therefore, the steep cobble/rock acoustic classification is an important habitat type that was routinely identified by the acoustic system.

The cobble/sparse algae classification appears to represent a relatively hard but rough bottom substrate. At shallow depths (<50 m) this signal was often associated with low-density macroalgae concentrations. However, at greater depths a similar classification of the acoustic backscatter signal did not have macroalgae associated with it. In spite of these obvious biological differences, we expect both habitat types will be of importance to juvenile cod. It was also possible to distinguish between very soft bottoms versus less soft bottoms, which may be a combination of mud with some gravel, versus a hard gravel bottom. In each case, all are low relief and relatively smooth. Distinguishing between such seabed habitats may be important for flatfish and other benthic species.

The QTC VIEW seabed classification system is "trained" to recognize specific seabed types based on the calibration files built into the calibration catalogue. This approach to seabed classification assures the user that seabeds will be classified correctly with respect to the original calibration files. However, the capabilities of the system will be limited by the extent to which the original calibration files adequately represent all seabed types to be classified. The QTC VIEW system classifies each return signal. Therefore, seabed types not explicitly represented in the calibration catalogue will be classified incorrectly. Ideally, a calibration catalogue would contain all seabed types that would occur within an area to be surveyed. However, this may be impossible without extensive and detailed prior knowledge of seabed habitats within an area of interest. In addition, it may prove difficult to collect high-quality calibration data files when seabed habitats of interest are small in area, such as high-relief slopes. Therefore, it may be necessary to develop postclassification procedures for most applications.

Acoustic classification by the QTC VIEW system appears to hold promise as an important tool for surveying and mapping seabed habitats. Once calibrated, it offers a relatively low-cost, nonintrusive method of surveying seabed habitats. Further refinement and extension of our calibration

files should lead to a real-time classification system that is capable of distinguishing among all important habitat types.

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Environmental Factors, Spatial Density, and Size Distributions of 0-Group Fish

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Abstract

Data from the August-September 1985-1998 joint Norwegian-Russian annual 0-group survey in the Barents Sea and adjacent waters 1985-1998 are used to describe and discuss the spatial density and size distributions of 0-group fish in relation to temperature, salinity, and daylight. The eight species of 0-group fish studied are cod, haddock, saithe, herring, redfish, capelin, polar cod, and Greenland halibut. The ambient temperature and salinity are calculated separately for each species in the Barents Sea and the Svalbard waters as well as the total area. The interannual variations of ambient temperatures are found to be greater than the corresponding variations of mean temperature at fixed stations along the Kola section, commonly used as the area's temperature index. This finding calls for caution when observations at fixed locations and depths are used to characterize variations in the environment of the organisms. Observed differences in mean length within and between years for each species are compared with the associated variations in ambient temperature and salinity. Polar front and thermocline form natural boundaries for the 0-group spatial density distribution, but the vertical density distribution of the 0-group may change with day and night. In all 5 years considered, the day-time vertical distribution of 0-group cod is about 10 m deeper, with significant differences in 3 out of 5 years.

Introduction

Sea temperature influences abundance and size of larvae and 0-group fish (i.e., age-0 fish) in the Barents Sea area (Nakken 1994; Loeng et al. 1994; Ottersen et al. 1994, 1998). Loeng et al. (1994) found that the length of 0-group cod, haddock, and herring mainly showed the same fluctuations since the time series were established in the late 1960s and that their

mean lengths tended to be longer in warm years than in cold years. Also the 0-group capelin increased in size with increasing temperature but with a different pattern than other species. This was explained in terms of the different environment inhabited by the capelin larvae in comparison to the other three species. Hylen et al. (1995) found a difference between the vertical density distributions of 0-group fish at day and at night, based on acoustic scattering values sampled at a fixed location.

The present paper is an attempt to describe and characterize the hydrographic environment of 0-group fish in the area in more detail than has been done hitherto in order to identify possible effects of temperature, salinity, and daylight on 0-group size, density, and abundance. The study is based on density estimates from pelagic trawl catches, depth distributions of 0-group densities obtained from acoustic scattering values, and temperature and salinity from CTD data. The species are cod, haddock, saithe, redfish, herring, capelin, polar cod, and Greenland halibut.

Materials and Methods

The present study uses data from the 1985-1998 joint Norwegian-Russian annual 0-group survey in the Barents Sea (ICES 1985-1996, Institute of Marine Research 1997-1998), which has been carried out annually in August-September since 1965. Gears and sampling procedures were standardized in 1985 (Nakken and Raknes 1996). The trawl stations from 1995 and 1996 are shown in Figs. 1 and 2. Since 1990 the acoustic backscattering values from 0-group fish are routinely obtained from data collected along the courselines (Knudsen 1990), but only the data from 1994 to 1998 are used here. No acoustic sampling was done in a small area west and south of Novaya Zemlya, but the warm-water fish, e.g., cod, have low population density there. Temperature and salinity were sampled at all trawl stations.

Trawl Data and Species Composition

The standard trawl haul procedure includes a towing distance of 0.5 nautical miles (nm) at each of 3 depths with the headline at 0, 20, and 40 m, thus mixing the catches from each step (Fig. 3). Additional steps at 60 and 80 m and deeper are included when echo-sounder recordings indicate the necessity. Catches aggregate information about density, species, and length composition into two dimensions (2D) and provide no information on the depth distribution of the 0-group fish within the depth range of each haul. The vertical profile of 0-group density is recovered from acoustic backscattering values (Sa-values) described below.

Catch Density Index

Density indices of each species of 0-group fish are calculated from pelagic trawl catches. Assuming the vertical extension of the 0-group is completely covered by the sampling, we use the number of fish from a species in a

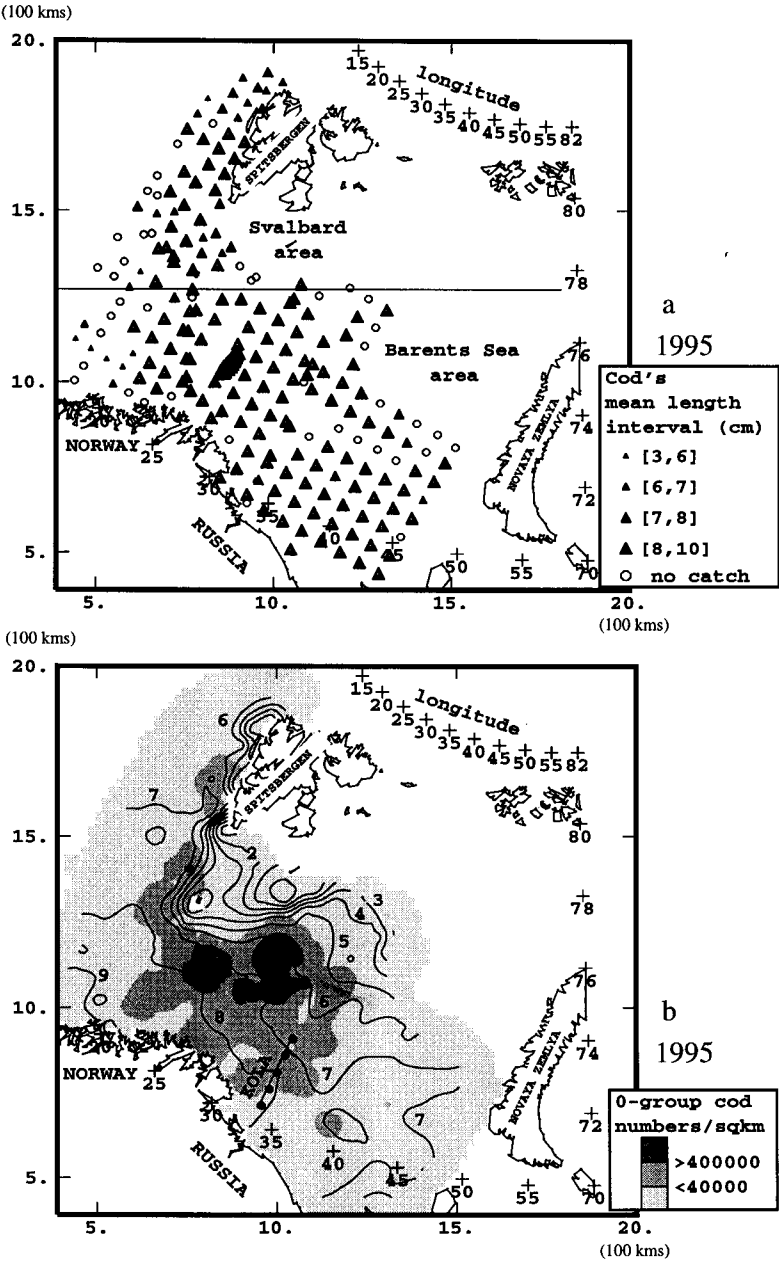


Figure 1. (a) Trawl stations and the mean lengths of 0-group cod at each station in 1995. (b) Isotherms at 30-m depth and density (numbers per km²) of 0-group cod from trawl catches in 1995. The position of the Kola section is indicated.

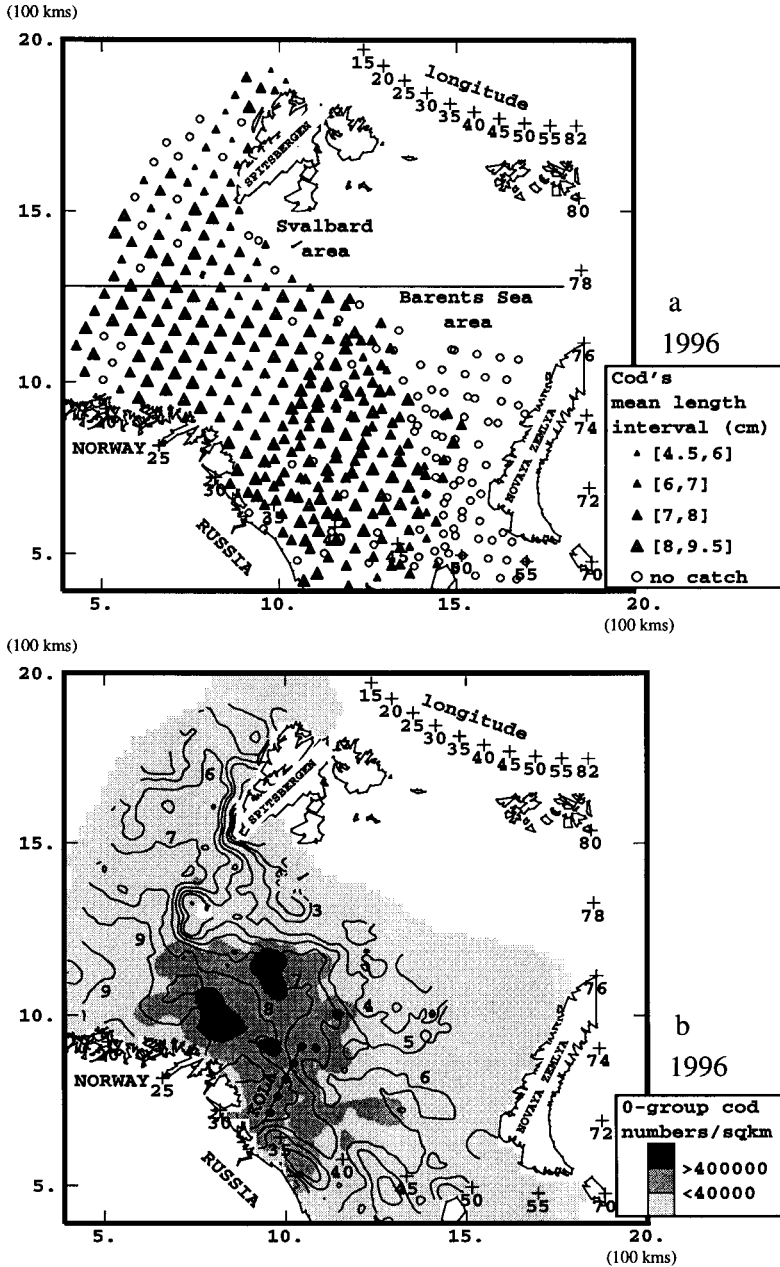


Figure 2. (a) Trawl stations and the mean lengths of 0-group cod at each station in 1996. (b) Isotherms at 30-m depth and density (numbers per km²) of 0-group cod from trawl catches in 1996. The position of the Kola section is indicated.

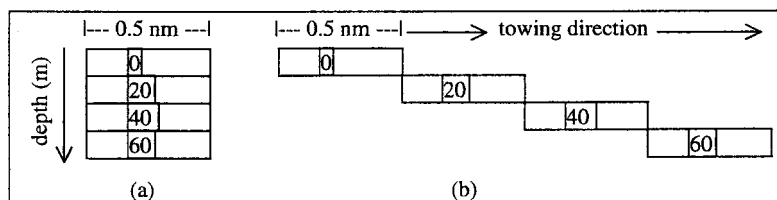


Figure 3. (a) Schematic representation of a trawl haul including 4 depth steps. (b) The way the haul is carried out.

trawl catch as an index of numbers in the water column per unit surface area regardless of the number of depth steps and total distance towed (Fig. 3). With this preferential sampling we use catch (per 0.5 nm) as a 2D density index. The older practice (dividing by the variable distance hauled) led to relative under- or overestimation as steps are added or cancelled; the dominance of 3-step hauls reduces the distortions thus introduced.

Acoustic Data and Vertical Density Profile

Column or area backscattering values were sampled with echo-integrators (Knudsen 1990, Foote et al. 1991). The Sa-values are partitioned as described by Nakken et al. (1995) into 0-group (except herring), 0-group herring, plankton, and others.

To obtain a detailed vertical density profile of 0-group Sa-values, the acoustic backscattering values per unit area (Sa-values) were re-aggregated from the archive echogram data in blocks of 5 nm long and 5 m deep from 10 m and downward. Using the trawl catch species composition of neighboring stations, the Sa-values of the 0-group were partitioned into each separate species according to the description by Nakken et al. (1995). Thus all species (except herring) must be assumed to have the same vertical Sa density profile (in relative terms). The information on the vertical Sa density profiles are used for two purposes: (1) to estimate the three-dimensional (3D) density distributions by distributing the catch data according to the vertical Sa-profile at each point, for a joint study of fish distribution, temperature and salinity; and (2) to investigate vertical day/night differences in the depth distributions of the 0-groups.

Estimation of Ambient Temperature and Salinity

The sampled data are values of regionalized stochastic variables. An unknown value at an unsampled location, e.g., at a point of the grid, is estimated on the basis of observed values from neighboring locations by applying the technique of geostatistics using the software ISATIS (Cressie 1991, Stensholt and Sunnanå 1996, ISATIS 1997).

We define the ambient temperature T_{amb} as in equation 1

$$T_{amb} = \frac{\iiint \rho(x, y, z) \times T(x, y, z) \times dx \times dy \times dz}{\iiint \rho(x, y, z) \times dx \times dy \times dz} \quad (1)$$

Here (x, y) are horizontal coordinates, z depth, $\rho(x, y, z)$ the fish density for a species, and $T(x, y, z)$ the temperature. The integrals are over the distribution volume of each species. In practice they are estimated by sums over 2D or 3D grids ($20 \text{ km} \times 20 \text{ km}$ or $20 \text{ km} \times 20 \text{ km} \times 5 \text{ m}$).

Three different estimates of T_{amb} are computed:

1. The estimate $T_{amb}(d)$. In summation over the 2D grid $\rho(x, y, z)$ is replaced by the catch density $\rho(x, y)$ and $T(x, y, z)$ by the average temperature from surface down to depth d .
2. The estimate $T_{amb}(thermocline)$. This is similar to 1, but with $T(x, y, z)$ replaced by the average temperature from surface down to the thermocline depth; this is defined as 10 m below the largest vertical temperature gradient.
3. The estimate $T_{amb}(acoustic)$. In summation over the 3D grid $\rho(x, y, z)$ is replaced by the estimated 3D density for the species as described above.

Similarly, for calculation of ambient salinity S_{amb} we use salinity $S(x, y, z)$ in equation 1 and the $S_{amb}(d)$, $S_{amb}(thermocline)$, $S_{amb}(acoustic)$ are computed.

In the Barents Sea, during late summer, there are large vertical temperature gradients in the upper 100 m where the 0-group is situated. Hence, T_{amb} in equation 1 is sensitive to the vertical profile of the density data used in the calculation. For this reason we regard the estimated $T_{amb}(acoustic)$ as the most accurate, but the acoustic samples are available only from 1990. Since the thermocline layer forms a natural boundary to the 0-group's vertical density distribution, $T_{amb}(thermocline)$ may offer an alternative T_{amb} value. $T_{amb}(d)$ is a rough estimate which may be useful if d is a good overall approximation of the 0-group's vertical extension. By comparing (validating) $T_{amb}(d)$ and $T_{amb}(thermocline)$ with $T_{amb}(acoustic)$ we get an impression of the accuracy of the first two estimates, which are simpler to calculate, and which may also be used in years when only trawl catch data are available. Moreover, $T_{amb}(d)$ informs about the 0-group's habitat where most of the stock stays: the more $T_{amb}(d)$ varies with d , the higher is the vertical gradient and the stronger is the water stratification.

Vertical Distribution of Fish Density

To investigate the influence of daylight on the vertical distribution of a particular species, "k," we select the acoustic samples near the trawl stations where the species "k" dominates in the catch; i.e., the catch contains more than 50% of species "k" (after conversion to Sa-values [Aglen 1996])

and, moreover, the catch exceeds 10 specimens (Table 1). As the sun was above or below the horizon, each acoustic sample was classified as a day or night sample. To normalize the large spatial variation in absolute values, we get from acoustic sample s the relative number $P(s,i)$ (%) of fish in the depth interval $[5(i-1), 5i]$, and accumulate from 10 m down to 5ν meters, i.e., $C(s,\nu) = \sum_{i=3}^{\nu} P(s,i)$. At each depth level 5ν , $\nu = 3, 4, \dots, 20$, we compare the day and night distribution of the values $C(s,\nu)$ over s , i.e., over the selected samples. The median and the interquartile ranges of the day/night $C(s,\nu)$ for each depth level are presented.

The method can be applied in general for comparing the day/night vertical density profile for a fish species known to have its main vertical distribution in the observed depth interval.

Mean Length

The mean length of a species at a grid point was taken as the mean length in the catch at the closest trawl station. Mean lengths over areas were then computed using the trawl catch density index as weight in the computation.

Results

Spatial Distribution of 0-Group Fish

Maps showing the horizontal distribution of the trawl catch density (using number of trawl catch per nautical miles index) of each particular species are given in the annual reports (ICES 1985-1996, Institute of Marine Research 1997-1998). Figure 4, which is based on the annual distribution maps, demonstrates the commonly observed horizontal distribution of 0-group fish in the area. These distributions reflect the transport routes of spawning products from the spawning fields of the various species. All studied species spawn in early spring. Cod, haddock, herring, redfish, and saithe spawn off and along the Norwegian coast in areas south of those covered by the map. Capelin spawns along the northern coasts of Norway and Russia while polar cod has two main spawning areas: one in the south-eastern Barents Sea and another in the very northern part of the Barents Sea east of Svalbard (Spitsbergen).

The polar front and thermocline form natural boundaries for the 0-groups; their location varies from year to year (Figs. 1, 2, and 5). The horizontal and some vertical distributions of 0-group acoustic scattering values (Sa-values) for 1995 and 1996 (Fig. 5) are presented as examples. The recordings in Fig. 5 are totally dominated by cod (Table 1 and Figs. 1 and 2) except for the easternmost area in 1995 where polar cod is predominant.

Vertical distributions of 0-group cod as well as the mean vertical temperature profiles are shown in Fig. 6 for the years 1994-1998. In all years 85% or more of the 0-group cod were observed at depths between 0 and 60 m, and with a clear tendency of diel vertical migration that apparently

Table 1. Number of stations selected for studying the vertical distribution of 0-group fish. The selection criteria are: (1) the catch of the species considered should exceed 10 specimen; and (2) the acoustic scattering (Sa-value) corresponding to that catch should exceed 50% of the acoustic scattering corresponding to the total catch of 0-group fish.

Year	Cod	Haddock	Saithe	Redfish	Herring	Capelin	Polar cod	Total stations
1994	100	4	0	20	3	0	20	216
1995	141	0	0	24	5	0	3	245
1996	158	25	0	0	14	40	61	393
1997	116	1	0	0	11	30	29	264
1998	28	49	0	4	44	21	10	166

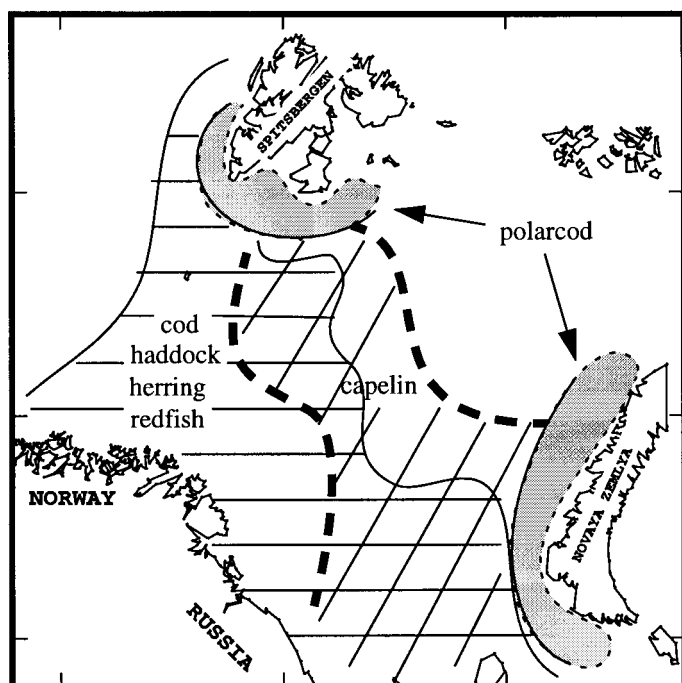


Figure 4. Schematic representation of the horizontal distribution of the various species for all years 1985 to 1998.

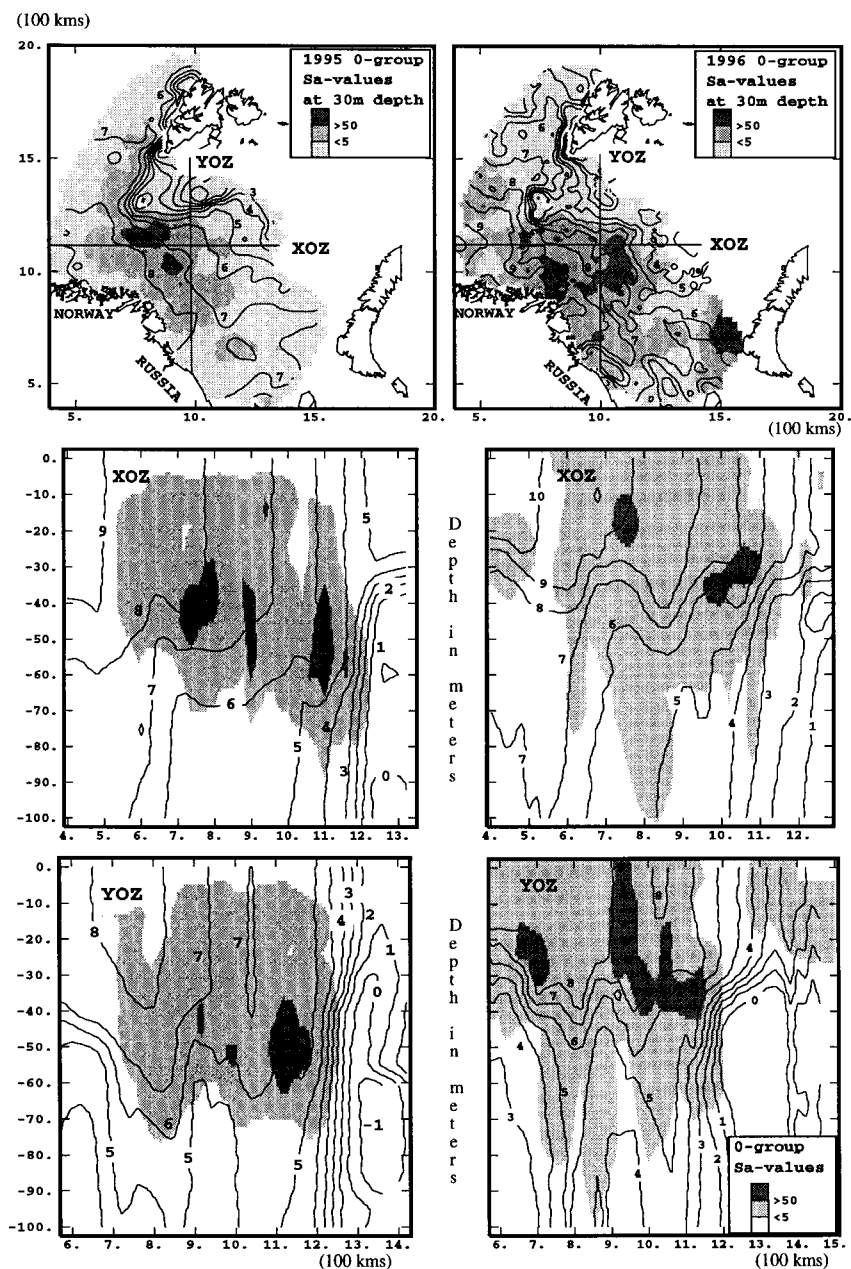


Figure 5. Spatial distribution of 0-group fish acoustic density (all species combined) and temperature in 1995 and 1996. Maps show acoustic scattering (Sa) from the 25- to 30-m depth layer and isotherms at 30 m and location of the vertical sections.

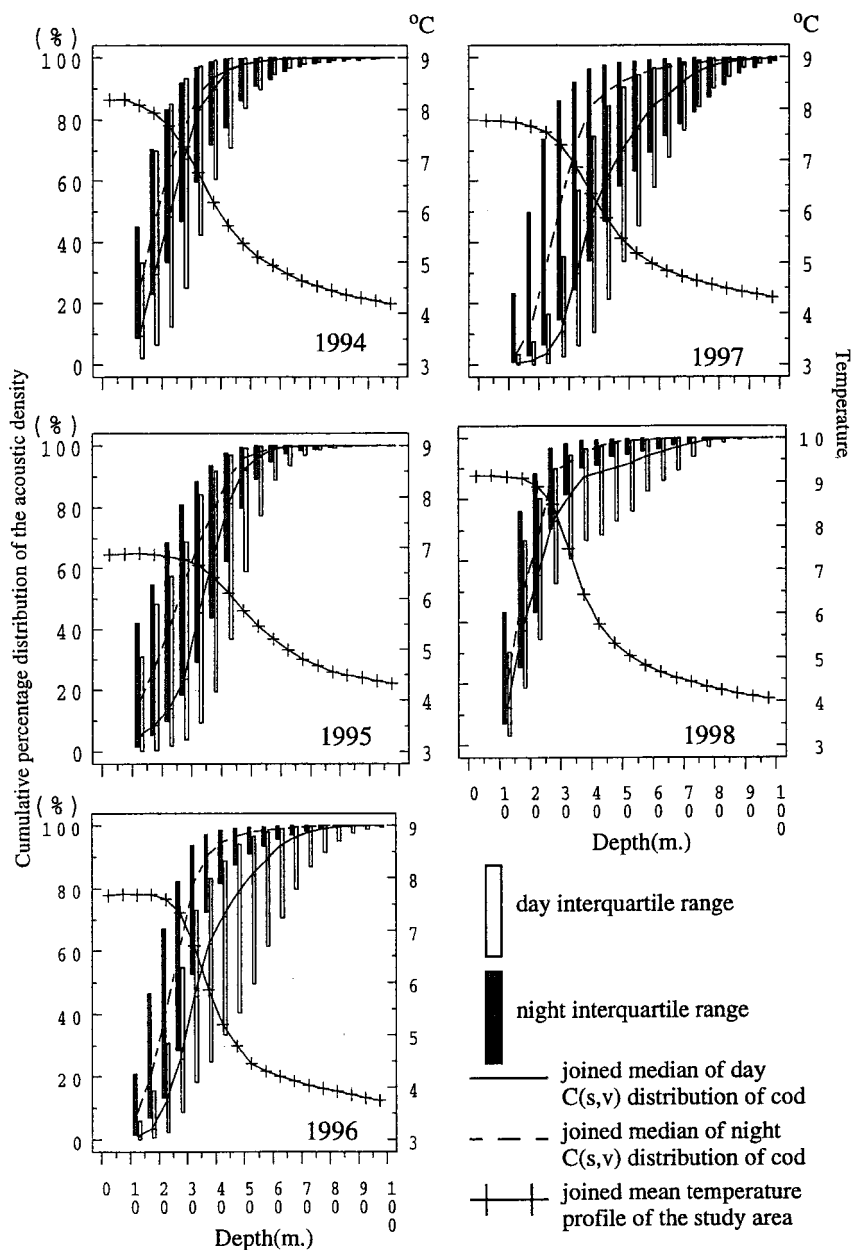


Figure 6. Distribution over day/night stations of the acoustic density (Sa-values in percent) accumulated downward from 10 to 5j meters, $j = 3, \dots, 20$, with the corresponding vertical profiles of temperature means over the study area.

differed between years. In 1994 and 1995 the fish was only a few meters higher up in the water column at night than during the day, while in 1996, 1997, and 1998 the day/night depth difference amounted to 10-15 m.

Ambient Temperature and Salinity

The estimated values are presented in Table 2 together with the mean temperature at the Kola section (Figs. 1 and 2). Time series of estimates of ambient temperatures and mean temperature at Kola are displayed in Fig. 7. Despite the difference between the estimates they generally deviate the same way from the Kola section values. Moreover, the agreement improves if the same area is used; e.g., if $T_{amb}(thermocline)$ is calculated over the area of acoustic sampling. Sometimes they show substantial variations independent of those for Kola.

The interannual distribution of the ambient temperature for each 0-group species and the mean temperature at Kola are presented in Fig. 8, and reflect that polar cod and Greenland halibut are distributed farther east and north and consequently in colder water masses than the gadoids and herring (Fig. 4). The estimates of ambient temperatures show generally greater variations from year to year than the corresponding variations at Kola.

The range of the $T_{amb}(d)$, $d = 10, 15, \dots, 100$, within each year shows that some species (cod, haddock, saithe, capelin) mainly stay in waters with a higher vertical temperature gradient than others (redfish, Greenland halibut, polar cod). For species with diel vertical migration the ambient temperature varies from daytime to nighttime within the range of variation in $T_{amb}(10)$ to $T_{amb}(100)$. The different estimates of T_{amb} seem to agree well in general. The $T_{amb}(thermocline, acoustic)$ which is $T_{amb}(thermocline)$ restricted to the area covered by acoustic sampling as described above, is used for comparison with $T_{amb}(acoustic)$.

Fish Length and Ambient Temperature

In general the warm-water fish (cod, haddock, redfish, and herring) caught at most sampling stations in the Svalbard area have smaller mean length and lower density than the fish caught in the Barents Sea (Figs. 1 and 2). Figure 9 presents the scatter plots of $T_{amb}(thermocline)$ against the corresponding estimates of mean length of the 0-group, for the two areas separately. In general, within the same year, the fish in the Svalbard area are smaller and also inhabit a colder environment than those in the Barents Sea. The figure leaves an impression of a positive relationship between ambient temperature and length for most species with the exception of capelin.

Discussion

The main features of the spatial distribution of 0-group fish in the area are shown in Figs. 4 and 5 and were outlined 30 years ago (Dragesund 1970). However, the results in the present study include observations that should

Table 2. Time series of estimated ambient temperature, salinity, and the mean length of 0-group cod over total area (A), Barents Sea area (B), and Svalbard area (S) together with the mean temperature, 0-50 m, at Kola section.

Year	Total area (A)						Barents Sea area (B)				Svalbard area (S)			
	$T_{amb}(50m) ^\circ C$	$T_{amb}(thermocline) ^\circ C$	$T_{amb}(acoustic) ^\circ C$	$T_{amb}(thermocline, acoustic) ^\circ C$	$T_{amb}(50m) ^\circ C$	$T_{amb}(thermocline, acoustic) ^\circ C$	$T_{amb}(thermocline) ^\circ C$	$T_{amb}(acoustic) ^\circ C$	$T_{amb}(thermocline, acoustic) ^\circ C$	$T_{amb}(50m) ^\circ C$	$T_{amb}(thermocline) ^\circ C$	$T_{amb}(acoustic) ^\circ C$	$T_{amb}(thermocline, acoustic) ^\circ C$	$S_{amb}(thermocline) A$
85	7.1	6.7	6.5	—	—	—	7.0	6.9	—	5.6	5.4	—	—	34.86
86	7.5	6.6	7.1	—	—	—	6.7	7.2	—	5.2	5.1	—	—	34.59
87	6.2	7.1	7.0	—	—	—	7.2	7.2	—	5.1	5.0	—	—	34.65
88	7.0	7.8	8.3	—	—	—	7.8	8.4	—	5.4	5.1	—	—	34.31
89	8.6	7.1	7.4	—	—	—	7.2	7.5	—	4.7	4.6	—	—	34.52
90	8.1	8.5	9.2	—	—	—	8.5	9.3	—	6.2	6.2	—	—	34.77
91	7.7	6.7	6.5	—	—	—	6.9	6.7	—	6.2	6.1	—	—	34.90
92	7.5	6.4	6.6	—	—	—	6.5	6.7	—	6.1	6.1	—	—	34.85
93	7.5	5.9	6.2	—	—	—	6.2	6.6	—	5.4	5.2	—	—	34.69
94	7.7	7.4	7.4	7.4	7.4	7.4	7.4	7.5	7.5	6.3	6.4	5.9	6.1	34.84
95	7.6	6.9	6.7	6.7	6.7	6.7	6.9	6.7	6.7	6.1	6.1	6.2	6.1	34.88
96	7.6	7.0	7.3	6.7	7.3	7.3	7.0	7.3	6.7	6.1	6.1	6.1	6.1	34.75
97	7.3	7.3	7.5	6.7	7.5	7.5	7.3	7.5	6.7	4.5	4.7	4.5	4.7	34.82
98	8.4	7.4	7.5	8.3	8.1	8.1	7.5	7.5	8.4	6.8	7.0	6.9	7.0	34.69

$T_{amb}(50m)$ = average of mean temperature from surface to 50-m depth weighted by trawl catch density index. $T_{amb}(thermocline)$ = average of mean temperature from surface to thermocline depth weighted by trawl catch density index. $T_{amb}(acoustic)$ = 3D average of temperature weighted by 3D density index. $T_{amb}(thermocline, acoustic)$ = $T_{amb}(thermocline)$ over the acoustic sampling zone. Similarly for ambient salinity (S_{amb}).
a Mean length from ICES (1985-1996), Institute of Marine Research (1997-1998).

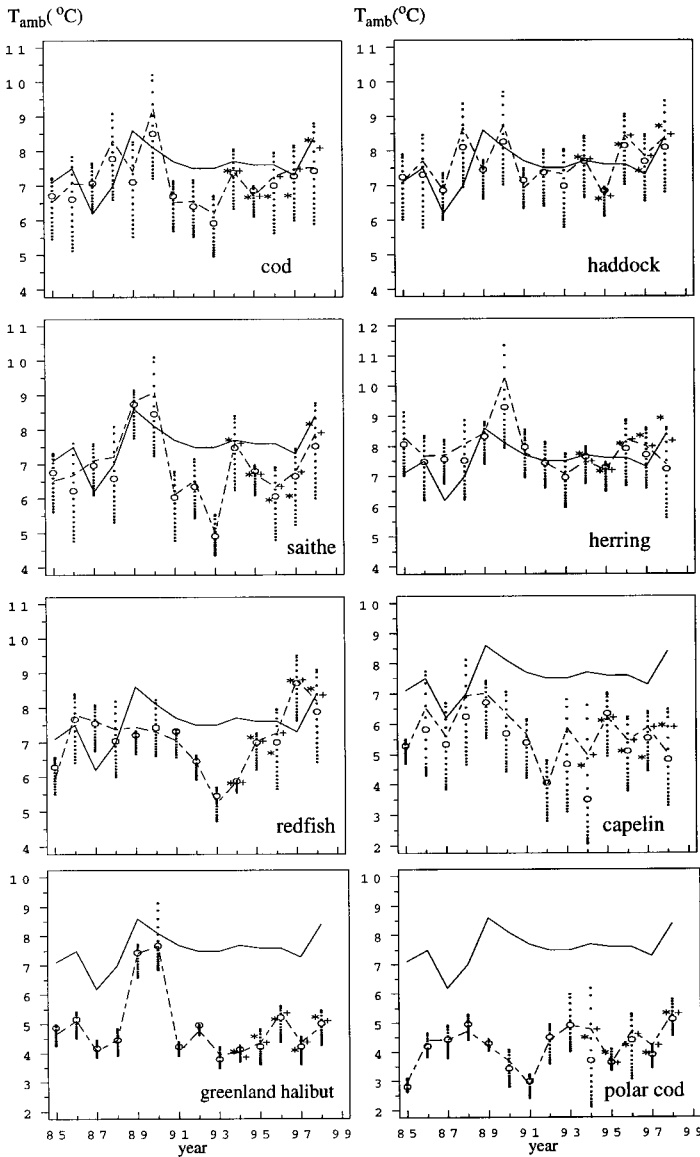


Figure 7. Time series of ambient temperature estimates. $T_{amb}(d)$ [T_{amb} (thermocline)]: average of mean temperature from surface to d meters depth [thermocline depth] weighted by trawl catch density index. T_{amb} (acoustic): average of temperature weighted by density index using 3D data. Black dot (\bullet) represents $T_{amb}(d)$, $d = 20, 25, \dots, 100$; open circle (\circ) represents $T_{amb}(50m)$; asterisk (*) represents T_{amb} (acoustic); plus sign (+) represents T_{amb} (thermocline) over acoustic survey area. Broken line joins T_{amb} (thermocline) over total area; solid line joins Kola section 0- to 50-m average temperature.

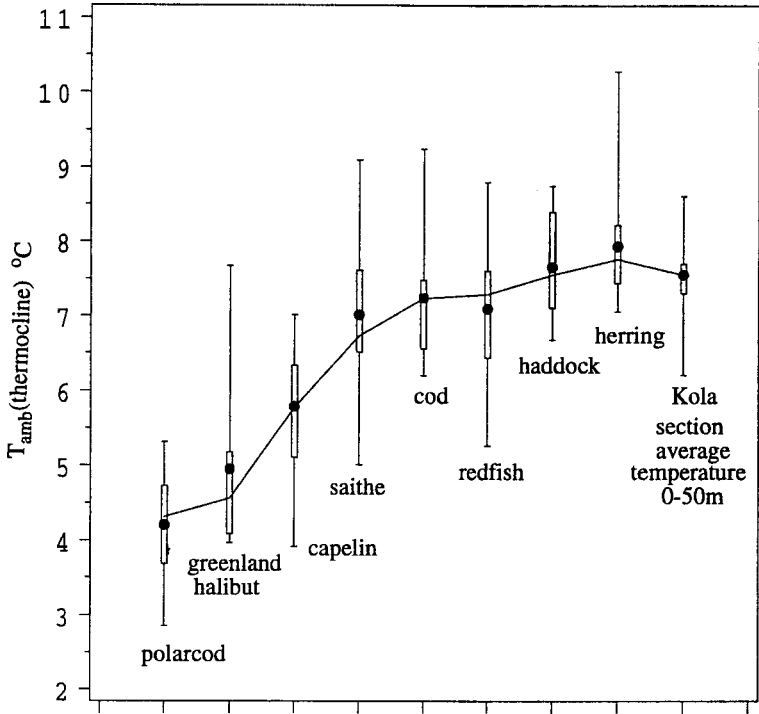


Figure 8. Interannual distribution of $T_{amb}(\text{thermocline})$ for each 0-group species compared to the interannual distribution of average temperature from 0 to 50 m at the Kola section during 1985-1998. Solid line joins median values and black dots (•) indicate mean values. Boxes show interquartile and whiskers show full range.

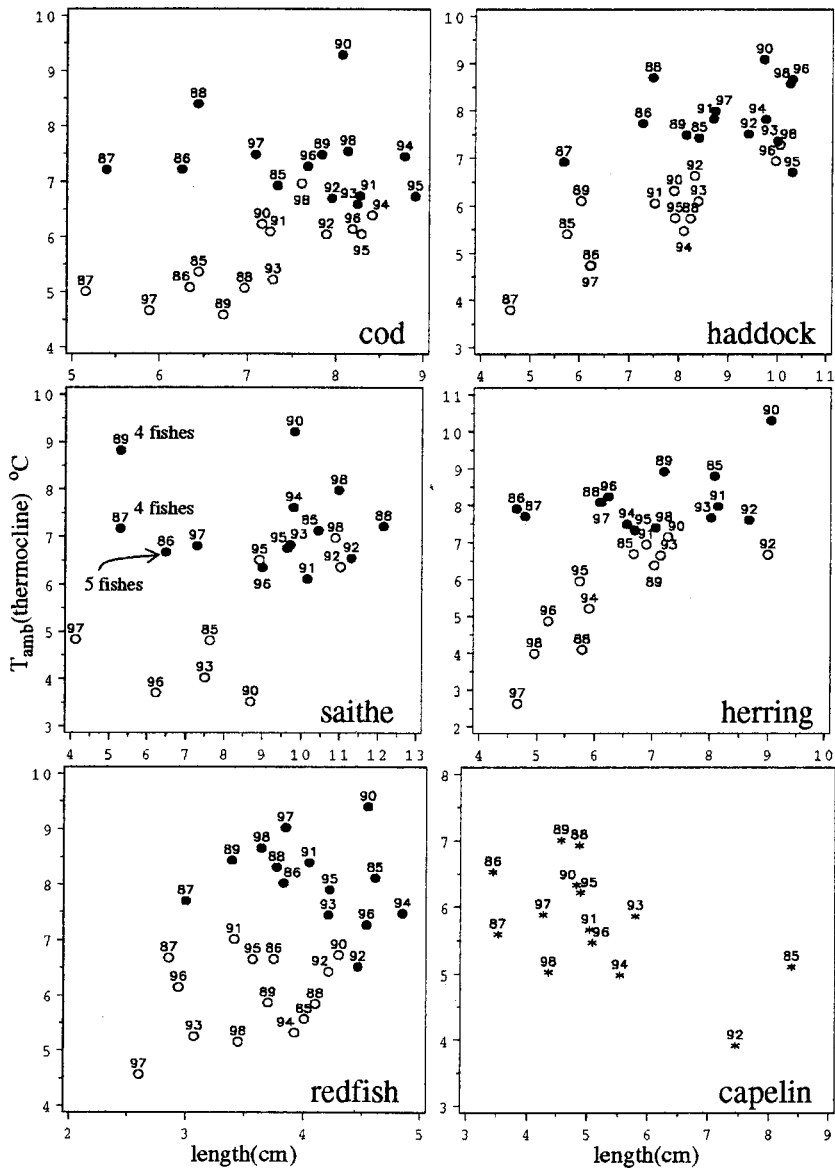


Figure 9. $T_{amb}(\text{thermocline})$ and mean lengths of 6 species from 1985 to 1998. Black dot (•) represents Barents Sea area, open circle (o) represents Svalbard area, asterisk (*) represents total area, numbers indicate years.

be given attention in future work. The observations are summarized and quantified to give an overall picture in terms of graphic presentations or numerical values. The interpretation and reliability of these results depend on the station coverage over the study area and the number of studied species caught at each station. For cod, haddock, redfish, herring, and capelin the sampling and area coverage were satisfactory. For saithe, polar cod, and Greenland halibut the survey covers only a fraction of the total distribution area and caution must be exercised in drawing conclusions for these species.

Vertical Sampling and Computation of Abundance Indices

The standard trawl sampling scheme adopted for the surveys, with each haul covering three depths or more, seems satisfactory. It has previously been shown that the 0-group undertakes diel vertical migrations (Beltestad et al. 1975, Godø et al. 1993, Hysten et al. 1995) and that the 0-group scattering layer may be close to the surface at night. Much of the fish will then be too shallow to be recorded by the echo sounder and thus the Sa-based vertical nighttime density distributions will be biased. To some extent this may also affect the estimates of ambient temperature, although the effect is thought to be minor since the vertical temperature gradient in the uppermost 10-15 m as a rule is small (Fig. 6).

Estimates of Ambient Temperature

The various estimates of ambient temperature (Table 2, Fig. 7) demonstrate the necessity of knowing the vertical distributions of fish as well as temperature in order to characterize the habitat quantitatively. We consider $T_{amb}(acoustic)$ as the most reliable estimate since the acoustic data are the best source for the vertical density profile. The results indicate that the other estimates, based on "assumed" vertical density profiles of the 0-group, may be useful substitutes to $T_{amb}(acoustic)$ in the analysis of historical data. They also show that the Kola temperature should not be used as an index of the ambient temperature of the various 0-group species. Results for cod aged 1-7 years (Ottersen et al. 1998) also show that caution should be exercised when using temperatures at fixed stations or sections as indicators of the habitat of a species.

As stated previously the estimates of ambient temperature of saithe, polar cod, and Greenland halibut (Figs. 7 and 8) are biased because of incomplete coverage. The bulk of 0-group saithe is distributed in Norwegian coastal waters south of the survey area where temperatures in August-September are higher than in the Barents Sea. Thus the actual ambient temperature for saithe might be substantially higher than shown in Figs. 7 and 8. For polar cod the situation is opposite since much of the 0-group is

distributed north and east of the survey area in waters of lower temperatures (Fig. 4).

0-Group Length and Ambient Temperature

The positive relation between mean length and ambient temperature appearing in Fig. 9 (cod, haddock, saithe, herring, redfish) is mainly a result of separating the data set for the two areas, Svalbard and the Barents Sea (Figs. 1a and 2a). When mean values for each of the two areas are considered separately no such relation is evident for the period we have studied. However, the difference between the two areas is clear. As pointed out in the introduction, Loeng et al. (1994) have shown a positive relationship between 0-group mean length of several species and the mean temperature at the Kola section when using longer time series and mean lengths for the entire 0-group population, indicating increased growth prior to the 0-group stage in warm years as compared to cold years.

The age distributions of the 0-group in the two areas have not been established. If we assume that the 0-groups in the two areas have an approximately common origin (spawning field and hatching time [Gjøsæter et al. 1992]) then the temperature difference is most likely one factor causing, directly or indirectly, the observed differences in mean lengths between the Barents Sea and the Svalbard area within the same year. The fish drifting north experience lower temperature and grow more slowly throughout the summer than the fish that drift east (Figs. 1, 2, and 9).

The plot for capelin in Fig. 9 shows an opposite tendency to that observed for the other species; the larger mean lengths are associated with low ambient temperatures. In the annual distribution maps there is a tendency for capelin to be larger when they move offshore. The growing capelin migrate farther north into colder waters. Thus the observation is interpreted as an effect of the age of the 0-group. Capelin have a rather long spawning period (March-June) and the pre-0-group history of the fry is not known for each particular year. It is thus difficult to draw a conclusion on the causes for the opposite tendency appearing in Fig. 9 for capelin.

Comparison of mean lengths (over the total area) of 0-group cod estimated in this paper with the estimates given in the annual reports reveals some differences that may be caused by differences in the way the density index is calculated from the trawl catches.

Acknowledgments

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Spatial Distribution of Atlantic Salmon Postsmolts: Association between Genetic Differences in Trypsin Isozymes and Environmental Variables

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Abstract

This study is the first attempt to investigate the distribution of different trypsin isozyme characteristics of wild Atlantic salmon postsmolts in natural marine ecosystems. Aquaculture studies have shown genetic differences in growth and food utilization affected by variations in trypsin isozyme patterns in the pyloric caeca of Atlantic salmon. Postsmolts, caught as bycatch from a pelagic trawl survey in the northeastern Atlantic Ocean during summer 1995, were divided into three groups: pattern 1 (TRP-2*100/100), pattern 2 (TRP-2*100/92), and pattern 2' (TRP-2*92/92), according to differences in the expression of the trypsin isozyme TRP-2*100 and the trypsin variant TRP-2*92 in the pyloric caeca revealed by isoelectric focusing on agarose-IEF gel.

The survey was carried out in two main areas: off the Hebrides (56-60°N, 11°W-2°E) in June and in the Norwegian Sea (62-72°N, 16°E-7°W) in July. The proportions of postsmolts possessing trypsin patterns 1, 2, and 2' off the Hebrides area, where the ambient temperature was around 10.2°C with relatively high ichthyoplankton indices (as determined acoustically), were 0.25: 0.50: 0.25 with mean weights of 64 g: 62 g: 58 g, respectively. In contrast, the proportions found in the Norwegian Sea under lower ichthyoplankton densities were 0.50: 0.34: 0.16 with mean weights of 133

g: 137 g: 234 g for postsmolts possessing trypsin patterns 1, 2, and 2' at the ambient temperatures of 9.3°C, 8.7°C, and 7.7°C, respectively. Postsmolts of pattern 2' caught at ambient temperatures $\leq 8^\circ\text{C}$ in the Norwegian Sea were on average larger, while they were found smaller at ambient temperatures $> 10^\circ\text{C}$ off the Hebrides, compared to the postsmolts of pattern 1 and pattern 2 caught in the same area.

During sea migration and if the availability of suitable food is reflected in the ichthyoplankton index, growth of Atlantic salmon postsmolts seemed to be affected by food utilization at different ambient temperatures and to be dependent on the trypsin phenotypes possessed by individuals. The hypothesis that trypsin variant TRP-2*92 is important for food utilization at temperatures $\leq 8^\circ\text{C}$ and the trypsin isozyme TRP-2*100 at $> 8^\circ\text{C}$, which have been observed in aquaculture systems, is supported.

Introduction

Differences in the expression of different trypsin isozymes in the pyloric caeca of Atlantic salmon (*Salmo salar* L.) are influenced by water temperature very early in life, during egg incubation and the first feeding period (Rungruangsak-Torrissen et al. 1998). Establishment of the trypsin isozyme pattern of individual salmon at the early life period affected food utilization and growth during the whole life cycle (Torrissen 1991, Torrissen and Shearer 1992, Rungruangsak-Torrissen et al. 1998). The effect of trypsin isozymes on growth could be observed within 3-5 months after the first feeding (Torrissen et al. 1993). High food conversion efficiency and growth rate, due to increased rate of digestion and utilization of dietary protein (Torrissen and Shearer 1992, Torrissen et al. 1994), were associated with the presence of trypsin variant TRP-2*92. The effects on food utilization and growth were pronounced when the water temperatures were $\leq 8^\circ\text{C}$ and especially below 6°C (Rungruangsak-Torrissen et al. 1998). Without this trypsin variant, the fish showed low food utilization and growth at temperatures $< 8^\circ\text{C}$. The presence of the common isozyme TRP-2*100, on the contrary, was associated with temperatures $> 8^\circ\text{C}$ (Rungruangsak-Torrissen et al. 1998). Atlantic salmon with the variant TRP-2*92 have an advantage in utilizing food at a restricted ration (Torrissen and Shearer 1992, Torrissen et al. 1994, Rungruangsak-Torrissen et al. 1999), and probably with a low-quality dietary protein (Bassompierre et al. 1998). Atlantic salmon of pattern 2 possessing both isozyme TRP-2*100 and variant TRP-2*92 should have a greater advantage of living in areas with variations in food abundance and quality, and with varying temperatures.

The above observations were performed in captive aquaculture systems. In order to study the effects of different trypsin isozymes in natural systems, wild Atlantic salmon postsmolts caught in the northeastern Atlantic Ocean during early migration in summer 1995 were screened for different trypsin isozyme patterns. This represents the first attempt to relate trypsin characteristics of wild Atlantic salmon with different envi-

ronmental factors, such as sea temperature, salinity, and plankton abundance, in natural marine ecosystems.

Materials and Methods

Wild Atlantic salmon postsmolts during early migrations were obtained as bycatch in two areas in June and July 1995 from a pelagic trawl survey by the Norwegian research vessel *Johan Hjort*. Catches were performed by using the relatively large Åkra pelagic trawl fitted with floats on the wings and headline developed for surface mode sampling at depths of 0-25 m (Valdemarsen and Misund 1995, Holm et al. 2000). The trawl was rigged to fish with the headrope at the surface, with a vertical opening of approximately 25 m, towing speed of 3-4 knots, and haul duration of 30 minutes. The sampling area was designed to cover the distribution of the Norwegian spring spawning (NSS) stock during its feeding season.

The first survey area (June 1995) covered the shelf edge north and west of the British Isles (56-60°N, 11°W-2°E), and was conducted to study the relation between currents and migrating mackerel along the shelf edge. A total of 39 surface hauls were made and a total of 46 Atlantic salmon postsmolts were caught. The second area (July 1995) covered the Norwegian Sea (62-72°N, 16°E-7°W) and was an acoustic survey for herring. A total of 60 surface hauls were made and a total of 62 postsmolts were caught. Details are further described in Holm et al. (2000).

Weights of individual postsmolts were measured on board, and the fish were immediately frozen. Once ashore, pyloric caeca samples were dissected and kept frozen at -80°C for the analysis of trypsin isozyme pattern by isoelectric focusing on agarose-IEF gel as described by Torrisen (1984). The age of the Atlantic salmon at transfer/migration from fresh water into the marine environment was determined from scales and otoliths.

Seawater temperature and salinity were obtained from CTD stations (Seabird 911 Plus with Seasoft version 4.246, Sea-Bird Electronics, Inc., Bellevue, WA), with data recorded at 1-m depth intervals to 500-1,000 m immediately before or after each fishing station (Institute of Marine Research 1996a, Gjertsen 1995). An index for plankton density was derived from the integrated echo intensity of planktonic organisms (including fish larvae, etc.) at the echo-sounder frequency primarily used for fish, -38 kHz. The integrated echo energy, expressed as the area backscattering coefficient (S_A), was aggregated over 5 nautical miles for each 50-m depth layer. This was the data allocated as "plankton" during the scrutinizing of the echograms, recorded by the Bergen Echo Integrator (BEI) system (Foote et al. 1991, 1992). It should, however, be noted that the "plankton" category is marked as "lowest precision level," code 3, and was mainly used to isolate the backscattering from the plankton (ichthyoplankton layer) from the backscattering from the herring schools, which was the main target species in the surveys. This is also evident from the nonstandardized use of acoustic threshold level for removal of "unwanted" echoes, $S_v = -73$ dB

and $S_v = -79$ dB for the data recorded in June and July, respectively. The fish density at each sampling station was determined as the number of fish per unit towing distance assuming the same surface trawl opening. Temperature, salinity, and plankton density data were available in 3 dimensions. Locations given in geographical coordinates (latitude, longitude) were projected onto the plane by a polar stereographic projection. In order to quantify the relationship of the fish density and environmental variables, all these variables were interpolated onto the 2-dimensional grid system of 20 km by 20 km (and 5-m depth bins for 3 dimensions), using kriging or linear model kriging, so that they represented the spatial distribution of each variable in the study area (Cressie 1991, Stensholt and Sunnanå 1996, ISATIS 1997). The ambient temperature (salinity) is a kind of average temperature (salinity) of the water-mass in which the majority of fish live. It is defined as an average temperature (salinity) weighted by fish density (Stensholt and Nakken 2001). To obtain a good estimate of the true ambient temperature for a fish stock, it is important that the survey cover its total distribution area. One survey then represents a snapshot of the ambient temperature of the stock at time t . For growth analysis, serial snapshots should be available. For a 2-dimensional grid system we defined the ambient temperature as a double integral over the study area:

$$\frac{\iint \rho(x, y) \times T(x, y) \times dx \times dy}{\iint \rho(x, y) \times dx \times dy}$$

where $\rho(x, y)$ was the estimated fish density at (x, y) -grid point (block) and $T(x, y)$ was the average temperature (salinity) for the depth interval within which $\rho(x, y)$ was estimated. The fish were only caught in the surface (0-25 m) trawls in these surveys, and the thermocline had a range from 20 m to 50 m. Assuming that the fish lived above the thermocline, the ambient temperatures presented here were computed using the average temperature (salinity) from the surface to 25 m, and from the surface to 50 m.

In practice the integral values are approximated by summation over the 2-dimensional grid. Calculations and spatial data analysis were performed using the ISATIS software (1997) together with developed programs in the SAS (SAS 1993). To calculate the ambient temperature for fish with each type of trypsin the estimated density of fish with that trypsin phenotype was substituted into the equation above. Due to the spatial correlation of the regional variables, we assumed the same fish weight composition at the nonsampling locations around the sampling stations in calculating the mean weight over the study area.

Only a single sample was collected at each sampling location; i.e., one trawl haul per station. Thus, for the total study area, there was only one realization of fish density, temperature, and salinity, producing a single value of the estimated ambient temperature (salinity) for a given depth range in the definition of average temperature (salinity).

Results

Trypsin phenotypes were identifiable in 88 out of 108 samples, representing 81.5% of total postsmolts caught during the survey. The fish recorded with empty stomachs were mainly postsmolts with nondetectable trypsin phenotypes. Within each fishing area (either off the Hebrides or the Norwegian Sea) the postsmolts were divided into three groups according to differences in the expression of trypsin isozymes TRP-2*100 and TRP-2*92 in the pyloric caeca: pattern 1 (TRP-2*100/100), pattern 2 (TRP-2*100/92), and pattern 2' (TRP-2*92/92) (see details in Rungruangsak-Torrissen et al. 1998).

Off the Hebrides

The estimated ambient salinity of postsmolts caught off the Hebrides area was 35.26, and the estimated ambient temperature was 10.2°C with an isotherm of 8°C passing about 300 km north of Scotland (Fig. 1). Vertical temperature profiles indicated that the thermocline was not clearly differentiated in this area. Distributions of postsmolts caught and plankton abundance are shown in Fig. 2. Plankton abundance varied at different depths. Distributions of ichthyoplankton density at 0-50 m depths ranged from 200 to 2,000, and all caught postsmolts were in the area with density values ≥ 500 (Fig. 2).

Trypsin phenotypes were identifiable in 44 individual salmon, out of 46 postsmolts caught in this area, with frequency distribution of 0.25: 0.50: 0.25 for patterns 1: 2: 2' (Table 1). Fish weight ranged from 39 to 126 g with average weights of 63.9 ± 7.1 g (mean \pm SEM), 62.4 ± 3.2 g, and 57.9 ± 4.8 g for patterns 1, 2, and 2', respectively (Table 1). The pattern 2' salmon were on average smallest, albeit insignificant ($P > 0.05$ by ANOVA at 95% significance level). Different ages of 1+ smolts ($n = 5$), 2+ smolts ($n = 36$), and 3+ smolts ($n = 3$) were observed, and all pattern 1 fish caught were of 2+ smolts (Table 2). One postsmolt of pattern 2' (1+ smolt of 52 g) was a cultured fish. Spatial distributions of postsmolts possessing different trypsin phenotypes are shown in Fig. 3. Salmon with different trypsin phenotypes were in some cases captured in the same tows. Distributions of different trypsin phenotypic groups were overlapping; therefore the ambient temperature ($\sim 10.2^\circ\text{C}$) and salinity (~ 35.2) were similar among different trypsin phenotypes in the area off the Hebrides (Table 1). The ambient temperature was $\sim 0.3^\circ\text{C}$ lower, and the ambient salinity ~ 0.02 higher when calculated at 0-50 m compared to 0-25 m depth.

The postsmolts possessing the trypsin variant TRP-2*92 (patterns 2 and 2') caught off the Hebrides area where ambient sea temperature $> 10^\circ\text{C}$ tended to be smaller than the salmon lacking the variant (pattern 1).

Norwegian Sea

The postsmolts caught in the Norwegian Sea at 0-25 m depth range had estimated ambient temperature (9.0°C) and salinity (35.03) somewhat lower

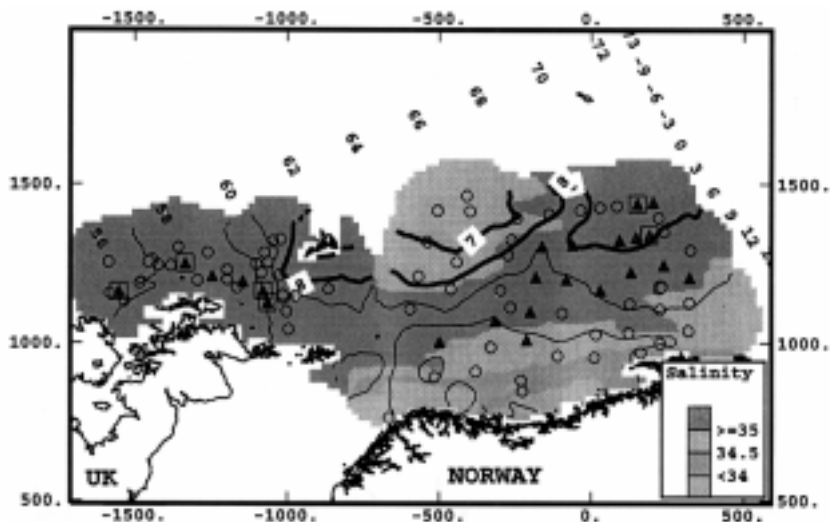


Figure 1. Isolines of average temperature and salinity, within 25 m sea-depth, in the area off the Hebrides (June 1995) and in the Norwegian Sea (July 1995). The isotherms of 7°C and 8°C are labeled, and each isotherm is a 1°C step with the thick and thin lines representing lower and higher levels, respectively. Salinity variations are indicated by different gray shades. Sampling stations without postsmolts caught (○), with postsmolts caught (▲), and with caught postsmolts of pattern 2' (□), are indicated. The distance in kilometers is indicated on the frame.

than those of postsmolts caught off the Hebrides area (10.2°C and 35.26, respectively) (Fig. 1). The thermocline was clearly differentiated in the Norwegian Sea and ranged between 20 m and 50 m in depth. Distributions of postsmolts caught and plankton abundance are shown in Fig. 2. The ichthyoplankton index in the Norwegian Sea at 0-50 m depth in July ranged from 5 to 60 (Fig. 2).

Trypsin phenotypes were identifiable in 44 individual salmon, out of 62 postsmolts caught in this area. Fish weight ranged from 54 to 303 g with average weights of 132.6 ± 12.2 g, 136.5 ± 14.9 g, and 234.3 ± 24.9 g, at a frequency of 0.50: 0.34: 0.16, for salmon of patterns 1, 2, and 2', respectively (Table 1). On average, postsmolts of pattern 2' were significantly larger than salmon of patterns 1 and 2 ($P < 0.01$ by ANOVA at 95% significance level), and the pattern 1 salmon were smallest. Different ages of 1+ smolts ($n = 17$), 2+ smolts ($n = 23$), and 3+ smolts ($n = 4$) were observed, and the pattern 2' fish caught were of 1+ and 2+ smolts (Table 2). Two postsmolts (1+ smolt of pattern 1 [302 g], and 1+ smolt of pattern 2 [225 g]) were cultured fish. Spatial distribution of postsmolts (Fig. 3) indicated that

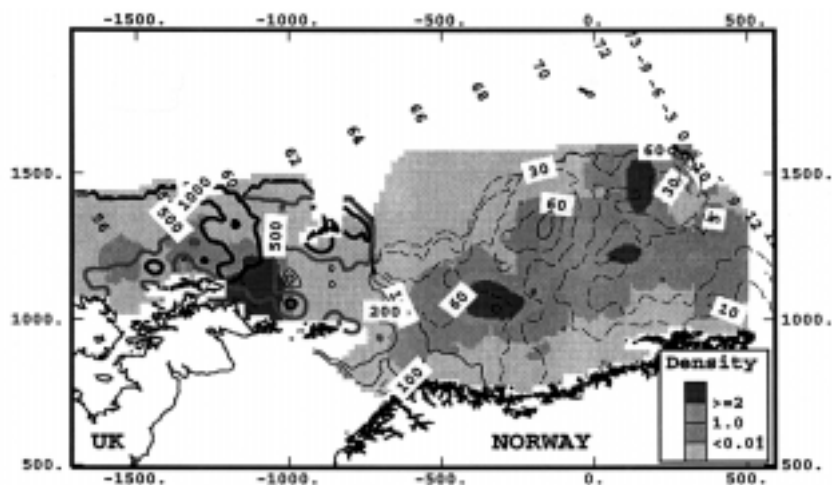


Figure 2. Spatial distributions of plankton abundance off the Hebrides area (June 1995) and in the Norwegian Sea (July 1995) at 0-50 m sea-depth, showing with the distribution of Atlantic salmon postsmolts caught in the corresponding areas. The S_A values for plankton are indicated on the isolines. Numbers of postsmolts caught per nautical mile are indicated by gray shades. The distance in kilometers is indicated on the frame.

the Atlantic salmon possessing patterns 1, 2 and 2' had estimated ambient temperatures of 9.3°C, 8.7°C, and 7.7°C, respectively (Table 1). High dispersion of the TRP-2*92 salmon (patterns 2 and 2') was observed in the area where sea temperatures were $\leq 8^\circ\text{C}$ (patterns 1: 2: 2' = 0.26: 0.35: 0.39), while high dispersion of salmon with pattern 1 was observed at sea temperatures from $> 8^\circ\text{C}$ to 11°C (patterns 1: 2: 2' = 0.637: 0.357: 0.006). Salmon with pattern 2' in the Norwegian Sea were not caught at temperatures $> 9^\circ\text{C}$ (Fig. 3). The ambient salinity (~ 35.1) was similar between different trypsin phenotypes at 0-25 m (Table 1), and the values were ~ 0.02 higher when calculated at 0-50 m depth. The ambient temperatures were $\sim 0.4^\circ\text{C}$ lower for each phenotype calculated at 0-50 m, compared to 0-25 m depth.

In contrast to the Hebrides area, the postsmolts possessing trypsin variant TRP-2*92 (patterns 2 and 2') caught in the Norwegian Sea, at lower ambient temperature, were larger than the salmon lacking this variant (pattern 1).

Discussion

The weight compositions (if reflecting growth at site) relative to ambient temperatures of postsmolts possessing different trypsin phenotypes in

Table 1. Spatial distribution of Atlantic salmon postsmolts, possessing different trypsin isozyme patterns in the pyloric caeca, caught off the Hebrides in June and in the Norwegian Sea in July (1995), and the ambient temperature and salinity of each trypsin phenotype within 25 m sea-depth.

	Pattern 1 (TRP-2*100/100)	Pattern 2 (TRP-2*100/92)	Pattern 2' (TRP-2*92/92)
Off the Hebrides:			
Average weight (g)	63.9 ± 7.1	62.4 ± 3.2	57.9 ± 4.8
Weight range (g)	39-126	44-96	41-96
Number of fish identified	11	22	11
Estimated ambient temperature (°C)	10.17	10.19	10.24
Estimated ambient salinity	35.24	35.25	35.25
Norwegian Sea:			
Average weight (g)	^a 132.6 ± 12.2	^a 136.5 ± 14.9	^b 234.3 ± 24.9
Weight range (g)	57-302	54-249	129-303
Number of fish identified	22	15	7
Estimated ambient temperature (°C)	9.30	8.74	7.70
Estimated ambient salinity	35.03	35.02	35.06

The values with different superscript (a or b) are significantly different ($P < 0.01$ by ANOVA at 95% significance level).

Table 2. Average weights (in grams) and smolt age of Atlantic salmon postsmolts, possessing different trypsin isozyme patterns in the pyloric caeca, caught off the Hebrides in June and in the Norwegian Sea in July (1995). The numbers of fish with different smolt age are in parentheses.

	Off the Hebrides			Norwegian Sea		
	1+ smolt	2+ smolt	3+ smolt	1+ smolt	2+ smolt	3+ smolt
Pattern 1		63.9 ± 7.1 (11)		153.0 ± 24.5 (8)	116.0 ± 15.4 (11)	139.0 ± 21.1 (3)
Pattern 2	80.7 ± 8.0 (3)	67.9 ± 3.2 (18)	55 (1)	154.0 ± 29.7 (6)	123.1 ± 17.3 (8)	139 (1)
Pattern 2'	74.0 ± 22.0 (2)	53.1 ± 4.4 (7)	58.5 ± 4.5 (2)	237.0 ± 40.4 (3)	232.3 ± 36.9 (4)	

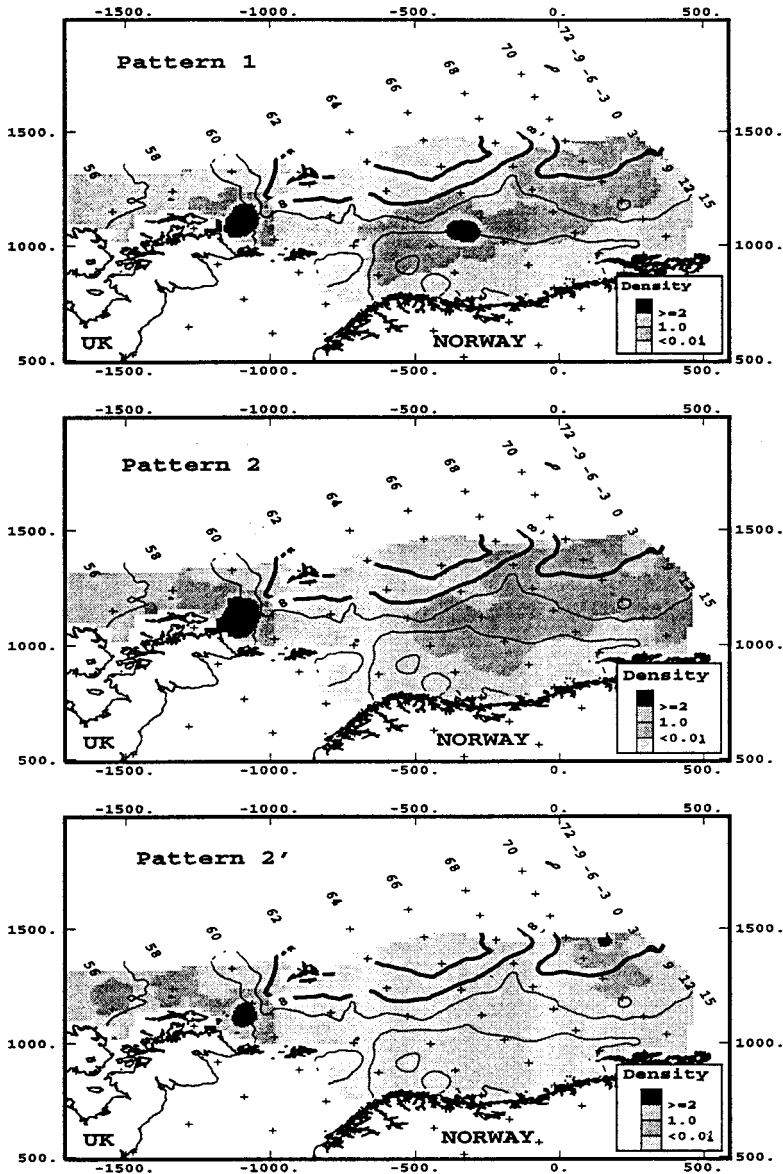


Figure 3. Spatial distribution of postsmolts with pattern 1, pattern 2, and pattern 2' at different sea temperatures off the Hebrides area (June 1995) and in the Norwegian Sea (July 1995). The isotherm of 8°C is labeled, and each isotherm is a 1°C step with the thick and thin lines representing lower and higher levels, respectively. Numbers of postsmolts caught per nautical mile are indicated by gray shades. The distance in kilometers is indicated on the frame.

the northeastern Atlantic Ocean correspond with the findings of Rungruangsak-Torrissen et al. (1998) that trypsin isozyme TRP-2*100 and the variant TRP-2*92 are associated with more efficient growth of Atlantic salmon at temperatures $> 8^{\circ}\text{C}$ and $\leq 8^{\circ}\text{C}$, respectively. In contrast to the postsmolts of pattern 1, the salmon of pattern 2' captured at sea temperatures $\leq 8^{\circ}\text{C}$ in the Norwegian Sea were largest on average while they were smallest at sea temperatures $> 10^{\circ}\text{C}$ off the Hebrides, when compared to the other trypsin phenotypes caught in the same area (see Table 1). The pattern 2 salmon in both surveyed areas dispersed in moderate sea temperatures with mean sizes in between those of pattern 1 and pattern 2' fish, and very similar to the pattern 1 (see Table 1) suggesting an influence of the isozyme TRP-2*100 at temperatures above 8°C . The influence of the variant TRP-2*92 might have been shown in the pattern 2 salmon if the fish had mainly dispersed and been caught in the areas with temperatures below 8°C . The fish possessing pattern 2 were significantly larger ($P < 0.01$ by ANOVA at 95% significance level) in the areas close to the 8°C isotherm above 68°N ($188.0 \pm 18.9 \text{ g}$ [$n = 6$]) compared to the rest of the same trypsin phenotype ($102.2 \pm 11.4 \text{ g}$ [$n = 9$]) caught in the Norwegian Sea.

On average, postsmolts of trypsin pattern 1 and pattern 2 caught in the Norwegian Sea in July were about 2 times larger, while the fish of pattern 2' were about 4 times bigger than the fish of the same trypsin phenotype caught off the Hebrides in June. All postsmolts of pattern 2' ($n = 7$) in the Norwegian Sea were caught during 23-24 July 1995 with an average weight of $234.3 \pm 24.9 \text{ g}$ (Table 1) while the postsmolts of patterns 1 and 2 ($n = 18$) caught about the same time (23-31 July 1995) had an average weight of $164.4 \pm 10.3 \text{ g}$, indicating that the higher weight of pattern 2' fish was not due to the catching of the fish near the end of the survey. Although the fish caught in the Norwegian Sea were on average larger, they tended to be younger (38.6% as 1+ smolts, 52.3% as 2+ smolts, and 9.1% as 3+ smolts) than those off the Hebrides (11.4% as 1+ smolts, 81.8% as 2+ postsmolts, and 6.8% as 3+ smolts) (Table 2). Generally, salmon from middle and southern Europe (principally the British Isles, France, and Iberian Peninsula) dominate in the western Norwegian Sea while postsmolts from northern Europe (principally Norway) are represented in the eastern Norwegian Sea (Holst et al. 2000). Based on size and smolt age distribution of postsmolts in both areas in the current investigation, the fish from central or southern Europe dominated the catches (Holst et al. 1996, Holm et al. 2000). A wild fish tagged in April 1995 on the River Test, near Southampton, southern England, was recaptured on 23 July 1995 at $70^{\circ}54'\text{N}$, $2^{\circ}27'\text{E}$ (Holst et al. 1996). This postsmolt weighed 249 g and was identified to have trypsin phenotype of pattern 2 (TRP-2*100/92). According to the trypsin isozyme assumption, it would not be surprising to find the fish from central Europe in the areas where sea temperatures are below 8°C if the fish possessed the "cold temperature" variant TRP-2*92 as well as the "warm temperature" isozyme TRP-2*100. As many of the postsmolts caught were assumed to come from central or southern Europe, it is interesting to note that the

other trypsin variant TRP-1*91 having temperature characteristics of somewhat higher than the variant TRP-2*92 and dominating (> 40%) in a Scottish Atlantic salmon population from the River Shin in northeast Scotland (see Rungruangsak-Torrissen et al. 1998), was not observed in any of the postsmolts caught in the current experiment. An adult salmon of 2,645 g possessing the trypsin variant TRP-1*91 was caught off the Hebrides. Atlantic salmon populations do not seem to disperse randomly in the sea, and we do not know whether survival rate differs among different phenotypes or if they enter the sea at different time or migrate in different directions. Almost all postsmolts caught were wild fish. Although they were of different ages, it is likely that the sizes of postsmolts for the first sea entry were similar as fish sizes at different smolt age were within the same range, and 1+ smolts seemed to be larger than the older smolts (Table 2). Growth is rapid at sea in the early weeks and a critical time for growth and survival opportunities seems to be during summer (Holst et al. 2000), indicating an importance of distribution of salmon relative to sea temperatures suitable for optimum growth.

Variation in plankton abundance between the Hebrides and in the Norwegian Sea indicated that the abundance was very dynamic in the top layer of 0-50 m depth during June and July. The low plankton s_A values observed in the Norwegian Sea, compared to off the Hebrides (Fig. 2), may be due to grazing. According to Institute of Marine Research (1996b), smaller zooplankton (<2 mm), mainly copepods, dominate the upper layers while larger zooplankton (>2 mm), mainly euphausiids, dominate at deeper layers during summer in the Norwegian Sea. Vertical migrations in these layers occur, but are relatively moderate in summer. The overlap between hydrographic conditions, postsmolts, and plankton abundance in the Norwegian Sea (Fig. 2) is located in favorable areas with respect to growth. Since the majority of catches in the current work occurred during daylight hours, some fish might have been deeper than 25 m. Atlantic salmon is a column feeder and should be expected to feed at any depth above the thermocline. Vertical distribution of postsmolts may affect sampling efficiency and as groups of postsmolts were seen moving close to the surface during twilight (Holm et al. 2000), salmon may also feed during the night.

Almost all salmon were caught in areas of salinity ≥ 35 . The apparent lack of fish with a high river age (3+ and 4+ smolts) originating from cold rivers in middle and northern Norway (Holst et al. 1996, Holm et al. 2000) might be because the survey was limited in the north and northwest directions. Data from the northern parts of the Norwegian Sea would therefore be interesting with respect to our hypothesis. The high frequency of postsmolts carrying the variant TRP-2*92 off the Hebrides area might be due to the area being an important intermediate feeding zone with high density of food organisms. When temperature is high, and food abundant, the advantages of certain trypsin variants seem to be reduced. More data from this area, also spanning the entire temperature scale, would be valuable.

In the Norwegian Sea, food organisms dominating in the postsmolt stomachs were crustaceans (*Parathemisto* spp.), krill, herring, and redfish larvae, whereas off the Hebrides blue whiting larvae were the only food item identified (Holst et al. 1996) due to the very strong 1995 year class of blue whiting spawned earlier in the year (ICES 1998, Jacobsen and Hansen 2000). In addition, some size-selective predation and selective feeding strategy of postsmolts may have occurred (Holst et al. 1996, Jacobsen and Hansen 2000). Distribution of Atlantic salmon in the sea seems to be dependent on environmental factors, such as temperatures (Reddin and Shearer 1987, Reddin and Friedland 1993), currents (Reddin and Friedland 1993, Holm et al. 2000), and probably food organisms and density since growth and survival are also important fitness characters (Hansen and Jacobsen 2000, Jacobsen and Hansen 2000). Abundance, type, and size of food may force the fish to stay in the area with high occurrence of food organisms, and due to the lack of a "warm temperature" isozyme (TRP-2*100) in salmon of pattern 2', the fish tended to be smaller in the area off the Hebrides. Under these circumstances the relative "advantage" is reduced. There are also other trypsin isozymes in the pyloric caeca, and their temperature effects are unknown. The assumption that trypsin in the pyloric caeca of Atlantic salmon is a rate-limiting enzyme for food utilization and growth (Rungruangsak-Torrissen et al. 1998, Rungruangsak-Torrissen and Male 2000) should be valid not only in captive aquaculture but also in natural marine ecosystems. The present investigation, however, did not have enough background data on the origins of the analyzed fish and total stock distributions to enable solid conclusions. Postsmolts have been observed to migrate in small shoals (Holm et al. 1998, Holm et al. 2000), at least in coastal areas. The possessions of similar trypsin phenotypes observed in the current investigation might indicate a common origin. The high catches taken near the northwest boundary of the survey area in the Norwegian Sea indicate that the total distribution of salmon postsmolts might not be well described by this survey (Figs. 1 and 3). Further investigation where salmon are the target species is then needed.

Genetic differences in trypsin expressions could be affected by the differences in gene sequences (Rungruangsak-Torrissen and Male 2000) and/or at gene expression levels dependable on environmental factors such as temperature (Rungruangsak-Torrissen and Male 2000) and dietary quality (Haard et al. 1996, Peres et al. 1998) at the very early life stage. Trypsin-specific activity is shown to be related to ability of food utilization and fish growth (Lemieux et al. 1999, Sunde et al. 1998, Rungruangsak-Torrissen et al. 1999, Rungruangsak-Torrissen and Male 2000). Trypsin activates chymotrypsinogen to active chymotrypsin, another major proteolytic enzyme, and the specific activity ratio of trypsin to chymotrypsin (T/C ratio) indicates the digestibility quality of the dietary protein (K. Rungruangsak-Torrissen and others, unpubl. data) and the digestion ability of the fish (K. Rungruangsak-Torrissen and Male 2000, Rungruangsak-Torrissen and Sundby 2000, K. Rungruangsak-Torrissen and others, unpubl. data). Effects

on growth, mainly described in farmed fish, are also likely to develop in natural populations. The data analyzed seem to support the hypothesis when food is limited. The relative advantage is, however, less if food is abundant, as in the southern area analyzed.

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Critical Habitat for Ovigerous Dungeness Crabs

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Abstract

The Dungeness crab, *Cancer magister*, supports an important fishery in the northeastern Pacific Ocean, yet there is limited knowledge of ovigerous female brooding locations and brooding behavior. Our earlier research suggests that ovigerous crabs aggregate at the same brooding locations for many years. Within these locations, ovigerous females occur in high densities, with the majority of the aggregation buried within the sediment. These locations often have similar water depths and sediment types and appear to be critical for this life history stage. Our study was designed to examine the bathymetric distribution of Dungeness crabs in bays with and without sea otters at eight locations within the Glacier Bay area by conducting transects with a video-equipped manned submersible. Two of the bays investigated contained large aggregations of ovigerous females. At both sites the substrate was composed primarily of sand. However, only a small percentage of the 33 km of transects were classified as sand. These data suggest that sand substrate may be a limiting resource. Since crab brooding aggregations represent a large portion of the crab population within a small area, and because they are a critical component of Dungeness life history, areas with these characteristics need to be investigated, mapped, and protected from development or exploitation. The areas requiring protection from the impact of anthropogenic wastes, fishing, and logging activities could be quite small, thus limiting conflict with alternative users.

Introduction

The Dungeness crab, *Cancer magister*, is an important commercial fishery species in Alaska and the northeastern Pacific. Their range extends from the Pribilof Islands to Baja California (Jensen and Armstrong 1987). The total monetary value generated by the fishery (Alaska, British Columbia, Washington, Oregon, and California) in 1997-1998 was \$83,665,600 (Pacific Fishing 1999). In Alaska, this represented a harvest of \$5,685,000, with \$4,500,000 coming from southeastern Alaska (Pacific Fishing 1999). The Dungeness crab fishery in Alaska is managed by sex, size, and season. Males with a hard carapace of 165 mm width (excluding 10th anterolateral spines) or greater can be legally harvested. Males become reproductively active in their third or fourth year while they are still sublegal in size, allowing them one year to mate prior to reaching a legally harvestable size (Cleaver 1949).

In Alaska, several aspects of the Dungeness crab reproductive cycle differ from those at lower latitudes. Egg incubation is longer, hatching is considerably later (Shirley and Shirley 1988), and not all reproductive females produce a clutch every year (Swiney 1999). Other aspects of mating and egg extrusion are similar to Dungeness crabs found in other parts of their range. Mating and egg extrusion in Alaska occurs from August to January, when the adults migrate to shallower waters (Shirley and Shirley 1988). Females reach sexual maturity in their second year (Hoopes 1973) and mate, but their gonads are not sexually mature, so eggs are not extruded until the following year (T. Shirley and G. Kruse, unpubl. observations). Mating occurs between hard-shell males and females in a soft-shell condition (Snow and Neilsen 1966, Hoopes 1973). Females mate with males that are at least two molts larger (T. Shirley and G. Kruse, unpubl. observations). In Alaska a portion of the females do not extrude eggs every year (Swiney 1999). The females that do reproduce will follow one of two pathways, depending on their size. If the females are smaller than 141 mm in carapace width, the majority will mate and subsequently extrude eggs once their shells have hardened. If the females are larger than 141 mm, many will not mate, but will rely instead on stored sperm and extrude their eggs (Swiney 1999).

Spermatophores are stored in the spermathecae and eggs are fertilized during extrusion (Cleaver 1949, Hoopes 1973, Shirley et al. 1987). Sperm may be stored for up to 2.5 years (Hankin et al. 1989). Eggs are deposited onto the pleopods (Wild 1980) and an egg clutch may contain as many 1.5 million to 2 million eggs (Hoopes 1973, Wild 1980, Hankin et al. 1989). Females must be partially buried for the eggs to form an egg mass (Wild 1980). The large clutch size forces the abdominal flap away from the thorax, making locomotion awkward (O'Clair et al. 1996). When eggs are first extruded they are bright orange, but darken with time. Just prior to hatching they are brown or black as a result of lipid depletion and the formation of the eyes (Cleaver 1949, Hoopes 1973). Eggs for both size classes of

females usually hatch between May and June (Shirley et al. 1987, Swiney 1999). Alaskan Dungeness crabs may not produce an egg clutch every year (Swiney and Shirley 2001) as a result of the longer brooding times and their reduced feeding activity when in an ovigerous state (female with an egg clutch) (O'Clair et al. 1990, Schultz and Shirley 1997). Molting and thus mating probability also decreases with increasing carapace width (Hankin et al. 1989).

Although many aspects of Dungeness crab biology and life history have been investigated, knowledge of the attributes of brooding location and the behavior of ovigerous females is limited. Our study was prompted by observations made in a study designed to measure the impact of sea otters on the bathymetric distribution of Dungeness crabs in several bays near or within Glacier Bay (Scheding, M.S. thesis in progress). Two of the bays investigated, Excursion Inlet and St. James Bay, contained large aggregations of ovigerous females. Both sites were near the mouths of rivers in water less than 10 m in depth with a primarily sand substrate. Of the 33 km of seafloor transected, only a small percentage was classified as sand substrate. These data suggest that a sandy substrate may be a limited resource in inner coastal waters. The objectives of our current study were: (1) to quantify the substrate by area within each bay; (2) to compare assessments of substrate type made from submersible videos, with grain size analysis from cores collected by scuba divers at two aggregation sites; and (3) to characterize habitat variables at the aggregation sites.

Methods

The eight study sites were selected because they had similar bathymetric profiles and waters deeper than those normally commercially fished for Dungeness crab. For several locations we also had data on both sea otter and Dungeness crab population densities.

Three of the sites had resident sea otter populations (Dundas Bay, Port Althorp, and Idaho Inlet), two sites (Bartlett Cove and the Beardslee Islands) were used over the winter months by transient otters (Jim Bodkin, U.S. Geological Survey, pers. comm.), and the other three sites (Excursion Inlet, Tenakee Inlet, and St. James Bay) did not have sea otters and served as controls. An additional site, Sunshine Cove, was added the following year for quantitative sediment analysis of an aggregation site, in addition to the St. James Bay site. These two locations were selected because of their proximity to Juneau (Fig. 1).

All transects were conducted with a two person submersible, the R/S *Delta* (Delta Oceanographics Inc.). The submersible operator sat in the navigation station, which was located in the middle of the submersible's fuselage. The scientific observer occupied the forward portion of the fuselage in a prone position. Ports provided views port, starboard, and forward. An external video camera was mounted on the starboard side to provide a video record of the transects. The camera angle of view is perpendicular to

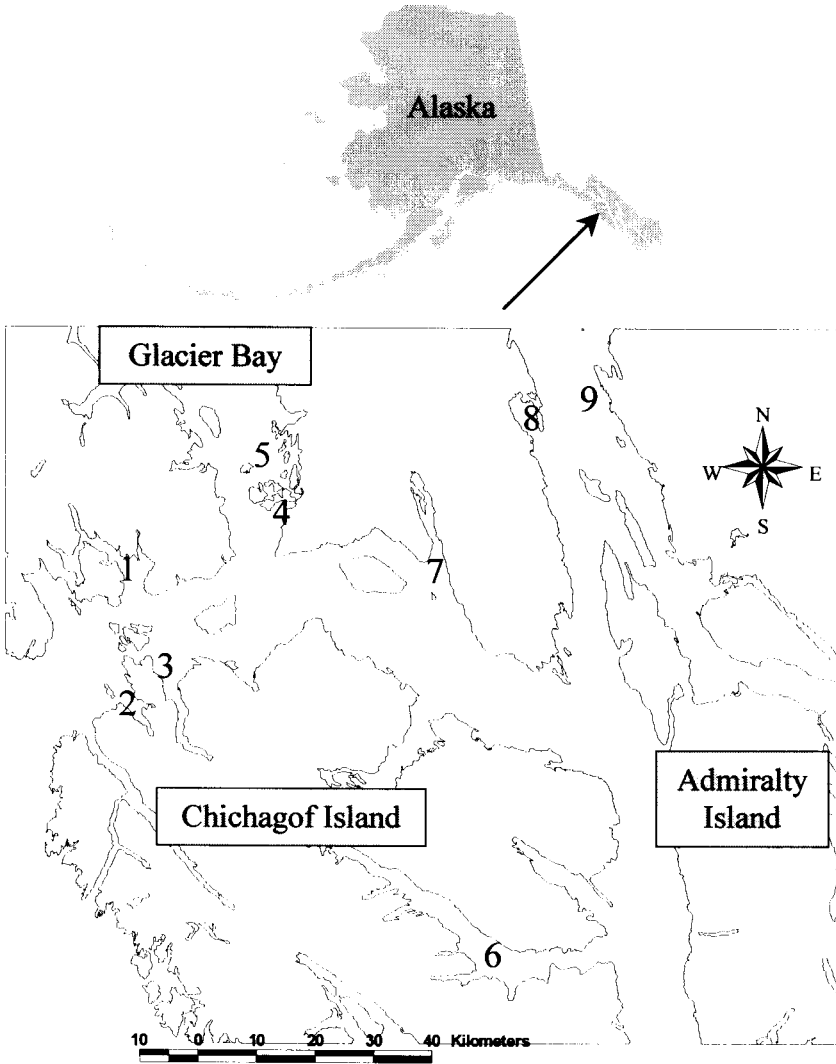


Figure 1. Study sites in the Glacier Bay area. Bays with sea otters: 1, Dundas Bay; 2, Port Althorp; 3, Idaho Inlet. Bays used seasonally: 4, Bartlett Cove; 5, Beardlee Islands. Bays without sea otters: 6, Tenakee Inlet; 7, Excursion Inlet; 8, St. James Bay. Additional site for quantitative analysis: 9, Sunshine Cove.

the direction of the submersible. An audio description by the observers was recorded onto "hi-8" videotapes along with physical variables including depth, height above bottom, and water temperature.

The manned submersible was deployed beginning May 9, 1998; sediment and hydrographic data were collected by divers on the same calendar dates in 1999. These dates coincide with a time when the commercial fishery is closed and prior to most females hatching their eggs.

Sixty-three transects (500 m each) were completed at a cruising speed of approximately 0.257 m per second over 8 days. Transects were conducted at predetermined bathymetric contours in each bay. The method of following a depth contour was selected to reduce habitat variability within transects and to control for bays with different maximum depths. Transects began at the 10 m contour, followed by 25 m, and then increased in 25 m increments to a maximum of 200 m, depending upon the depth of the bay (all depths corrected to MLLW datum). Most commercial fishing occurs in waters less than 25 m deep. The first four categories (10-75 m) are within the diving capability of sea otters, while the 100 m category is close to the limit of their diving range (Newbry 1975). Depths greater than 100 m are unlikely to be foraged by sea otters.

The R/V *Medeia*, a 34-m-long Alaska Department of Fish and Game research vessel, was the support ship. Macrofauna and substrate types of the video-taped transects were quantified immediately after each dive onboard the research vessel and in more detail in the laboratory after the cruise. All species observed were either identified to the lowest possible taxon or placed into broad categories when identifications could not be made. Specific habitat variables were recorded, including gradient, substrate type, and biogenic activity or evidence of benthic activity (e.g., burrows, mounds, tracks). Seafloor gradient was classified into four categories: flat (0-5%); shallow (6-15%); steep (16-30%); and very steep (>30%). Substrate type was classified into 10 categories: macroalgae; shell; mud (including clay and silt), 1-62 mm; sand, 62 mm to 2 mm; granule, 2-4 mm; pebble, 4-64 mm; cobble, 64-256 mm; boulder, >256 mm; bedrock; and rockwall. Particle size classification followed the Wentworth scale. To quantify the amount of each substrate we first estimated the transect area. The area was calculated by multiplying the length of the transect (determined by the O.R.E. Trackpoint II system and GPS) by the width of the camera's field of view. Transect width was determined from the average height of the camera above the seafloor (0.57 m) and the camera declination of 37 degrees from the horizontal. Visibility and seafloor gradient also affected transect width. To obtain an accurate estimate of the area surveyed, each transect was sampled every 20 m for height off the bottom, visibility, and seafloor gradient. A matrix of width values was calculated for a range of gradients and visibilities and each 20 m increment was assigned a width accordingly. The area for each increment was calculated and summed to provide the area of each transect. To determine substrate type and gradient, examples with the correct scale were referred to.

Several edaphic variables were examined to characterize physical parameters that might be important for brood site selection. Divers collected sediment core samples and interstitial water samples. The aggregation site at St. James Bay was relocated in 1999 with GPS coordinates recorded in 1998. Ten core samples were randomly collected at each aggregation site. Modified 50 ml syringes were used by divers to extract substrate samples which were immediately placed in plastic bags. The samples were collected either within a crab pit (crab burial site) or on the edge of a pit. Ten additional samples were collected at Sunshine Cove in June 1999. On this later sampling trip, five cores were from within the aggregation and five others were collected approximately 20 m away from the site at the same depth.

Water samples were collected at both sites by inserting a 15 cm canula into the sediment and extracting an interstitial water sample. Dissolved oxygen, temperature (both measured with YSI 55 oxygen meter [± 0.2 mg per liter at calibration temperature]) and salinity (measured with Atago refractometer [$\pm 0.5\%$]) were measured from the interstitial water samples and from sea surface water samples.

In the laboratory, core samples were transferred to glass jars. Samples were left to settle for 24 hours and then excess seawater was removed with a syringe. The samples were desiccated in drying ovens on aluminum trays at 60°C until a constant weight was obtained. These samples were randomly assigned to two equal groups. One set of samples was used for grain size analysis and the other was used to determine percent organic matter in the sediment. For particle size analysis, the dry weight of each sample was recorded prior to being placed in a sieve shaker for 15 minutes; sieve sizes used were: 4 mm, 2 mm, 1 mm, 500 μm , 250 μm , 125 μm , and 64 μm . The percentage by dry weight of each size class was calculated.

To measure organic content, samples were treated with an acid wash to remove carbonates (Holme and McIntyre 1971) prior to combustion of the samples at 600°C in a Thermolyne muffle furnace. Samples were transferred to 250 ml beakers and 1.0 M hydrochloric was added to each sample to form a thick slurry. Glass lids were placed on the beakers to prevent sample loss while drying. The samples were then dried on hot plates in a fume hood. The weight of the samples was recorded prior to and after combustion in a muffle furnace for 24 hours; percent organic content was calculated from the weight loss.

Results

The three sites with ovigerous female aggregations (Excursion Inlet, St. James Bay, and Sunshine Cove), all had similar bathymetric profiles. Aggregations were found in shallow waters 10 m in depth or less and sand was the main substrate type. The aggregation site at St. James Bay began at 2 m in depth on a flat seafloor and continued down slope at a gradient of ~25% to 5.5 m in depth. The aggregation density was highest on the slope but was more unevenly distributed than the aggregation at Sunshine Cove.

However, the overall size of the aggregation at St. James Bay appeared to be larger than the aggregation at Sunshine Cove. At the latter site all of the aggregation was on the shelf, and the slope had a more gradual incline. This aggregation site began at approximately 3 m in depth and extended to approximately 10 m in depth. Female densities for the St. James Bay and Excursion Inlet aggregations were 0.86 (43 crabs per 50.1 m²) and 0.75 (10 crabs per 13.4 m²) crabs per m² respectively, estimated from crabs counted on videotapes.

The area surveyed in each bay was initially categorized by depth (Fig. 2). Large differences existed among bays with respect to area surveyed. The smallest area surveyed was Bartlett Cove (731 m²), followed by the Beardslee Islands (1,918 m²), Excursion Inlet (2,155 m²), Idaho Inlet (2,519 m²), Port Althorp (2,709 m²), St. James Bay (5,669 m²), Dundas Bay (6,068 m²), and Tenakee (9,893 m²). Part of the reason for areal differences was the variation in depths among bays. Bartlett Cove and the Beardslee Islands are both shallow bays with maximum depths of 50 m. Idaho Inlet, Excursion Inlet, and St. James Bay had intermediate maximum depths that were 75 m, 100 m, and 100 m, respectively. Port Althorp (150 m), Tenakee Inlet (200 m), and Dundas Bay (200 m) were the deepest bays (Fig. 3). The variations in depth resulted in the number of transects within each bay varying from 6 to 10. The first five depth categories (10-100 m) had similar area surveyed (approximately 5,000 m²), but the average for the next four depth groupings (125-200 m) was only 1,750 m². Note, however, that the deepest four depth categories were found in only three bays (Port Althorp, Dundas Bay, and Tenakee Inlet). The depth differences explain most of the variation in area among bays, but visibility and seafloor gradient also contributed. For example, Dundas Bay and Tenakee Inlet had the same lengths of transects surveyed, but a large difference in area covered (6,068 m² versus 9,893 m²) existed. The majority of the difference was due to variation in visibility among the two bays. Average visibility in Tenakee Inlet was higher than in Dundas Bay (3.5 m compared to 2.5 m).

Mud was the predominant substrate type at all depth categories (Fig. 4). In the 10 m category mud composed 43% of the total substratum, with macroalgae being 34%. The other two common substrates for this depth were shell at 14% and sand at 8%. Mud was the primary substrate for all other depth categories, varying from a low of 76% to a high of 98%. Sand composed only a small percentage of the total area and was restricted to shallow water. In the 10 m category, sand composed only 8% and decreased rapidly with depth, to 2% in the 25 m category. Pebble, cobble, and boulders were more prevalent in the intermediate depth ranges, along with rockwalls and bedrock. At deeper depths, mud was the predominant substrate.

Dissolved oxygen (DO) content for both St. James Bay and Sunshine Cove was low in the interstitial water. St. James Bay had 1.32 mg per liter of oxygen and Sunshine Cove 2.93 mg per liter (100% saturation for the water characteristics at both sites would be approximately 6.83 mg per liter).

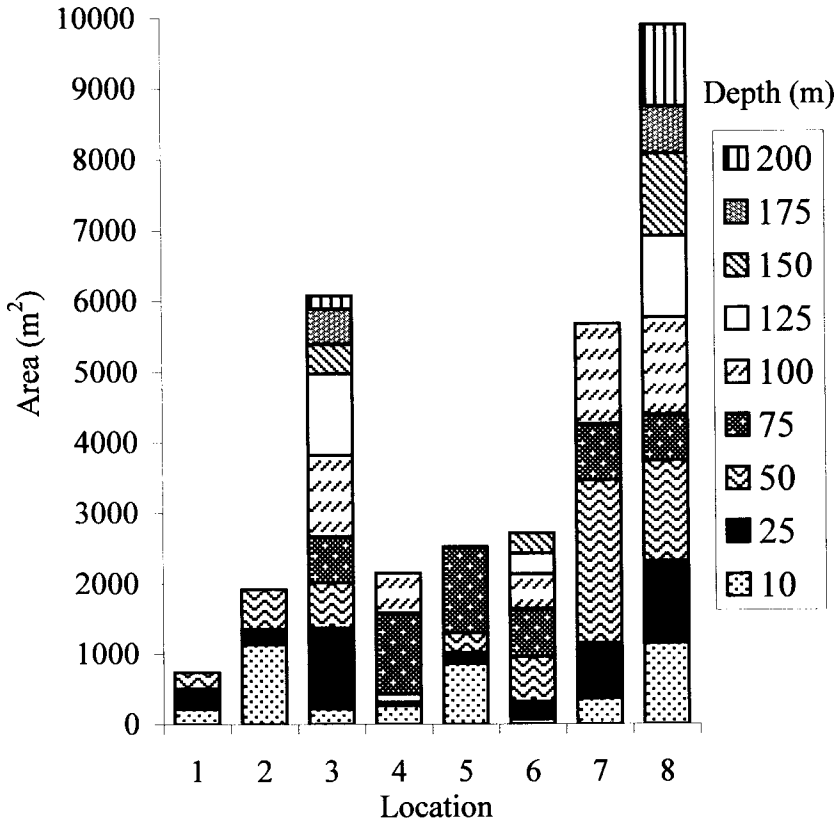


Figure 2. Distribution of area surveyed in each bay by depth. 1, Bartlett Cove; 2, Beardslee Islands; 3, Dundas Bay; 4, Excursion Inlet; 5, Idaho Inlet; 6, Port Althorp; 7, St. James Bay; 8, Tenakee Inlet.

Salinity of interstitial water at St. James Bay was higher (33‰) than the surface salinity (24‰), probably due to freshwater discharge layering above the denser saline water. Sunshine Cove had the opposite trend (25.5‰ and 30‰), but it is not adjacent to a river. Temperature at St. James Bay was higher in the interstitial water: 12.3°C compared to 9.3°C at the surface.

Substrate data collected from submersible videos and the quantitative data from the scuba core samples were similar. The only differences were the larger percentage of granule size particles in the submersible data (13.9% compared to 2.6%) and the smaller amount of mud (2.2% compared to 20.1%). These differences are probably due to the slight differences in core sample collection locations in relation to the transect locations. Given the accuracy of the navigational equipment, it is unlikely that the divers could

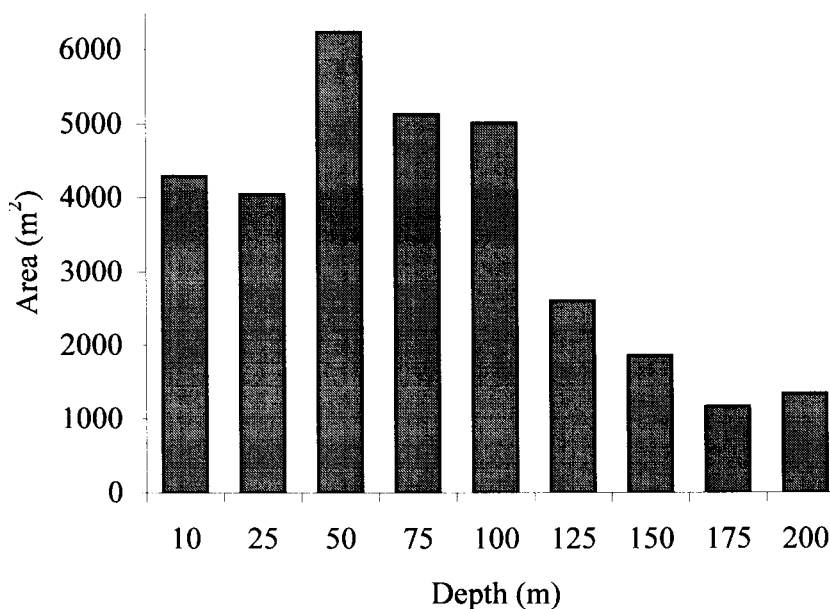


Figure 3. Distribution of area surveyed by depth for all bays combined.

sample the exact locations of the submersible transects. The majority of the initial submersible dive was on a steep slope with a gradient of about 25%. The divers sampled both from the slope and above the slope on the relatively flat seafloor.

The majority of the substrate of the aggregation sites was primarily fine and very fine sand. The St. James Bay grain size distribution was finer than Sunshine Cove. Both had similar amounts of very fine sand particles (St. James Bay, 37.6%; Sunshine Cove, 35.8%), but St. James Bay had a smaller fraction of fine sand particles (15.4% compared to 44.8% for Sunshine Cove) and so had a larger silt/clay fraction (20.1% compared to 3.1%).

Core samples collected at Sunshine Cove within the aggregation and those collected 20 m away have almost identical particle size distributions. Both samples were primarily fine sand (within the aggregation, 50.9%; away, 43.9%), with lesser amounts of very fine sand particles (within the aggregation, 36.1%; away, 37.7%).

The percentage of organic matter in the sediment affects the oxygen availability to the crab and, more critically, to the eggs being brooded. The amount of organic material was relatively high at both aggregation sites, ranging from a low of 6.3% at Sunshine Cove in May to a high of 11.5% in June at a location 20 m away from the aggregation site at Sunshine Cove. Measurements at St. James Bay and Sunshine Cove were not significantly

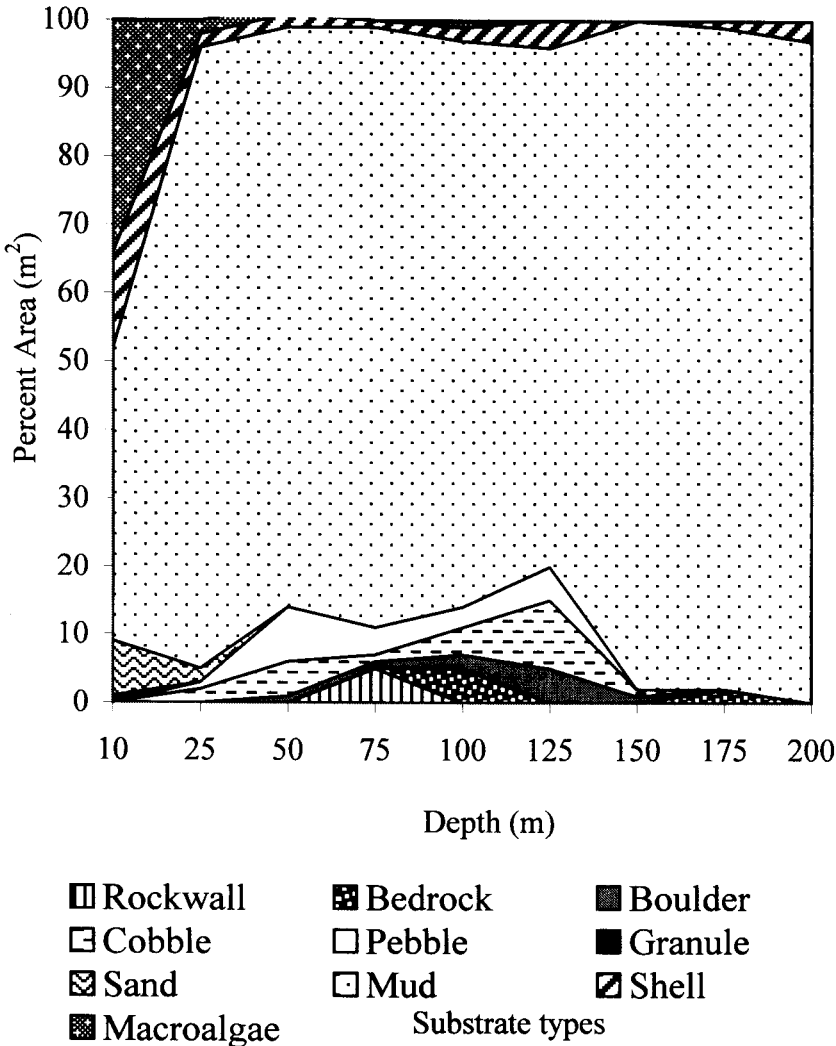


Figure 4. Distribution of substrate types by depth and percent area covered for all bays combined.

different in May 1999 samples (8.1% and 6.3%) ($P = 0.1013$; arcsin transformed single factor Anova) and between the later dives at Sunshine Cove (11.2% and 11.5%) ($P = 0.8441$). However, there is a significant difference when all samples are compared ($P = 0.0035$). This suggests the differences are probably temporal. A likely explanation is that the differences were caused by sedimentation after the onset of the spring bloom. To obtain a more consistent estimate of percent organics within the sediment and possible effects on oxygen availability, it may be better to collect samples prior to the spring bloom sedimentation.

Discussion

Overall density estimates for Dungeness crabs not found within an aggregation vary from 0.00 to 0.02 crabs per m^2 for males and <0.01 to 0.02 for nonovigerous females (O'Clair et al. 1996). These estimates were determined by counting crabs along scuba transects in five bays within or near Glacier Bay over five seasons. The density estimates for the two aggregation sites of ovigerous females found in our study were much higher: St. James Bay (0.86 crabs per m^2) and Excursion Inlet (0.75 crabs per m^2). Even these estimates are biased low for a number of reasons. Some ovigerous females were disturbed by the presence of the submersible, and the rapid departure of one crab would often elicit the same behavior from conspecifics. Thus some of the crabs immediately ahead of the submersible may have scattered prior to being recorded by the video. Also no attempt was made to uncover any of the buried crabs. Ovigerous Dungeness crabs spend much of their time brooding either partially or completely buried within the sediment (O'Clair et al. 1996). Investigations previously made by one of the coauthors (C.E. O'Clair, unpubl. data) have found ovigerous females buried as deep as 0.5 m within the sediment. A mesh enclosure was used by O'Clair to prevent ovigerous crabs from escaping from the aggregation site; densities as high as 20 crabs per m^2 were found. Finally, transects in our study were straight line transects, set to follow a depth contour, so the densest part of the aggregation may not have been intersected.

Brooding locations appear to be used on an annual basis. The aggregation site in St. James Bay was found in the same location in 1998 and 1999; similarly, the Sunshine Cove aggregation was found from prior knowledge of this site (D. Russell, University of Alaska Southeast, Juneau, pers. comm.). Aggregations of ovigerous Dungeness crabs have been reported to have high interannual site fidelity to specific brooding locations (O'Clair et al. 1996). In a 4-year study examining 13 dense aggregation sites at several bays in Glacier Bay, 77% of these sites were reused at least once (O'Clair et al. 1996). Brooding locations with the highest densities were primarily in sand substrate, with four located near the mouths of rivers. Two of our sites were near river mouths (Excursion Inlet and St. James Bay) and all three had substrate composed primarily of sand.

Sand for brooding sites may be a limited resource. Our study of over eight bays found that sand substrate covered only 1% of the transect area and 80% of this was at a depth of less than 10 meters. This zone is well within the sea otter's diving range. It is interesting to note that no crabs were observed in a sand habitat found in shallow water at Idaho Inlet. Since Idaho Inlet is a bay with sea otters, one explanation may be that the absence of crabs is the result of sea otter predation. Aggregations have been suggested to act as a group defense mechanism when ovigerous females are at a vulnerable stage in their life history. O'Clair et al (1996) reported that when ovigerous crabs were initially disturbed, they seemed reluctant to move, probably because of the size of their egg clutch, making movement awkward and slow. However, after a sufficient number had been disturbed, neighboring crabs scattered until the entire aggregation site was deserted. These aggregations may not be an effective defense against an intelligent predator like sea otters. Sea otters might deplete a breeding population within a short period of time where brooding aggregations are in shallow water and are occupied year after year. Adult sea otters in Prince William Sound were documented consuming an average of 14 Dungeness crabs per day with subadults consuming 10 crabs per day (Garshelis et al. 1986). For 1980-1981 this resulted in an estimated annual consumption of 370,000 crabs, half of these being of legal size. In Prince William Sound this level of predation eventually led to the closing of Orca Inlet which had been an important source of Dungeness crabs (Kimker 1984).

Given the locomotive difficulties of ovigerous females and their increased risk from predation, it may not be surprising that several studies have found that ovigerous females have a reduced activity rate, and use less of the available habitat, and that feeding bouts tend to be shorter and less frequent (O'Clair et al. 1990, Schultz and Shirley 1997).

Several hypotheses have been proposed as to why sand is the preferred substrate for ovigerous females. Coarser sediment is difficult to bury into, while finer sediments might cause fouling of the egg clutch, thereby limiting oxygen availability to the eggs (O'Clair et al. 1996). Sand may allow for increased interstitial water flow and therefore increased dissolved oxygen availability (O'Clair et al. 1996). However, we found that the oxygen content for both sites was relatively low, in the range of 19-43% saturation. This could have resulted from the high percentage of organic matter in the sediment (6.3-8.1%), which would have reduced oxygen availability to eggs.

Alternately, low oxygen content has been proposed as a mechanism of decreasing the metabolic rate of the eggs for *Cancer pagurus*, keeping eggs in diapause for an extended period. This could help to retard hatching of larvae until more favorable conditions prevailed later in the season (Naylor et al. 1999). Whether this is the case for Dungeness crabs is unknown, since no studies have investigated how varying levels of oxygen affect the behavior of the adult crab, or what effects oxygen availability have on embryo development. However, *C. pagurus* is a congener of *C. magister*

and they have similar behaviors when in an ovigerous state. Both species spend most of the 6-9 months of their ovigerous state either partially or completely buried within the sediment, with reduced feeding and activity rates (Naylor et al. 1997, Schultz and Shirley 1997). Developmental stage may play an important role in how embryos will be affected by temperature and oxygen levels (Naylor et al. 1999). The ovigerous females appear to be able to detect critically low levels of oxygen (especially at later stages of embryo development) and change their behavior accordingly, by ventilating the egg mass with their pleopods in a raised position above the surface of the sediment. This behavior was observed primarily at night and was prolonged as embryo development progressed (Naylor et al. 1999). Burial within a sand substrate may allow the females maximum control over embryonic development.

As indicated by the previous example, aggregating behavior is not unique to Dungeness crabs. Several other species in Alaska form aggregations, some of which are formed at different life history stages. However, it is a common behavior exhibited by ovigerous females. Tanner crabs (*Chionoecetes bairdi*) also exhibit aggregating behavior, with ovigerous females aggregating diurnally and then dispersing to feed nocturnally (Stevens et al. 1994). These aggregations have been observed at the same location for several years consecutively, but the substrate characteristics do not appear to be determinants in selection of the aggregation sites, since the surrounding environment (level, mud substrate) appears to be homogeneous for many kilometers (Stevens et al. 1994). The aggregating behavior may be a way of attracting mates, since males were seen mating with females on the periphery of an aggregation (Stevens et al. 1994), but the aggregations are primarily thought to be a method of releasing larvae above the benthic substrate (B. Stevens, National Marine Fisheries Service, Kodiak, pers. comm.).

Juvenile red king crabs (*Paralithodes camtschaticus*) also exhibit aggregating behavior, forming pods of individuals from the same year cohort. They continue this podding behavior until they reach maturity, forming tight aggregations during the day, then dispersing at night to feed (Dew 1990). This behavior may be a way of avoiding predation. Ovigerous, female red king crabs continue to aggregate into large pods, probably for reasons similar to those of Tanner crabs (Stone et al. 1993).

The common feature of the aggregating behavior of these species may be predator avoidance at a vulnerable life history stage. When aggregations are disturbed, crabs tend to scatter. However, burial within sediments in Alaska for extended periods of time appears to be unique to Dungeness crabs, and may be an adaptation to compensate for their large clutch size which makes quick movements more difficult. Both king and Tanner crabs can maintain their abdominal flap tight against their thorax. Selection of sand as the preferred primary substrate may be a way for Dungeness crabs to exert maximum control over their environment by allowing them to burrow readily and deeply within the sediment, while minimizing fouling of their eggs by smaller particle sizes.

Conclusions

Our study suggests that sand may be a limiting resource for ovigerous Dungeness crab aggregation sites. Dungeness crab brooding aggregations represent a substantial portion of the crab population, in a vulnerable life history stage, concentrated within a small area. Nearshore areas with physical attributes of aggregation sites (sand and shallow water) delineated in our study should be explored, mapped, and protected from development or damage that might result from vessel anchorage, discharge of anthropogenic wastes, fishing, and log storage or transfer activities. Aggregation sites appear to be small, thus limiting alternate use conflicts.

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Large-Scale Long-Term Variability of Small Pelagic Fish in the California Current System

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Abstract

A number of recent studies have suggested that ocean-climate interactions can drastically change the productivity of small pelagic fish populations in different current systems, with seemingly parallel variations in the biomass of phytoplankton, zooplankton, and other fish.

Sardinops and *Engraulis* populations, occurring in most eastern and western boundary currents, seem to be sensitive to climate-driven interdecadal regime shifts in the systems, and have been associated with long-term changes in distribution. Particularly, when sardine population size (*Sardinops* sp.) within a current system is high, it dominates the entire neritic zone. Alternatively, when the population size is low its distribution is greatly reduced or even totally absent from some areas. This spatial process is known as expansion-contraction.

Live-bait boats fishing for tuna from the California coastline in the north to Cabo Corrientes in the south, including the Gulf of California, use as bait clupeoid fish caught alongshore. The records include catch of California sardine (*Sardinops caeruleus*) and northern anchovy (*Engraulis mordax*). For this wide region, the CPUE pattern for live-bait species, used as a proxy of abundance, is analyzed during a 49-year period (1931-1979) on large- and mesoscale basis, and related to environmental variability (SST anomalies were the proxy).

Our large-scale long-term analysis in the California Current System suggests that when the sardine population size increased during warming conditions, the bulk of its biomass and the center of distribution were in the north. Before the 1960s, when the population size was decreasing during transition and cooling conditions, the center of distribution and bulk of abundance shifted from north to south and a part of it entered the

Gulf of California during the cold 1960s. This population movement gave rise to a new fishery inside the Gulf of California. When the sardine population size decreased during the end of cool conditions, the bulk of its biomass and the center of distribution were in the south. The spatial process described here is different from that of homogeneous spread resulting from simple expansion and contraction.

Sardine population changes are related to environmental variability, while a spatial pattern of anchovy abundance alongshore is seen assuming that the sardine is deleterious to the anchovy. Northern anchovies colonized and increased in abundance where the sardine population level was low or absent. Thus, concerning the long term and large scale, neither sardine nor anchovy populations conformed to the simple expansion-contraction model of range changes with population increase-decrease.

The same information analyzed only for a restricted geographical area shows limitations and would lead to different conclusions.

Introduction

Time series of California sardine (*Sardinops caeruleus*) and northern anchovy (*Engraulis mordax*) scale-deposition rates in anaerobic sediments of the Santa Barbara Basin reveal natural long-term fluctuations in the abundance of both species (Soutar and Isaacs 1974, Baumgartner et al. 1992). Natural changes in abundance of small pelagic fish populations have been associated with major changes in their geographical distribution (Lluch-Belda et al. 1989, Parrish et al. 1989).

The "regime problem" hypothesis (Lluch-Belda et al. 1989) suggests that fluctuations in landings of sardines (*Sardinops* spp. and *Sardina pilchardus*) and anchovies (*Engraulis* spp.) are dominated by long-term environmental variations, which cause large-scale and prolonged changes that give rise to persistent regimes of high or low abundance of the species. Since the interdecadal regime variation in small pelagic fish was described, similar natural patterns of variability have been noted in a wide variety of marine populations, and it has become a mainstream element of scientific thought (Hunter and Alheit 1995, MacCall 1996, Botsford et al. 1997).

The regimes of high and low abundance of small pelagic fish populations seem related to large-range expansions and contractions. Particularly, sardines extend their spawning areas into cooler regions during warm periods, which results in increased abundance. For the California Current, empirical models have been developed to support the idea of range expansion-contraction with changes in spawner abundance for the California sardine (Lluch-Belda et al. 1991, 1992a), and northern anchovy (MacCall 1990). Such models have been mostly derived from commercial landings of adult fish or from egg and larvae surveys.

Data from commercial fishing, although relatively continuous in time for each port, have different time-area coverage, particularly from north

(Canada) to south (Mexico; Murphy 1966, Sokolov 1974, Radovich 1982). Thus, no comparative indices for periods of high and low abundance are available between ports, even less between the extreme north and south. Geographically, data are spatial representatives of fishing areas around their landing ports, often having important gaps between some of them.

Although California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys, the main source of egg and larvae data, began in 1950 on a basic station plan, changes in the frequency and coverage of cruises occurred from monthly to quarterly scales, and in geographic extent from large-scale surveys covering most of the basic station plan to small-area coverage (Hewitt 1988, Smith 1990, Hernandez-Vazquez 1994). Cruises in some areas were rather sporadic and do not provide continuous time series. Thus, studies about large-scale long-term fluctuations in both of those species are limited. Besides, information before 1950 during the sardine high abundance regime is lacking.

Further, knowledge about *S. caeruleus* and *E. mordax* population dynamics is fragmentary, because it is mainly derived from surveys of egg and larval stages or from sampling of adult individuals that make up the bulk of the commercial catch. The need for study of the biology and ecology of juvenile stages has often been noted (e.g., Pitcher and Hart 1982, Hunter and Alheit 1995).

Vessels fishing for tuna with poles and lines and live bait (also called tuna clippers or baitboats) have been operating widely since the 1930s in the coastal area of the eastern central Pacific, from southern California to northern Peru (Alverson and Shimada 1957). A number of species of fish are used as live bait, mostly clupeoid fish that occur abundantly in inshore waters (Schaefer 1956). A remarkable characteristic of bait is the predominance of young fish (Howard 1952, Wood and Strachan 1970, Maxwell 1974, Baldwin 1977). The staff of the Inter-American Tropical Tuna Commission (IATTC) compiled a database containing tuna and live-bait catch records from clippers operating in 28 statistical areas in this wide geographical region from 1931 to 1979 (Alverson and Shimada 1957). The available database contains monthly catch by area for individual species or mixed species in "scoops" (a scoop is approximately 4.5-6.8 kg), and corresponding standardized effort (in searching days).

Since small pelagic fish are not the target species of tuna clippers, the amount of live bait required for their operation is relatively insignificant compared to that of purse seiners in the commercial sardine-anchovy fishery. Tuna clippers concentrate their effort looking for tuna schools near the sea surface, but they do not search for a particular kind of bait nor in a particular location. When needed, they replenish their fishponds at the nearest possible location (Ortega-Garcia 1987). Fishing for tuna with pole and line depends completely on a constant supply of live bait and on its survival until needed for the fishing operation (Ben-Yami 1980). Thus, their small pelagic fish catch data are mostly devoid of the bias induced by searching for large schools in high-abundance areas (Hilborn and Walters 1992).

In this paper, the wide distribution of live-bait catch by boats fishing for tuna off California and Baja California and in the Gulf of California during a 49-year period, which includes regimes of high and low abundance of California sardine and northern anchovy, is analyzed. Also, available sea surface temperature data are examined and an attempt is made to relate them to species abundance and distribution.

The analysis of the historical changes in abundance of sardine, anchovy, and tropical species on a large geographical scale, including the interspecies interactions between them and their relation to indices of marine climate, leads to different interpretations of the spatial process than the ones made from the stock analysis for restricted geographical areas.

Although our results agree in general with the suggestion that changes in abundance of small pelagic fish are associated with shifts in their distribution, those variations occurring on a decadal time scale and over a major geographical area differ from the homogeneous spread that is normally expected from an expansion-contraction process about a fixed geographical center. The simple expansion-contraction model emerged from time series analysis of recoveries and collapses of sardine-anchovy stocks harvested within a limited geographical scale, or from abundance changes inferred through scale-deposition rates obtained at a specific core site.

Data and Methods

We used the IATTC database of live-bait records for 1931-1979. We analyzed 14 of the 28 statistical areas of the eastern central Pacific containing catch records of California sardine (*Sardinops caeruleus*) or northern anchovy (*Engraulis mordax*), ranging from southern California in the north to Bahía Banderas-Cabo Corrientes in the south and including the Gulf of California. Besides these species, others caught in the region are herring (*Harengula thrissina*), thread herring (*Opisthonema* spp.), and anchoveta (*Cetengraulis mysticetus*). Records of herring, thread herring, and anchoveta in each area were merged as tropical species.

We pooled the information in some areas, given the difficulty of establishing a latitudinal sequence among them. We thus merged the information of Bahía Magdalena, Bahía Almejas, and Bahía Santa María into one area. The same was done with the central part of the Gulf of California, originally described as Guaymas, Yavaros, and Isla Macapule. In this paper we use 10 areas (Fig. 1): A, California waters; B, Mexican border to Punta Eugenia; C, Punta Eugenia to Cabo San Lázaro; D, Bahía Magdalena; E, Punta Redonda to Cabo Falso; F, Gulf of California West; G, Central Gulf of California; H, Gulf of California East; I, Bahía Banderas; and J, Southern Cabo Corrientes. Further, for part of the analysis area F (Gulf of California West) was combined with the California and Baja California areas (areas A-F). Other areas in the Gulf of California along the mainland were also latitudinally arranged (areas G-J).

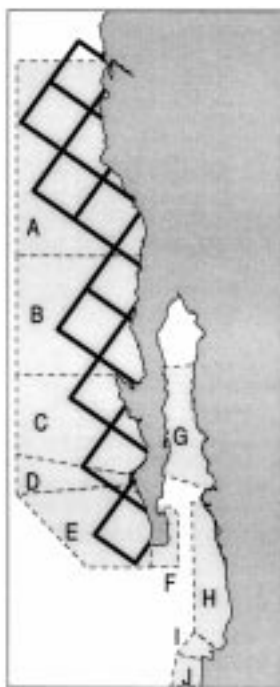


Figure 1. Live-bait fishery areas off California and Baja California, and in the Gulf of California (after Alverson and Shimada 1957), including squares of 2×2 degrees from which time series of SST were obtained from the COADS database.

For each of these areas, total monthly catch for *S. caeruleus*, *E. mordax*, and tropical species in scoops and their corresponding effort (in searching days) were extracted from the IATTC database for 1931-1979.

Annual CPUE by species (total annual catch per total annual effort) was estimated as a proxy of abundance for each area. Ten-year (decadal) averages were estimated from the annual CPUEs for areas A-F only.

Time series of sea surface temperature (SST) for the same geographical region, from San Francisco, California to Cabo Falso, Baja California (areas A-E), were obtained from the Comprehensive Ocean Atmosphere Data Set (COADS) (Mendelssohn and Roy 1996). Data for the Gulf of California (areas F-J) are too fragmentary through the analyzed period to provide annual resolution of temperature fluctuations.

We used the SST data in coastal 2 degree by 2 degree squares for each area (Fig. 1), estimated the mean annual cycle for 1900-1996 for each, and calculated their monthly anomalies as departures from the mean monthly

values. Yearly anomalies were then estimated as the average monthly anomalies for the year. The yearly global area index for the 1930-1980 period is the average of 13 individual annual anomalies, one by square. Smoothing was done by means of a Hamming window of 10 years. Decadal averages of yearly SST anomalies by area were also estimated.

Results

Smoothed time series of SST anomalies for areas A-E along California and Baja California coast are shown in Fig. 2, and abundance indices by species on a yearly basis for each live-bait fishery area for 1931-1979 are shown in Fig. 3.

At decadal spans and on a large geographical scale, live-bait species abundance variability along the 49-year period analyzed is shown in Fig. 4. Decadal averages of yearly SST anomalies by area are coupled to species abundance and time series of SST anomalies for the full coastal area is shown enclosed.

Discussion and Conclusions

Smoothed yearly SST anomalies for areas A-E (Fig. 2) show similar trends. A shift from cooling to warming during the early 1920s, cooling from the early 1940s to 1975, and a new shift from low to high temperatures since 1976. A brief warm event related to El Niño occurred during the late 1950s, followed by a cold period during the 1960s. The smoothed SST anomalies show a similar alternating pattern of warm and cool climate states described by Roden (1989), Hollowed and Wooster (1992), Ware (1995), and MacCall (1996).

Strong ENSO (El Niño-Southern Oscillation) events superimposed on these temperature regimes are the ones occurring about 1940 during a transition, in the midst of a cool period (1958-1959), and in the midst of a warm period (1982-1983 and 1992-1993). MacCall (1996) has pointed out that it is unclear how the low-frequency temperature regimes are related to ENSO events, although Ware (1995) mentioned that interactions between ENSO, bidecadal, and very low frequency oscillations produce a pattern of alternating warm and cold climate states.

Time series analysis of CPUE of species within each area (Fig. 3A-J), shows that the long-term changes in fish abundance between areas do not exhibit similar trends.

Relative abundances of small pelagic fish for the California area (Fig. 3A) shows an orderly sequence of *S. caeruleus* and *E. mordax* from 1931 to 1979 similar to the order and timing of fluctuations previously described for commercial catches of the same species in the area.

Sardines were abundant in California waters during the 1930s, with catch plummeting during the 1940s and not recovering until the end of the analyzed period. Anchovies showed increasing abundance from the 1950s through the end of the period. This general behavior, as well as the short-

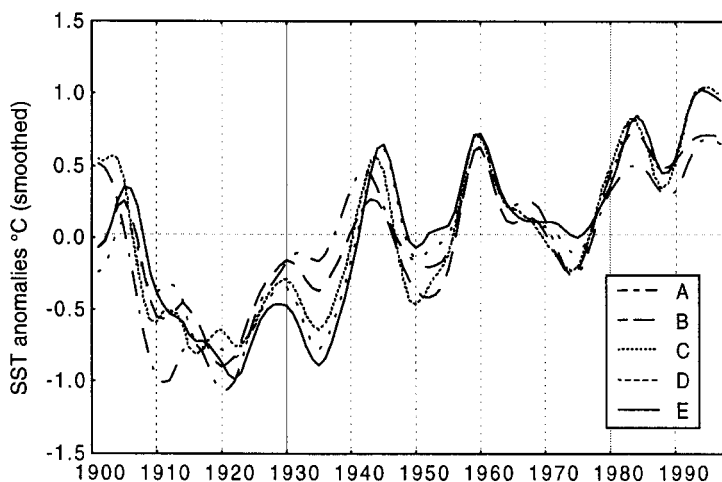


Figure 2. Time series of SST anomalies (smoothed) for live-bait fishery areas off California and Baja California (areas A to E).

term increase in sardine abundance during the late 1950s and the return to low stock levels (Clark and Marr 1955, Murphy 1966, Lasker and MacCall 1983), is also apparent. Similar behavior is shown in area B, but lags by about a decade.

Both California sardines and northern anchovies were in the central Baja California area (C) during the entire 49 years of the analysis, alternating in abundance between cold and warm periods. Although anchovy abundance increased during the 1960s, sardines were always present. This agrees with the hypothesis of a refuge area for a sardine population in this area where oceanographic conditions allow sardine spawning year-round (Lluch-Belda et al. 1992a, 1992b).

Bahia Magdalena is a temperate-tropical transition area. Here, as opposed to the northern areas, sardines alternate in abundance with tropical fish species and with anchovies. Sardines dominated during the 1940s, whereas tropical fish species were dominant particularly during the 1950s. Shortly after a short-term increase in sardine abundance during the early 1960s, northern anchovies became more abundant (Fig. 3D).

Short-term increases in sardine abundance in the northern areas (A-C) during the late 1950s have occurred during El Niño (Ware 1995), abundance lowering in the temperate-tropical transition area and returning to the former level when these events ended.

Along the southwestern coast of Baja California (area E) the data series by species begins in 1950, with earlier information available only for mixed catches, not useful for this analysis. In this area, anchovies were abundant

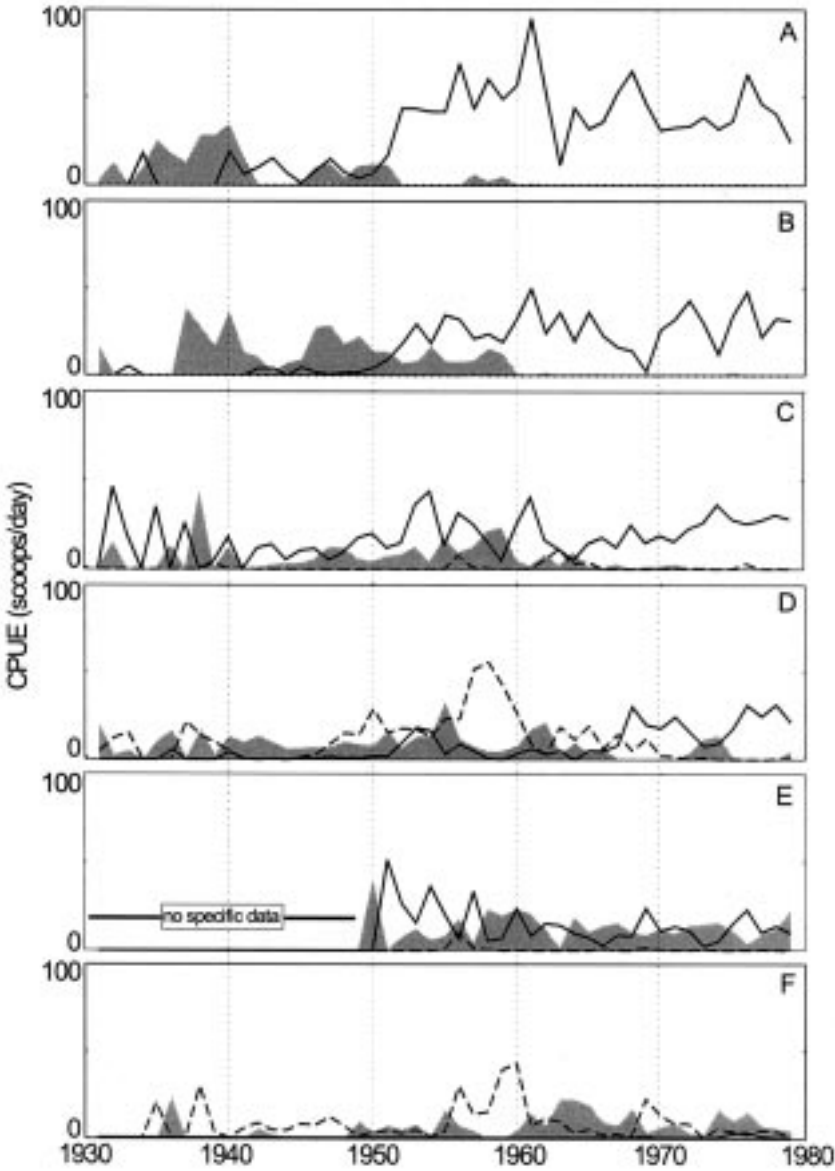


Figure 3. Time series of yearly abundance index for *Sardinops caeruleus* (shaded area), *Engraulis mordax* (thick line), and tropical species (dashed line) by live-bait fishery areas. Areas A-F: off California and Baja California (above). Areas G-J: Gulf of California and along the mainland (next page). Geographical limits are defined in the text.

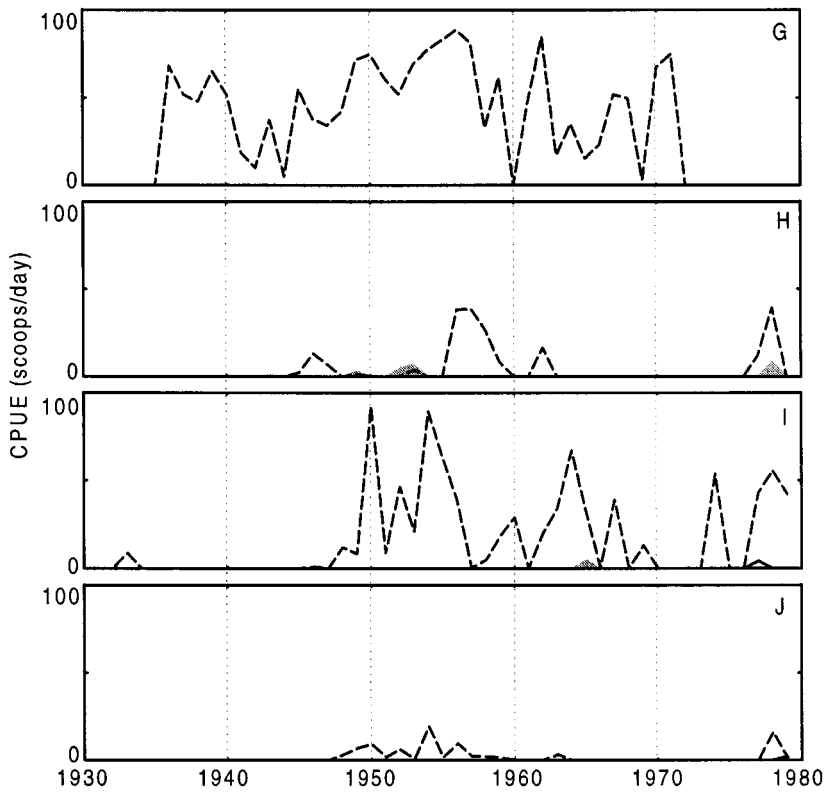


Figure 3. Continued.

through the 1950s, after a period during which consistent catches of sardine were obtained from the 1960s to the early 1970s.

In area F, along the southeastern coast of Baja California (Bahia de La Paz to Cabo Falso), the abundance of tropical species was high during the late 1950s. Consistent catches of California sardines were obtained during the 1960s and early 1970s.

The Gulf of California encompasses a temperate-tropical transition on the basis of fish fauna (Walker 1960). Concurrent to the dominance of tropical species in Bahia Magdalena, the catch of live bait was dominated by tropical fish in the central Gulf of California from the 1930s to the 1960s (Fig. 3G), then diminished toward the beginning of the 1970s, when simultaneously the local commercial catch of California sardine was increasing (Sokolov 1974).

Thus, hypotheses proposed from fish abundance variability from any single area alone may provide a limited representation of the condition of the entire population.

At decadal spans and on a large geographical scale (Fig. 4), live-bait species abundance suggests a low-frequency variability along the 49-year period analyzed, with abundance changes associated with major shifts in the distribution of small pelagic species.

The abundance index for *S. caeruleus* suggests that during the 1930s, while the population increased its geographic range north to British Columbia (not included in this analysis), the bulk of the sardine biomass and the center of its distribution were in the north (area A). When the range and abundance of this population was decreasing (1940s and 1950s), the center of distribution and bulk of abundance shifted from north to south and a part of it entered the Gulf of California during the cold 1960s. This population movement could have given rise to a new fishery inside the Gulf of California. In the 1970s, a period of lesser sardine abundance, the population was mostly confined to the southwestern coast of Baja California and the Gulf of California.

The range of the California sardine has been reported to extend poleward during warm periods as other sardine populations do in other eastern boundary currents. Equatorward extension has been reported only for sardines of the Canary Current and in the southeast Pacific (Lluch-Belda et al. 1989). The southernmost report of *S. caeruleus* is off Islas Revillagigedo (Whitehead and Rodríguez-Sánchez 1995), although no evidence of massive abundance has been reported.

It is during the warming period (1930s, Fig. 4) that decadal averages of yearly SST anomalies are well coupled to latitudinal distribution of sardine abundance. During the regime shift from high to low temperatures in the 1940s, sardine abundance declined in the northern areas as the first sign of ocean-climate-population interaction, with less apparent changes in the south. During the cool 1950s to 1960s, the relationship between sardine abundance and decadal SST anomalies is less clear. After the end of the cold regime in the 1970s, during which the sardine population was con-

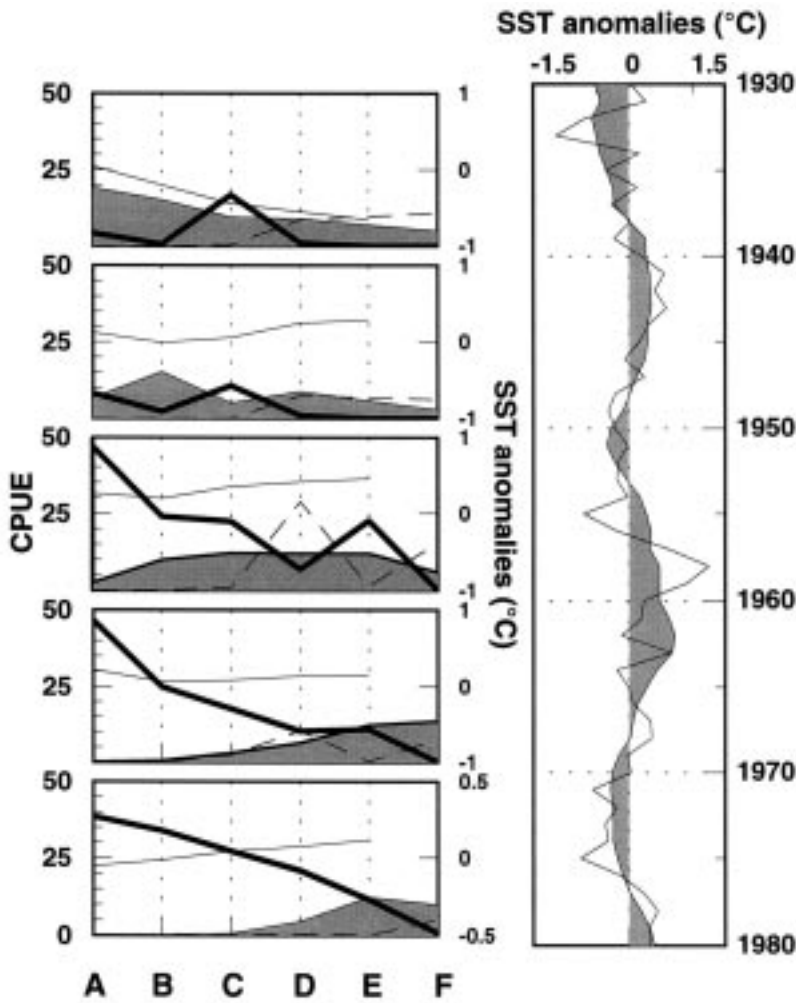


Figure 4. Interdecadal variability of SST anomalies and small pelagic fish abundance for live-bait fishery areas off California and Baja California: *Sardinops caeruleus* (shaded area), *Engraulis mordax* (thick line), tropical species (dashed line), decadal averages of yearly SST anomalies (thin line). For 1970s, scale in second Y-axis (SST anomalies) is changed. Time series of yearly (solid line) and smoothed (shaded area) SST anomalies for the full coastal area is enclosed perpendicularly.

finned mostly to the coast of Baja California (the refuge area), a new warming period began (Ware 1995, MacCall 1996), and again the latitudinal distribution of sardine abundance relates well to decadal averages of yearly SST anomalies.

It has been suggested that ocean temperatures are a simple proxy for the more complicated and poorly understood suite of oceanographic variables that influence biological populations (Lluch-Belda et al. 1989, MacCall 1996). Our results agree with this, because an empirical relation is evident only at the beginning and at the end of the sardine population movement, whereas no relationship is apparent when sardine abundance is shifting. Therefore, the sardine population seems to be important when tracking responses to regime shifts of temperatures, but not along sustained regimes. In other words, sardine abundance regimes are not those of the warm or cool periods, but those of warming or cooling periods.

Climatic indices (others than SST) have been used to correlate climate dynamics and fish population fluctuations (e.g., Bakun 1996, Klyashtorin 1998). They are still only faint indications of the mechanisms through which environmental changes act on population abundance. Most of the evidence rests on the simultaneity of events or empirical correlation. Nevertheless, hypotheses of the relationship between environmental variables and biological processes of importance for sardine population growth have not gone further than the early hypothesis of Kawasaki (1983) regarding the expansion of the feeding habitat or that of Lluch-Belda et al. (1989) of the expansion of the spawning habitat.

The relation of spatial distribution of decadal SST anomalies and anchovy or tropical species abundance is not apparent. Our results agree with a former hypothesis that *Sardinops* species are more susceptible to climate change than other small pelagic fish (Crawford et al. 1991). If it were true that sardine abundance is deleterious to the anchovy population (Radovich 1982), a spatial pattern of northern anchovy abundance along-shore should be observed.

When the bulk of the biomass and the center of distribution of the sardine population was in the north during the 1930s, anchovy abundance was high in the south (area C, Fig. 4). Later, when the sardine population decreased in the northern areas (1940s), anchovy abundance increased. During the 1950s, when the distribution of sardine abundance was more homogeneous, the anchovy abundance index suggests that besides increasing northward, anchovy also colonized southern areas. Nevertheless, during the 1960s and 1970s sardine population abundance shifted from north to south and with the bulk of biomass and center of distribution moving to the southern areas, anchovy abundance was prevented from growing. Finally, the retreat of the sardine population allowed anchovy abundance to grow in the north.

Recently, in the central Gulf of California (area G), an example of the sardine-anchovy relationship was apparent. There, sardine landings rapidly declined from 294,095 t during 1988-1989 to 6,431 t during 1991-

1992, while for first time since 1985-1986, northern anchovy were caught commercially. Anchovy landings increased from 39 t in 1986-1987 to 18,493 t in 1989-1990 (Cisneros-Mata et al. 1995). More recently, sardine landings have recovered and there are almost no anchovy landings. The sardine abundance changes in the Gulf of California were discussed by Cisneros-Mata et al. (1995) as a result of fishing pressure and competition with the anchovy.

Different long-term sources of information, analyzed under different methods (Lluch-Belda et al. 1989, 1991, 1992b; MacCall 1990, 1996), have shown that natural changes in abundance of small pelagic fish populations have been associated with major changes in their distribution. The live-bait catch information, incorporating interspecies interactions and physical environmental indices, also shows new interpretations of the spatial processes involved in low-frequency changes of metapopulation biomass. The same information analyzed only for a restricted geographical area shows limitations and would lead to different conclusions. This limitation should be considered in further analysis, especially when the focus is the prediction of sustainability (Botsford et al. 1997).

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Spatial Distribution and Selected Habitat Preferences of Weathervane Scallops (*Patinopecten caurinus*) in Alaska

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Abstract

Over the past 30 years, the weathervane scallop (*Patinopecten caurinus*) fishery, located from the Oregon coast to the Bering Sea, has largely been passively managed by state agencies without adequate information on the abundance or ecology of the species. My objective was to obtain information on the life history, distribution, and ecology of weathervane scallops in order to promote effective management of the resource. Selected commercial logbook information from the 1993-1997 fishery was compiled, analyzed using ArcView® GIS (geographic information system) and used to delineate and characterize scallop beds. In addition, scallop data were compared with sediment type data from U.S. Geological Survey (USGS) surveys. Average CPUE (catch per unit of effort) was highest on sand and clayey silt-to-silt substrates and lowest on bedrock. Depth did not appear to correlate with CPUE. These results suggest resource managers should consider sediment type as well as fishery effort when designing future scallop surveys.

Introduction

Overview

The weathervane scallop, *Patinopecten caurinus*, is the largest scallop in the world, growing to a maximum shell height of 250 mm with a corresponding adductor muscle weight of 0.34 kg (Hennick 1970a, Mottet 1978). Weathervane scallops occur from Point Reyes, California (38°N) to the Pribilof Islands (57°N) in the eastern Bering Sea in depths ranging from 20 to 300 m with highest densities found from 60 to 120 m deep (Foster

1991). Recent analysis of catch records from National Marine Fisheries Service groundfish trawl research cruises suggests that weathervane scallops occur as far north as St. Lawrence Island (62°N) in the Bering Sea and extend west to Amchitka Pass (180°W) in the Aleutian Islands. Since the inception of the commercial fishery in 1967, the scallop fishery has had few long-term participants and annual harvests have been highly variable (Shirley and Kruse 1995). In the future, the increase in industry-funded fisheries observed by biologists, and the decline in monies for traditional resource surveys, will likely force other researchers to utilize information derived from fishers in order to conduct management-oriented analyses.

Spatial Structure

Scientific investigations on the Alaska scallop resource have been few and often focused on general distribution patterns and growth parameters with little habitat or management information. However, in the past 5 years, abundance surveys using area swept methods have been conducted on two small beds, Cook Inlet and Kayak Island (Bechtol and Bue 1998). In all other areas, abundance surveys have never been conducted and distribution has not been investigated since the late 1960s.

Weathervane scallops, like most scallop species, tend to occur in spatially discrete aggregations characterized by higher densities than the surrounding area. These scallop aggregations, also referred to as "beds," are the most important commercial stock unit (Caddy 1989). Scallop fishing grounds may be composed of many beds surrounded by continuous low densities (i.e., subcommercial) of the resource. Fishers typically locate a scallop bed, and concentrate harvest from this bed until the catch rate drops below a certain level at which time the vessel begins to explore new grounds (Orensanz et al. 1991). Weathervane scallop aggregations or beds have not been formally located and described prior to this study. Instead, scallops have been managed by nine large geographical management areas since 1993 (Fig. 1). Guideline harvest levels were established for each management area based solely on the long-term average catches in each area (Kruse and Shirley 1994).

Although weathervane scallops are broadly distributed from northern California to St. Lawrence Island, Alaska, relatively few areas contain sufficient densities to support a commercial fishery. Since the data used for this analysis were derived from skipper logbooks, a primary assumption used for this study is that fishers seek commercially abundant scallop grounds. By analyzing fisher behavior we can pinpoint the location of known beds. Of course, it remains a problem to establish what level of density is meaningful in determining biomass, commercial distribution, or essential habitat. The primary question in this investigation in identifying and delineating weathervane scallop beds was determining the minimal level of fishing activity and subsequent catch within a geographical area that is important. Once these commercial aggregations are identified, appropriate and sustainable management approaches can be implemented.

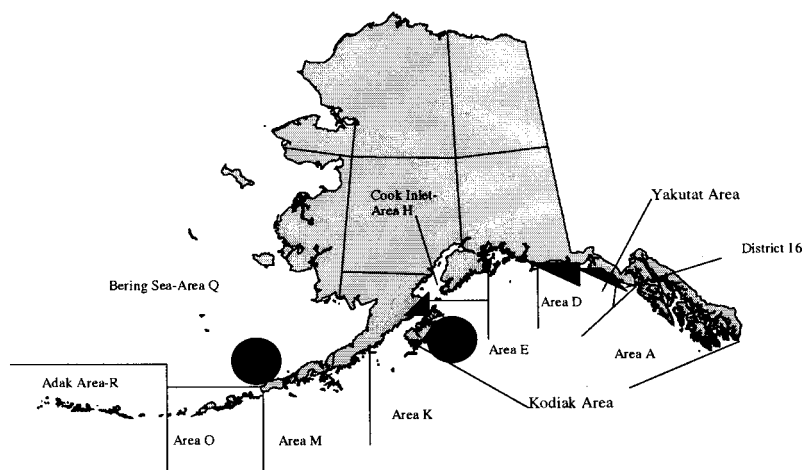


Figure 1. Areas of commercial scallop beds (lined areas) with associated Alaska Department of Fish and Game management areas.

Habitat

Environmental factors affecting scallop species distribution are complex and are not well studied. Substrate type, depth, water temperature, salinity, oxygen concentrations, food availability, interaction with predators, and ocean currents may play an important role in scallop distribution. Scallops are found throughout the world on a variety of substrate types; however, most commercial species tend to occur on harder substrates of gravel and coarse to fine sand (Brand 1991). Some species (e.g., *Argopecten gibbus*, *A. irradians*, and *Placopecten magellanicus*) occur in areas with silt or mud in the substrate but highest abundance and fastest growth rate occur in areas with little mud. Harder bottom substrates typically occur in areas with strong current flow. Sediment data are extremely limited from most areas of the world and are usually collected only through oil exploration research. Distinct sediment type information has been collected from the *P. magellanicus* fishing grounds on the East Coast. Results from these studies suggest juvenile and adult population densities were significantly higher on gravel substrate than on other sediment types (Thouzeau et al. 1991a,b).

During the initial development of the weathervane scallop fishery in Alaska, Hennick (1970a) noticed that scallops from the Yakutat area were found on different substrates than in the Kodiak area. Around Yakutat, scallops occurred on mud in contrast to Kodiak where they were found on sand and gravel. More recently, weathervane scallops have been characterized as dwelling on a wide array of sediment types ranging from uncon-

solidated glacial sediments to coarse gravel and rock (Kaiser 1986). Sediment type may also play an important part in influencing the incidental injury and mortality rate of noncaptured scallops during commercial fishing. Shepard and Auster (1991) found damage to noncaptured scallops was significantly higher on rock substrate compared to sand.

Depth is another important factor influencing distribution and abundance of many scallop species. Usually its ecological effects are coupled with variations in food availability or temperature (Brand 1991). Two studies by Haynes and Hitz (1971) and MacDonald and Bourne (1987) indicated *Patinopecten caurinus* growth and reproductive output were reduced in deep waters but the researchers did not measure scallop abundance. Since little analysis has been performed to define scallop distribution, consequently, habitat preferences have not been explored either.

In this paper, I provide a method to delineate spatially aggregated species using logbook data with only the start position available. Second, I characterize individual scallop beds based on size, fishing effort, and in certain areas, sediment type. Third, I identify patterns of abundance using CPUE as a proxy, in relation to sediment type and depth. As a result of these investigations, I provide recommendations for future scallop management.

Methods

Bed Identification and Delineation

Strict confidentiality rules prevented the state of Alaska from releasing data from a statistical area if three vessels or less fished in that area within a given year. Much of the published scallop information from the Alaska Department of Fish and Game (ADFG) is summarized by large management areas and has large data gaps due to confidentiality. Because of Alaska confidentiality requirements I had to solicit confidentiality waivers from vessel operators in order to acquire and use haul-by-haul data from commercial logbooks. In many cases, data were not obtained because vessel captains could not be located. Approximately 70% of the haul-by-haul logbook was obtained in this fashion. Logbook data covered the period from September 1993 to February 1997 with over 28,000 haul records.

Using ArcView® GIS version 3.0a (Environmental Systems Research Institute, Inc., Redland, CA) Spatial Analyst and Neighborhood Analyst extensions, scallop aggregations were identified spatially. Scallop beds were delineated based on the number of hauls (e.g., the start location) occurring within 1 km². A threshold of 3 hauls per km² was chosen to define a scallop aggregation. This number was selected after overlaying and reviewing the vessels' track line and bathymetry.

Once scallop beds were identified, individual beds were assigned a name. Because vessel operators are only required to record the start position of their harvest operation, the exact dredge track line could not be

identified. However, using the ArcView Animal Movement extension (Hooge and Eichenlaub 1997) an approximate track line was produced by connecting each start position sequentially. Track lines were then used to confirm the correct location and demarcation of scallop beds. The area (in square kilometers), total catch, total effort, and average CPUE (in kilograms per square kilometer) were calculated for each year fishing occurred.

Sediment Analysis

Two different methods were used to relate scallop CPUE to sediment type. The first analysis employed a qualitative descriptive approach by investigating the sediment type composition within previously defined individual beds. A second investigation using ArcView Spatial Analyst was performed to determine if scallop beds were located in proportion to the relative area of each sediment type that occurs in the 0-200 m depth zone.

Geographic distribution of sediment types in the Gulf of Alaska were digitized and mapped from U.S. Geological Survey (USGS) data. Original maps were produced by USGS using a compilation of many sediment surveys (Carlson et al. 1977, Evans et al. 1997). These data have not been ground-truthed with fishery data. Grain sizes were classified using the modified Wentworth and Udden scales (Evans et al. 1997). Ternary categorization was based on schemes modified from Shepard (1954) and Folk (1954). Sediment data coverage roughly extended from Yakutat in the eastern Gulf of Alaska to Chirikof Island southwest of Kodiak Island. Sediment maps (mercator scale 1:2,000,000, 0.5 mm = 1 km error) were digitized and imported into ArcView 3.0a and transformed into a coverage layer.

In areas where sediment data existed for the Gulf of Alaska, scallop beds were examined and the area of each sediment type was identified (Table 1). Using ArcView 3.0a X-tools extension scallop beds were geographically intersected with sediment data. The area of each distinct sediment type on each scallop bed was determined using the Animal Movement extension (Hooge and Eichenlaub 1997).

An analysis was performed to determine if the area of a particular sediment type occurring in the depth range 0-200 m was proportional to the area of scallop beds located on the same type of sediment. Total area for each sediment type occurring within the 0-200 m depth range was determined and compared with the total area of a particular sediment type occurring on scallop beds.

Depth

The depth recorded at the start position of each haul was used to characterize the entire dredge track. Depth was plotted as a function of CPUE for each known commercial scallop bed throughout Alaska, not just where sediment data existed, and aggregated with other beds within the same large ADFG management areas.

Table 1. Summary of number of scallop hauls by vessel and sediment type (n=17,785).

Vessel	BD	CS	GS	GM	SD	SM	SS	SC
1	2	615	356	23	714	679	239	1
2	0	884	19	39	1,041	704	65	1
3	133	1,435	490	34	691	182	429	0
4	8	808	388	30	1,171	142	145	2
5	2	0	193	0	5	0	138	0
6	7	370	125	1	225	16	81	0
7	132	2,265	459	39	1,473	306	478	0
Total	284	6,377	2,030	166	5,320	2,029	1,575	4

BD = Bedrock

CS = Clayey silt to silt

GS = Gravelly sand

GM = Gravelly mud

SD = Sand

SM = Sandy to muddy gravel

SS = Sandy silt to silt

SC = Silty clay

Results

Bed Delineation and Characterization

Thirty-seven scallop beds spanning from Cape Fairweather to Umnak Island in the Aleutian Islands and occupying 3,145 km² were identified using the criterion of 3 hauls per km². Scallop beds occurred in a variety of statistical and management areas. Some beds were located in bays or nearshore areas while others occurred at least 60 km offshore. The average size of an individual scallop bed was 85 km². Scallop bed size ranged from 6.02 km² located in bed "E" to the largest bed, "EE," comprising 694 km². Depth of scallop harvest by bed ranged from 58 to 127 m with an average of 82 m. The average area swept per bed per year was about 17.02 km².

The number of scallop beds found in current ADFG management areas ranged from 1 to 9 with an average of 4 beds per management area (Table 2). The average area of all beds combined within a management area was approximately 350 km². The average catch per year in whole weight for all beds combined in each management area ranged from a low of 9,656 kg in District 16 to a high of 842,000 kg in Area KSS with an overall average of 372,570 kg.

Sediment

Sediment data were available for 17 scallop beds in the Gulf of Alaska. All 8 sediment types occurred on 3 out of the 17 beds (Fig. 2). The silty clay

Table 2. Summary of bed characteristics by management area.

Management area	No. of scallop beds	Total area of beds (km ²)	Average total catch/year (kg)	Years fished
District 16	1	6.56	9,656.17	1
D	7	770.70	985,473.56	5
E	2	12.55	119,598.72	3
KNE	6	510.21	309,097.65	3
KSI	9	92.72	108,536.99	3
KSS	4	505.32	842,873.39	3
M	2	124.46	120,830.84	3
O	4	39.48	21,664.70	1
Q	2	1,083.02	835,401.28	3
Overall average	4	349.44	372,570.37	3
Total	37	3,145.00	3,353,133.30	

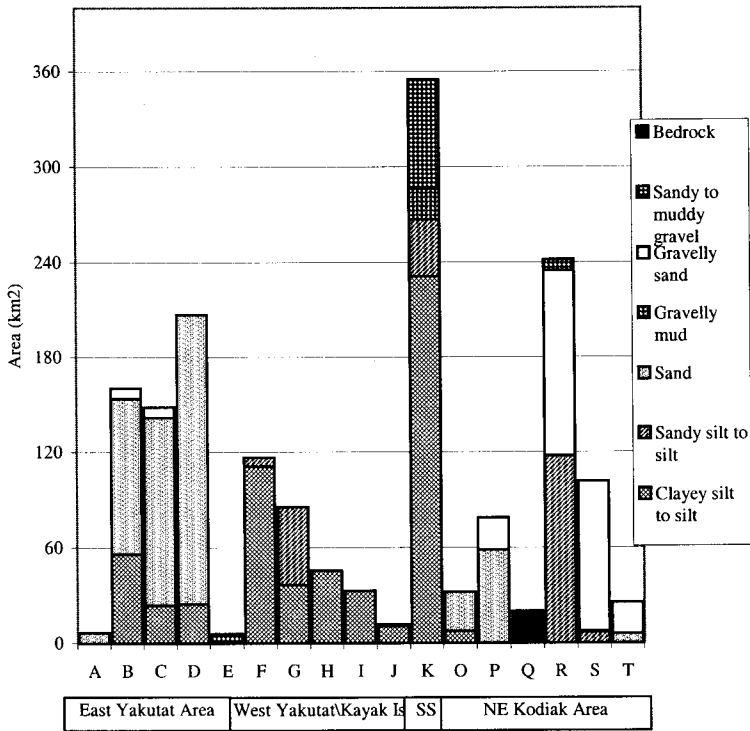


Figure 2. Size and sediment composition from selected scallop beds. Sediment type is arranged from largest (bedrock) to smallest (silty clay) particle size.

sediment type was fished at an extremely low rate, with only 4 hauls being made. Fishing effort was also relatively limited in areas where bedrock and gravelly mud occurred, but high for substrate types composed of sand, sandy to muddy gravel, gravelly sand, and clayey silt to silt. The average CPUE was highest on sand and clayey silt-to-silt substrates and lowest on bedrock. Scallop beds were most often located on sediment types containing clayey silt (CS) followed by sand (SD) and gravelly sand (GS) while occurring least frequently on bedrock (BD) and silty clay (SC) sediments.

Individual scallop beds occurred in a variety of sizes and over a wide spectrum of sediment types. It is interesting to note that sediment type changes as beds progress from east to west in the Gulf of Alaska. In the Yakutat area beds (A-D) were found most often in areas where sand predominates with some clayey silt to silt. In the Kayak Island or western Yakutat area (beds F-J) clayey silt to silt dominated the sediment type with some sandy silt to silt present (Fig. 3). Bed K, the only representative from the Shelikof Strait area, had a broad combination of sediments, composed of sandy to muddy gravel, gravelly mud, clayey silt to silt, and sandy silt to silt. In the northeast area of Kodiak, beds O-T displayed a more heterogeneous composition than in other areas. Beds O and P appear to have sediment types more representative of the eastern Yakutat area. Bed Q is the only scallop bed to be found on bedrock. However, the remaining beds (R-T) are often located on gravelly sand and gravelly mud sediments. In the case of beds G and F, the beds appear to avoid an area of gravelly mud. Likewise a large outcrop of bedrock in the vicinity of beds R & S is not part of these scallop beds.

Due to limited GIS coverages, the area in Shelikof Strait was combined with the Kodiak area coverage for analysis. In each area (Yakutat and Kodiak) the relative area of scallop beds occurring on a particular sediment type was plotted together with the overall total area for the region in the Gulf of Alaska in the depth contour 0-200 m (Fig. 4). In the Yakutat area, scallop beds occurred on sand in a higher proportion relative to available habitat. Sandy silt to silt followed as the second and clayey silt to silt was third in sediment type occurring in association with scallop beds.

In the Kodiak area, scallop beds occurred most often relative to available habitat on the clayey silt to silt substrate with gravelly mud and sandy silt to silt following behind. As in Yakutat, bedrock and silt clay were the least likely substrates where scallop beds could be found.

Depth

Scallops were caught in depths from 38 to 182 m spanning from Cape Fairweather in southeastern Alaska to the Bering Sea and Aleutian Islands with the largest effort occurring at depths of 108-112 m. Some scallop beds occupied a very narrow depth range, occurring from 60 to 80 m (beds J & I), while other beds (K & R) spanned over 100 m of depth.

In management area D, scallop beds occurred from 50 to 130 m. Some beds (B, E, F, G, H) had a very narrow depth range of less than 30 m while

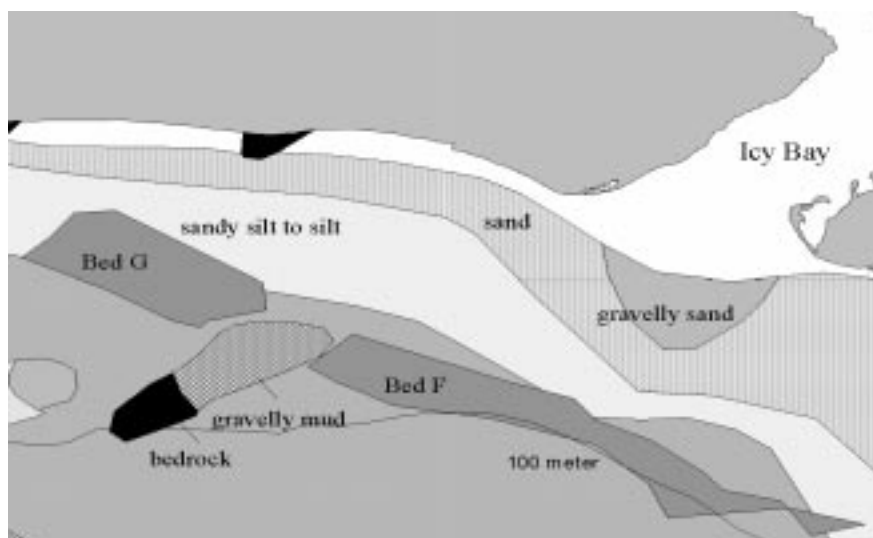


Figure 3. Individual scallop beds F and G in the Yakutat area with associated sediment type.

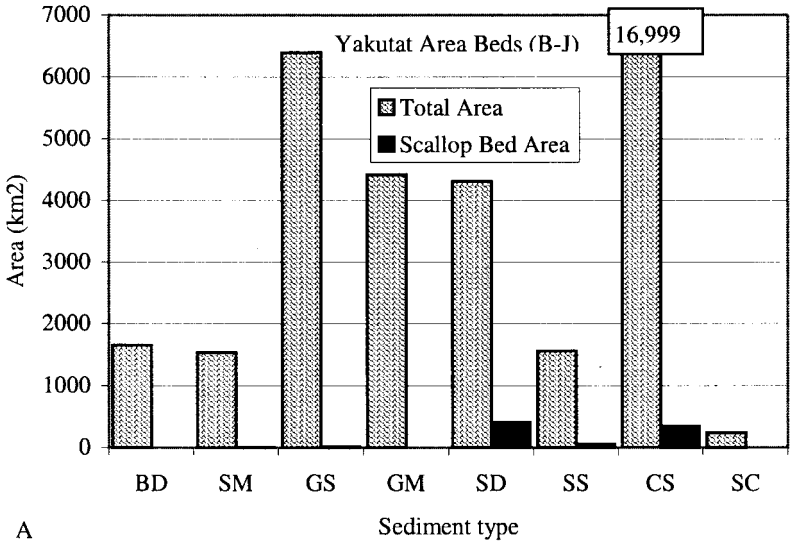
others (C-D) spanned over 70-100 m. In management area E around Kayak Island, both beds (I and J) occurred in depths from 60 to 90 m. Scallop beds in management area KSS occurred from 40 to 150 m deep. Bed K occupied this entire depth range while bed M primarily occurred from 60 to 85 m deep. Scallop beds occurring in management area KNE ranged from 70 to 180 m. Some scallop beds (O, P, Q, T) occupied relatively narrow deep ranges while larger scallop beds R and S occurred throughout the depth range.

Scallop beds in the Chignik area (KSI) occurred from approximately 40 to 140 m. All individual scallop beds occupied a moderate depth span of 40 m or less. In the vicinity of the Shumagin Islands (Area M), the depth ranged from 85 to 130 m with both beds (CC and DD) scattered throughout the depth range. The Bering Sea beds occurred between approximately 90 to 120 m deep for both beds (EE & FF). In the Aleutian Islands management area O, scallop beds occurred from 55 to 100 m deep with narrow depth ranges (less than 30 m) for all beds. In all areas, depth did not appear to be correlated with CPUE (Fig. 5).

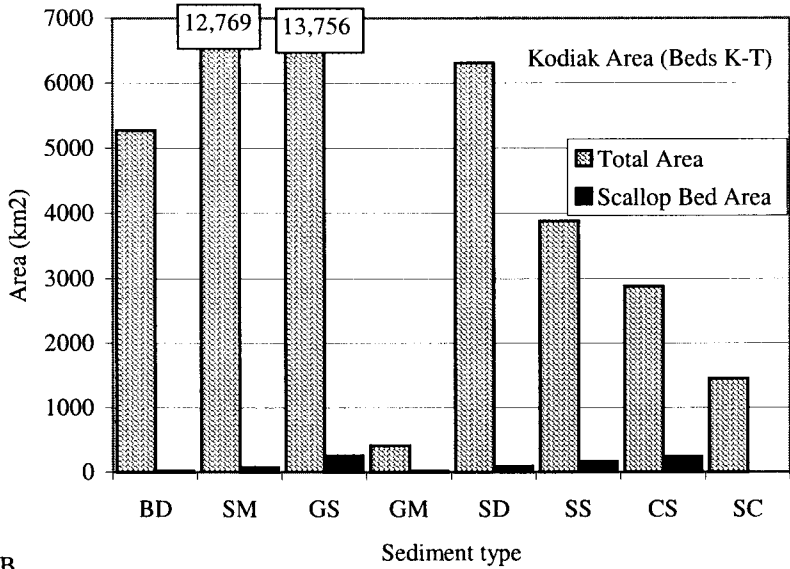
Discussion

Bed Identification and Characterization

Thirty-seven weathervane scallop beds located off Alaska were identified. Each individual bed was characterized by its size, depth, average yearly



A



B

Figure 4. Sediment type comparisons between available area (A) in Yakutat and (B) in Kodiak and areas occupied by scallop beds in the 0-200 m depth range.

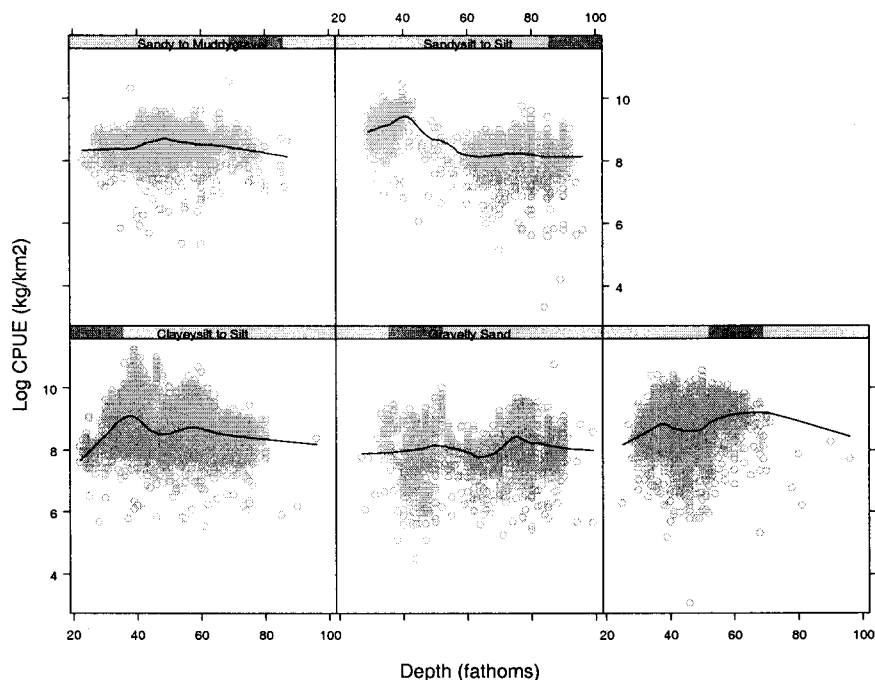


Figure 5. CPUE levels by depth (fathoms) and predominant sediment types.

fishing effort, and catch between July 1993 and February 1997. Previous researchers have identified differential growth rates of weathervane scallops between large areas of Alaska (Hennick 1970b), in British Columbia (MacDonald and Bourne 1987), and in Oregon (Haynes and Hitz 1971). Individual beds likely experience differences in productivity, associated bycatch, density, mortality, recruitment episodes, habitat, impacts from other fisheries, and growth parameters.

Scallop beds defined by using this technique are likely to underestimate the total area of the bed. Using a 1-km by 1-km grid to identify a minimum number of hauls to 3 as a critical value eliminated areas that were infrequently exploited. Historically productive scallop beds that were not fished during September 1993 to February 1997 were not enumerated or described in this investigation. In some areas where the vessel track line deviated outside a dense number of start positions, the area exploited was probably not included as part of the area of the scallop bed. Conversely, all of the area defined within a scallop bed is not likely to be dredged every year. In the future, additional scallop beds are likely to be either discovered or revisited by fishers and should be included in future analyses. To increase the precision of the dredge track line, the area of scallop beds and

associated densities, ADFG should require that both the start and end position of the vessel's track be recorded in the vessel's logbook.

Sediment Type

In general, adult weathervane scallops appear to have different sediment preferences than Atlantic sea scallops and many other scallop species. Studies in other parts of the world indicate most scallops prefer gravelly substrate. The weathervane scallop's tolerance of silty and sandy substrates is interesting in light of previous studies which suggest a lower CPUE for the majority of other scallop species in muddy and silty bottoms. The weathervane scallop has a low CPUE on gravelly sand (GS) and gravelly mud (GM) with the lowest catch occurring on bedrock (BD).

Weathervane scallops are found on all of the 8 sediment types in the Gulf of Alaska but in varying degrees compared to the available area of different sediment types. Scallop beds occur, proportionate to available area, most frequently on sand and sandy silt in the Gulf of Alaska.

Consistently from Yakutat to Kodiak Island to the Bering Sea, scallop beds are least often found on bedrock and silty clay substrates. The bedrock and silty clay sediment types are found at the extreme ends of the particle size continuum. There may be certain properties of these two sediment types that prevent scallop settlement or habitation.

Since the data set is derived from logbooks and not a systematic survey, it is difficult to draw conclusive results about adult scallop abundance on discrete sediment types. Fishers could be avoiding bedrock areas, not due to lack of scallop abundance, but because the rocky substrates snag or flip over dredges (Mark Kandianis, Kodiak Fish Co., Kodiak, AK 99615, pers. comm., June 1996). In addition, sediment data were not collected along the actual dredge path. The sediment data were sparse, with wide spaces between data points. Moreover, these data were digitized from paper charts, which have errors associated with the mapping process.

Because *P. caurinus* is found on a variety of substrates, sediment type may not be a sole limiting factor in their abundance. However in the future when other data may become available, analyses of bottom temperature, current speed, and phytoplankton availability may show that those factors also influence scallop settlement patterns.

Depth

Commercial aggregations of scallops occurred at depths of 25-195 m. Scallop beds usually occurred in fairly narrow depth ranges; however, the larger beds occupied wide depth ranges up to a 100-m spread. Since scallop beds were not consistently located in a particular depth range but varied from bed to bed, additional physical attributes (e.g., food availability, current) likely influence their distribution more than depth. Depth to some extent probably controls food availability and growth as has been demonstrated in previous studies. Future surveys should consider conducting meat weight

recovery and growth tests to compare shallow versus deep portions of larger beds.

Conclusions

In general this analysis is a very coarse comparison of variables that may influence scallop abundance. Since the entire haul is assigned an individual location at the start of the haul, this may bias these results if during the fishing process the dredge traversed over other sediment types and/or experienced highly varied depth strata. Further research surveys should collect not only abundance information on adults but also information on juvenile distribution and density related to sediment type. Additional physical information such as bottom temperature, salinity, current, and food availability may point to other significant correlations that influence distribution and abundance. Other environmental factors such as prey availability and hydrodynamics of larval flow and dispersal may also play an important part in scallop distribution.

Bed identification, delineation, and characterization may provide useful information such as stratification parameters when future research surveys are initiated. On the Canadian East Coast, prior to scallop research surveys, catch isopleths are generated from the previous year's commercial scallop fishing activity. Survey stratification and allocation are based on these isopleths to optimize vessel time and personnel (Robert and Jamieson 1986). More recently, Canadian fisheries managers have been limiting harvest on less productive beds until sufficient recruitment is available to support harvest (Ginette Robert, Department of Fisheries and Oceans, P.O. Box 550, Halifax, Nova Scotia, B3J 2S7, Canada, pers. comm., Dec. 1998).

Given the large discrepancies in size of individual beds, abundance, and effort, managers should review whether managing by large regions is an appropriate management strategy. Individual beds may be severely depleted, yet remain within the large management area guideline harvest levels since effort may be intensely localized on a particular bed or set of beds. Due to the small size of the scallop fleet, managers should have the means and discretion to manage on a bed-by-bed basis. In the Canadian East Coast scallop fishery, vessels are required to either carry an observer 100% of the time or be outfitted with a satellite tracking system. All vessels in the fishery now have a satellite tracking system that shellfish managers can access at any time. By having this device, resource managers are able to monitor fishing effort on an individual bed basis in real time. If effort is too high on a given bed, managers have the ability to close that particular area (Ginette Robert, Department of Fisheries and Oceans, P.O. Box 550, Halifax, Nova Scotia, B3J 2S7, Canada, pers. comm., Dec. 1998).

Finally, these findings may contribute to the ongoing work of defining essential habitat for federally managed fish and shellfish species as required under the 1996 Magnuson-Stevens (Fishery Conservation and Management Act). A promising area of future research will be to determine

environmental influences, genetic relationships, and larval dispersal on a particular bed or series of beds.

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Spatial Dynamics of Cod-Capelin Associations off Newfoundland

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Abstract

Statistical analysis of large-scale (1-1,000 km) predator-prey associations between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) is difficult because the spatial distributions of both species are heterogeneous and temporally dynamic. Statistics based on Ripley's *K*-function were used to describe the spatial association between cod and capelin off Newfoundland. The number of capelin prey around cod predators (potential contact) was computed from acoustic survey data for a range of possible cod ambits, from 5 to 100 km. Potential contact between cod and capelin varied seasonally in Placentia Bay, southeastern Newfoundland in 1998, being highest in June and lowest in January. This seasonal difference was largely attributable to an increase in the spatial association of cod and capelin at scales of 10-50 km in spring. A similar pattern was observed off the northeast Newfoundland shelf in 1991-1994 where postspawning cod migrated inshore in spring and encountered groups of capelin. As a consequence of this migration pattern, spatial association and potential contact between cod and capelin were dependent on survey timing relative to the timing of cod spawning.

Introduction

The interaction between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) is one of the best studied predator-prey interactions, and arguably the most important, in the northwest Atlantic ecosystem. Until the 1992 moratorium on fishing, cod were the most valuable commercial species in Atlantic Canada, and capelin are a major prey (review in Lilly 1987). Despite the importance of this interaction, relatively little is known about the association between cod and capelin distributions at large (>10 km) spatial

scales. Previous studies have used schematics (Akenhead et al. 1982) or expanding symbol plots (Lilly 1994) to graphically compare cod and capelin distributions with no formal statistical analysis. These and other studies suggest that the interaction between cod and capelin is spatially and temporally dynamic. The inshore movement of cod in spring (Rose 1993) coincides with the inshore spawning migration of capelin (Akenhead et al. 1982), and it has long been suggested that cod "follow" the movements of capelin at this time (Templeman 1965). At other times of the year (e.g., Turuk 1968) and in other areas (e.g., Casas and Paz 1996) consumption of capelin by cod is low, and little or no spatial association might be expected.

Previous quantitative studies of the association between cod and capelin were carried out at small spatial scales (<20 km), inshore, during the summer. In their study in southern Labrador, Rose and Leggett (1990) found that spatial associations were scale-dependent. Capelin and cod were positively correlated at the largest scales examined (>4-10 km), and negatively correlated at smaller scales, except when cod were actively pursuing capelin. Horne and Schneider (1994, 1997) did not detect spatial association between cod and capelin at any scale from 20 m to 10 km in 16 of 19 transects in Conception Bay, Newfoundland, and suggested that cod were not aggregating in response to capelin at these scales in this area (Horne and Schneider 1994). The dependence of association on spatial scale is typical of predator-prey interactions (Schneider 1992). Analysis at large scales may reveal patterns that would not be detected at smaller scales (Thrush 1991).

Our first aim in this study was to develop a statistical methodology to examine large-scale associations between cod and capelin from a variety of distributional data sets. Our second aim was to expand the temporal and spatial scales over which capelin-cod interactions have been examined.

Methods

Acoustic Data

Acoustic data on cod and capelin distributions were collected during research surveys in June 1991-1994, and in January (winter), March (early spring) and June (spring) 1998. Surveys in 1991-1994 mapped cod and capelin distributions on the northeast Newfoundland shelf (Fig. 1) using a Biosonics 102 dual-beam 38-kHz echo sounder calibrated with a tungsten carbide standard target. Surveys in 1998 covered Placentia Bay (Fig. 1) using a similarly calibrated Simrad EK500 split-beam 38-kHz echo sounder. Signals from cod and capelin were distinguished based on signal characteristics (LeFeuvre et al. 1999) and information from targeted fishing sets made using midwater and bottom trawls. Acoustic data were integrated in 100-m bins and scaled by target strength (TS) to give estimates of areal density (fish per square meter) of cod and capelin in each 100-m bin. Mean target strengths were calculated from fishing set length-frequency data

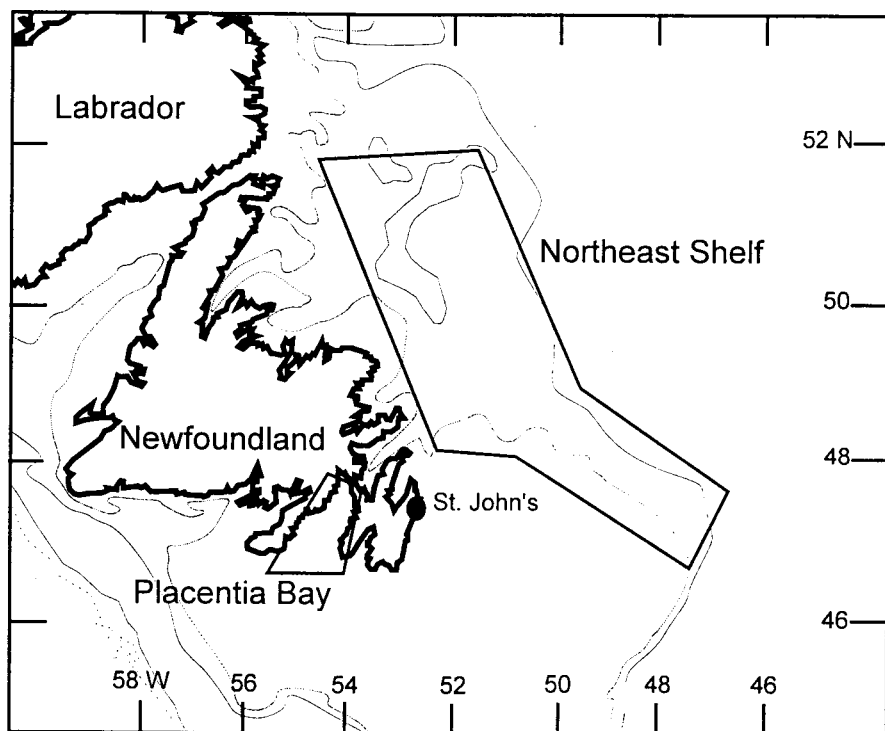


Figure 1. Map showing the location of the two study areas with major bathymetric contours.

using the relationship $TS = 20 \log L - 67.5$ (G.A. Rose, unpubl. data) for cod, and $TS = 20 \log L - 73.1$ for capelin (Rose 1998) where L is total length in centimeters. Areal density estimates were grouped into larger bins corresponding to 0.05 degrees of latitude by 0.05 degrees of longitude (equivalent to ~ 5.6 km by ~ 3.7 km at 49°N) prior to statistical analysis to reduce computational time and to compensate for differences in sampling intensity between areas.

Statistical Analysis

Potential contact is defined as the product of predator and prey abundance within the limits of some unit area (Schneider 1994). The general expression for potential contact is:

$$PC(r) = \frac{\sum_{x=1}^n (A_x B_x)}{\sum A_x} \quad (1)$$

A_x is the number of individuals of type A within an area x of size r , B_x is the number of individuals of type B within the same area x , ΣA_x is the total number of individuals of type A , and $\sum_{x=1}^n$ is a summation over all areas $x = 1 \dots n$ of size r .

Acoustic data provide estimates of density (fish per square meter) rather than numbers of individuals. The expected density of type B individuals (capelin) within distance t of any type A individual (cod), $E[b(t)]$ is:

$$E[b(t)] = \frac{\sum_{i=1}^n a_i \overline{(b_{ij})}}{\sum_{i=1}^n a_i} \quad (2)$$

where

$$\overline{(b_{ij})} = \frac{\sum_{j=1}^n I_t(u_{ij}) b_j}{\sum_{j=1}^n I_t(u_{ij})} \quad (3)$$

For each point i for which density estimates are available, all capelin densities (b_j) within distance t (indicator function $I_t(u_{ij}) = 1$ where distance $ij < t$, $I_t(u_{ij}) = 0$ otherwise) are averaged, and scaled by the density of cod at point i (a_i). This is repeated for all n points sampled. The result is then divided by the sum of the individual cod densities. It can be demonstrated (O'Driscoll et al. 2000) that equation 2 is analogous to the expectation term of Ripley's bivariate K function (Ripley 1981) for a spatial point pattern. Equation 2 is also equivalent to Lloyd's index of mean crowding for a single species (Lloyd 1967). However, unlike Lloyd's index of mean crowding, potential contact may be calculated at increasing spatial scales (increasing t) without arbitrarily grouping data (O'Driscoll et al. 2000).

By multiplying $E[b(t)]$ by the area enclosed by the circle with radius t ($= \pi t^2$), we obtain a measure of the potential contact between cod and capelin at scale, t .

$$PC(t) = \pi t^2 E[b(t)] \quad (4)$$

$PC(t)$ is the average number of potential capelin prey within an ambit of radius t of any cod. Potential contact increases as ambit size increases and is determined by the spatial association between cod and capelin as well as the overall density of capelin. Note that our definition of potential contact is based only on the relative spatial arrangement of cod and capelin and does not imply that cod encounter, or even have the ability to detect all capelin within their ambit. We assume, however, that at spatial scales similar to the foraging ambit of the predator that potential contact is a measure of feeding opportunity.

To test the hypothesis that there was association between cod and capelin at distance scale t , independent of capelin density, we generated 99 further realizations of the cod data by randomly reallocating cod density values to different points in the spatial distribution and recalculating $PC(t)$ for the randomized data. The results are expressed as the "extra contact" at distance t , $XC(t)$:

$$XC(t) = PC(t) - PC(t)_{ran} \quad (5)$$

$PC(t)_{ran}$ is the average potential contact from the random realizations. $XC(t)$ is the average number of "extra" capelin within an ambit of radius t . "Extra" capelin are those which are not expected if the cod sample densities were distributed randomly throughout the study area. $XC(t)$ has an expected value of 0 when there is no association between cod and capelin, $XC(t) > 0$ when cod and capelin are positively associated (correlated), and $XC(t) < 0$ when there is negative association. The upper and lower confidence intervals for $XC(t)$ were determined from the randomizations.

$$XC(t)_{95} = PC(t)_{95} - PC(t)_{ran} \quad (6)$$

$$XC(t)_5 = PC(t)_5 - PC(t)_{ran} \quad (7)$$

$PC(t)_5$ and $PC(t)_{95}$ are the values of the 5th and the 95th percentiles of potential contact from the random realizations.

Results

The distributions of cod and capelin in Placentia Bay in 1998 were spatially and temporally variable (Fig. 2). In January peak capelin densities were observed on the eastern side of the outer bay while cod were concentrated in the inner bay. In March the highest densities of both capelin and cod occurred in the inner bay. In June both species were present in large numbers in the outer bay. Average densities of cod and capelin in the study area in June 1998 were an order of magnitude higher than in the other two surveys.

In Fig. 3 potential contact with capelin is plotted as a function of ambit radius t for cod ambits of 5, 10, 15, ... 100 km. Little is known about the foraging ambit of cod, but Rose et al. (1995) measured mean swimming speeds of between 6.6 and 24 km per day, with a peak of 59 km per day during the spring migration. At ambits of radii < 60 km, potential contact between cod and capelin was highest in June, intermediate in March, and lowest in January (Fig. 3). These seasonal differences in potential contact were due to changes in spatial association between cod and capelin (Fig. 4) and changes in capelin density (Fig. 2). In January the association between

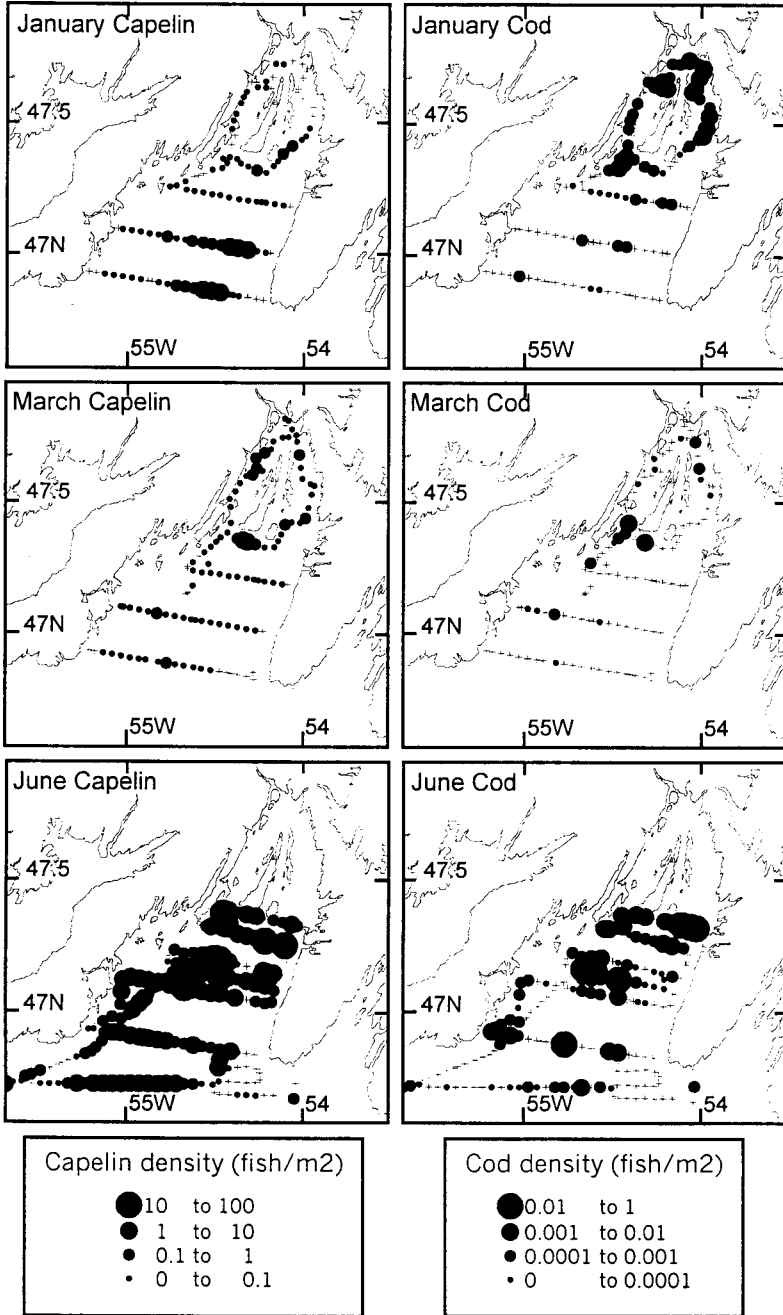


Figure 2. Expanding symbol plots of capelin and cod distributions from three acoustic surveys in Placentia Bay in 1998; + indicates no fish were detected.

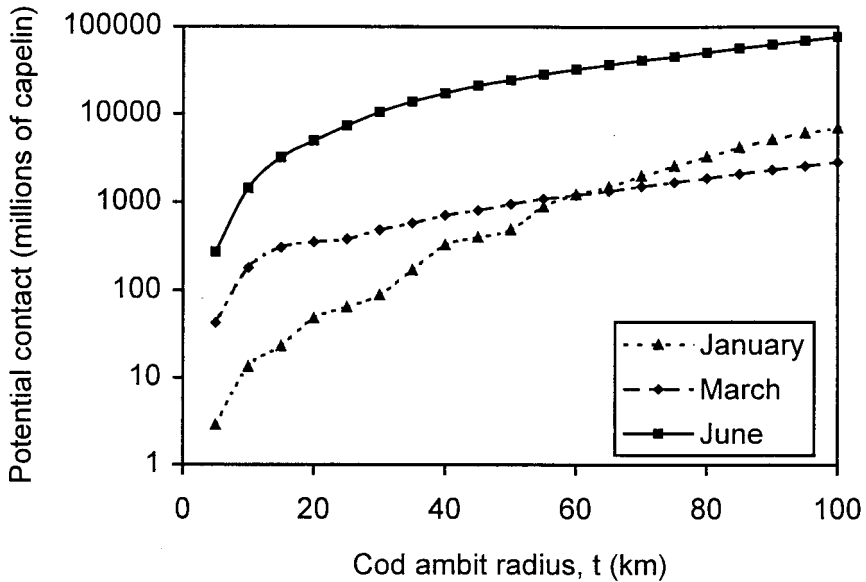


Figure 3. Seasonal variation in potential contact with capelin in Placentia Bay in 1998 over a range of possible cod ambits.

cod and capelin was negative over a range of spatial scales (Fig. 4), reflecting the segregated spatial distributions of predator and prey (Fig. 2). In March potential for contact between cod and capelin increased (Fig. 3), despite a decrease in the density of capelin in the bay, because the distributions of the remaining cod and capelin were similar (Fig. 2). There was positive association between the two species at spatial scales <20 km with a peak (maximum association) of 15 km in March (Fig. 4). Potential contact was highest in June when cod were positively associated with high densities of capelin. Spatial association was detected at scales of 10–50 km in June, with maximum association at 45 km (Fig. 4).

There was interannual variation in potential contact between cod and capelin off the northeast Newfoundland shelf in June 1991–1994 (Fig. 5). In 1991 and 1992 cod were observed offshore in spawning aggregations (Fig. 6). Because these large aggregations of cod were spatially segregated from areas of high capelin density (Fig. 6), there were fewer capelin surrounding each cod than would be expected in a random arrangement of cod (negative association, Fig. 7). Cod spawning was earlier in 1993 and cod were observed farther inshore (Fig. 6). There was positive spatial association (although not above the 95% confidence interval) between cod and capelin at scales <250 km (Fig. 7) and potential contact was high (Fig. 5). In 1994 densities of cod were very low (Fig. 6) and most fish were immature. There

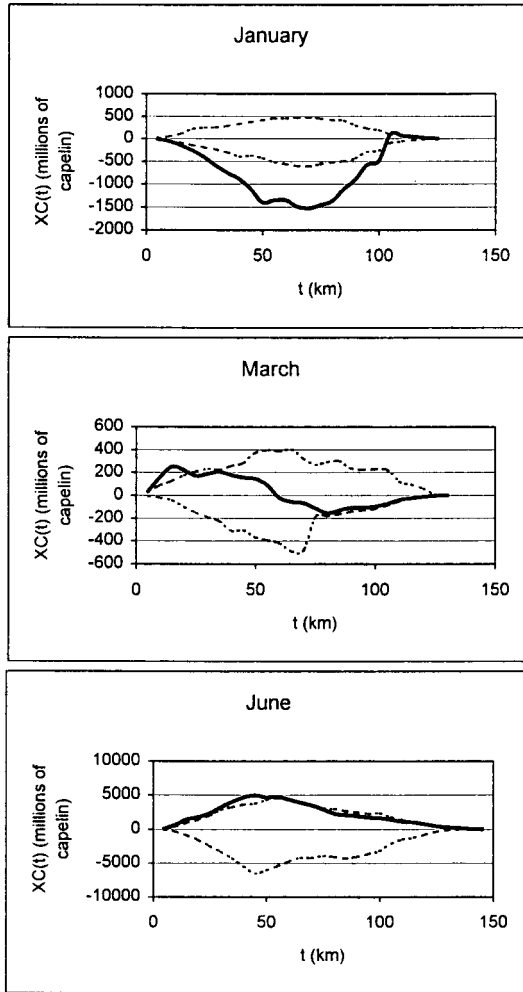


Figure 4. Seasonal variation in spatial association between cod and capelin in Placentia Bay. Plots show extra contact as a function of scale (solid line). Values greater than zero indicate positive association and values less than zero indicate negative association (segregation). Dashed lines are the 5% and 95% bounds for a random arrangement of cod generated from 100 randomizations of density increments.

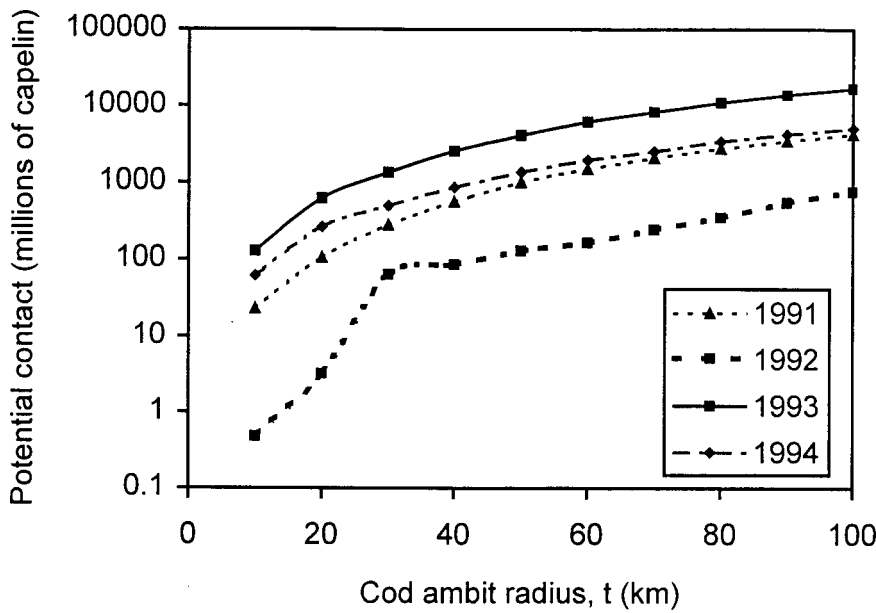


Figure 5. Interannual variation in potential contact between cod and capelin on the northeast Newfoundland shelf, June 1991-1994.

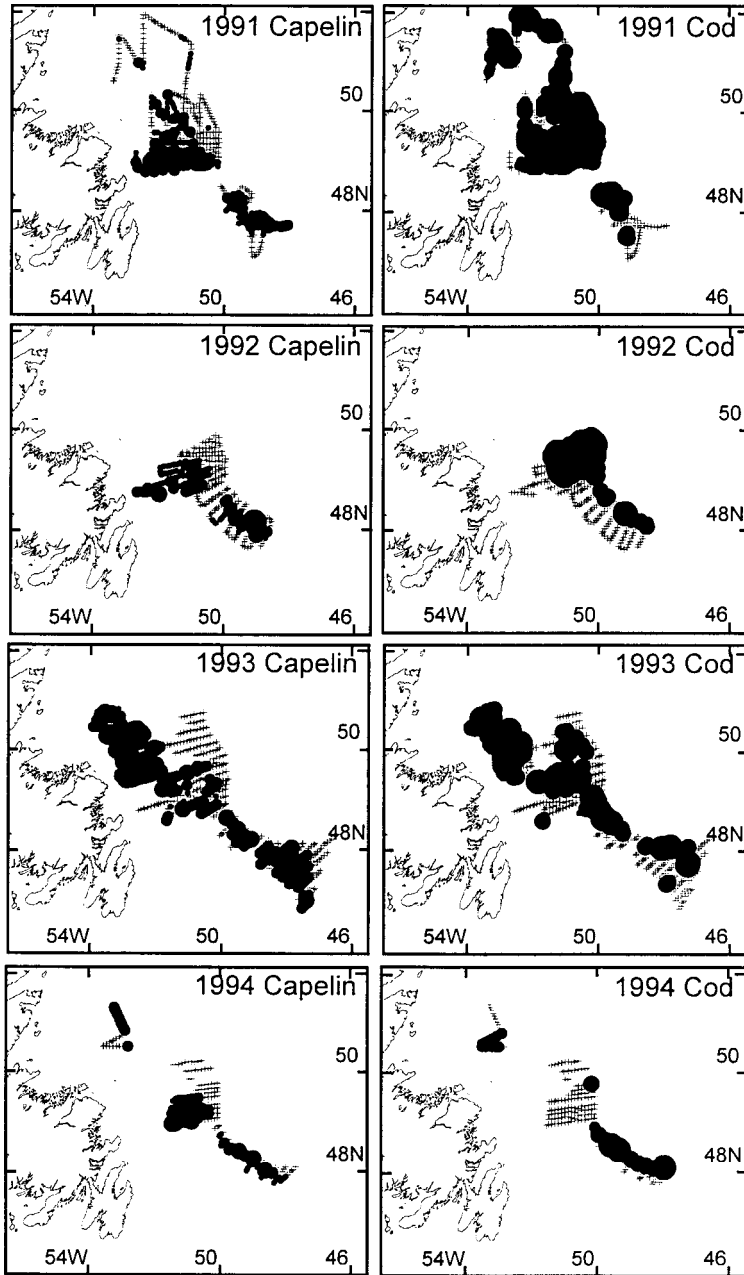


Figure 6. Expanding symbol plots of capelin and cod distributions on the northeast Newfoundland shelf from acoustic surveys in June 1991-1994. Key as for Fig. 2.

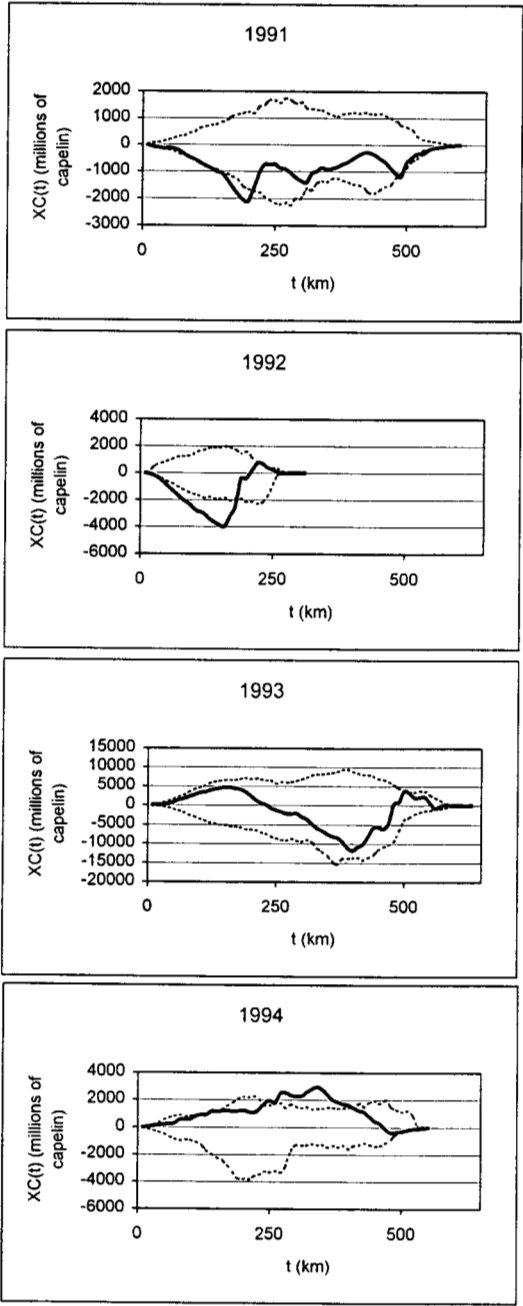


Figure 7. Interannual variation in spatial association between cod and capelin on the northeast Newfoundland shelf. See Fig. 4 for details.

was positive spatial association between cod and capelin at large scales (250-400 km, Fig. 7), but potential for contact between cod and capelin was lower in 1994 than in 1993 (Fig. 5).

Discussion

The predator-prey interaction between cod and capelin off Newfoundland was dynamic because of seasonal and interannual variability in the spatial distribution and abundance of both species. Potential contact provided a robust, quantitative measure of the overall influence of predator and prey distributions and prey abundance on potential encounter rates. A related measure, extra contact, assessed spatial association across a range of scales independent of density. Unlike alternative covariance-based methods such as spectral analysis (Rose and Leggett 1990; Horne and Schneider 1994, 1997), contact statistics are not sensitive to the presence of zero values and can be applied to areas with irregular sampling and/or boundaries. The statistical outputs are easily interpreted biologically as the potential for contact between predator and prey.

Our equation for potential contact (equation 4) is not corrected for edge effects. Edge effects arise when a sample point i is within distance t of a survey boundary. In these instances, part of the predator ambit centered on point i is outside the survey area and prey densities within the ambit cannot be evaluated without a certain bias (Haase 1995). Edge bias increases with increasing ambit size t . Our method used capelin densities within the portion of the cod ambit which was inside the survey area to estimate densities beyond the boundary. The implicit assumption is that capelin densities outside the surveyed area were similar to densities inside. This is clearly not the case when the survey area is bordered by land (e.g., Placentia Bay). We conducted simulations by adding zero values beyond the survey boundaries and found that at small cod ambits ($t < 40$ km) there was little evidence of edge bias. At larger cod ambits absolute values of $PC(t)$ overestimate potential contact when there are no capelin outside the survey area. Comparisons of relative values of potential contact at these larger ambits are still valid. Because the same assumptions are made for the data and for the random realizations, our measure of spatial association $XC(t)$ (equation 5) was not biased by edge effects.

Our data from Placentia Bay provide support for the hypothesis that cod "follow" capelin in spring (Templeman 1965). Between March and June 1998 there was an influx of both cod and capelin into Placentia Bay from outside the study area. Tagging studies also show that there is a postspawning migration from the inner bay spawning grounds to the outer bay (Lawson 1999). Potential contact was very high in June because there were high densities of capelin closely associated with cod. However, it should be noted that spatial association does not necessarily indicate cause and effect. There are at least three cod spawning sites in Placentia Bay and

spawning also occurs in spring (Lawson 1999). Some movements of cod may have been driven by reproduction rather than feeding.

Interannual differences in spatial association between cod and capelin off the northeast Newfoundland shelf were explained by differences in the timing of the acoustic surveys relative to the inshore postspawning migration of cod (Rose 1993). Although surveys in 1991-1994 were conducted at the same time of year, cod spawning was delayed in 1991 and 1992, possibly because of very cold water temperatures in these years. In 1993, spawning was earlier and the cod migration was more advanced. Cod were observed farther inshore and were associated with capelin. Little can be concluded from the 1994 survey because densities of cod were very low and the size structure of the population was different from previous years. These data emphasize the importance of understanding seasonal patterns in spatial association before attempting to quantify long-term trends in potential contact between predators and prey.

The observed movement patterns of cod on the northeast Newfoundland shelf and in Placentia Bay led to increased opportunities for feeding on capelin in spring. This is consistent with what is known about seasonality of feeding by cod. Templeman (1965) found that consumption of capelin by cod captured inshore at St. John's increased from May to June, was highest (capelin 88-99% of total cod food by volume) between mid-June and early August, and decreased again in the fall. Offshore, on the northeast slope of the Grand Banks, Turuk (1968) also recorded peak feeding on capelin from June to August. Little is known about cod diet in Placentia Bay, but our preliminary analysis of cod stomachs indicates that consumption of capelin is greater in spring than in late fall or winter. We intend to examine cod stomach data in more detail to compare our predicted contact rates with capelin consumption.

The statistical techniques described in this paper are applicable to any survey data where there are estimates of predator and prey density, providing the minimum separation between sample points is smaller than the spatial scale of interest (O'Driscoll et al. 2000). Sampling design is an important consideration when calculating contact statistics, as it is for any statistical method that relies on sample data. The separation between adjacent sampling points determines the minimum spatial scale at which potential contact can be assessed and also the precision with which we can describe association.

Contact statistics may also be calculated to describe scale-dependent spatial pattern in a single species (O'Driscoll et al. 2000) or to determine association with abiotic features such as habitat type (Bult et al. 1998).

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Spatial Patterns of Pacific Hake (*Merluccius productus*) Shoals and Euphausiid Patches in the California Current Ecosystem

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Abstract

In the summer, along the California Current Ecosystem (CCE) off the coastline of California, Oregon, and Washington, the battle line between actively feeding Pacific hake (*Merluccius productus*) shoals and large patches of euphausiids is drawn at the shelf break. In this paper we examine the summer spatial distribution of shoals of the dominant fish predator in this ecosystem (88% of trawl catch by volume) and its major prey species and suggest that the spatial proximity of these groups is dominated by their overlap at or near the shelf break (between 150 and 250 m depth).

Based on acoustic survey data collected by the National Marine Fisheries Service, Alaska Fisheries Science Center during summer 1995 and 1998, I used image processing methods and acoustic backscatter theory to distinguish patches of plankton from shoals of fish. Having multiple transects marching south to north from California to British Columbia provided a degree of pseudoreplication and gave us the ability to compare fish and plankton distributions over both space and time. I found evidence for an inverse relationship between fish and plankton over some regions. Of particular interest is the apparent northward shift of Pacific hake during the 1998 El Niño year and the accompanying increase in plankton abundance over part of the region (California, Oregon, and Washington). Two proximity-related tests were applied on a transect-by-transect basis. One, a nonparametric model of fish shoal biomass as a function of proximate plankton biomass, indicated a high degree of overlap in some regions and times, between high-abundance fish shoals and high-abundance plankton patches proximate to these shoals. This proximity has predator-prey implications, in that it suggests that the shelf break may be a dominant zone

for hake predation on euphausiids because high-abundance euphausiid patches and high-abundance fish shoals were most consistently found together near the shelf break.

Introduction

This paper distills results from acoustic surveys in summer 1995 and 1998 along the northern California, Oregon, and Washington continental shelf-break regions, concerning the spatial distribution of fish shoals, primarily Pacific hake (*Merluccius productus*), and euphausiids, which are their major prey over this region. (Fish and plankton are used interchangeably with Pacific hake and euphausiids, respectively. Pacific hake dominated the fish abundance with 90% [1995] and 89% [1998] of the targeted Aleutian wing trawl catch by weight [Wilson and Guttormsen 1997, 1998]. Euphausiids, because they are the largest plankton, dominated the plankton backscatter at 120 kHz [McKelvey 2000]. Much higher densities of smaller zooplankton would be necessary to be “seen” at 120 kHz.) While results are specific to this area, we hope that the methods and findings will be generally applicable to studies of shelf-ecosystem predator-prey spatial distributions and interactions.

Predator-prey dynamics in the nearshore ocean are played out in a labile, three dimensional space. This space also features mesoscale oceanographic features, such as fronts, jets, and eddies, and bathymetric features such as shelf breaks, trenches, and rises (Hickey 1998). In this extensive, but far from featureless, habitat, both fish and plankton form aggregations, which may provide them with advantages in either finding and utilizing their prey or escaping from their predators (Partridge 1982, Pitcher and Parrish 1993) or both. Recent improvements in ocean sensing, including satellite imagery (Simpson and Harkins 1993), low-frequency sonar systems, acoustic doppler current profilers (Pierce et al. 1999), and long-lived buoy-based hydrographic monitors (Hickey et al. 1997), have improved our understanding of the importance of ocean features in structuring nutrient, temperature, phytoplankton, and current dynamics. Still, our understanding of biological interactions in the highly productive shelf regions of our world's oceans is far from mature. Attempts have been made to model such explicit spatial phenomena as larval drift (Hermann et al. 2001) and juvenile fish feeding by adding passively moving biota onto mesoscale-level ocean models, which can resolve, but not predict, such features as jets, fronts, and eddies (i.e., they are mimics rather than predictors of observed oceanic phenomena). Predation by fish, another spatially explicit process, is clearly an active process where both the fish and their prey (be it fish or zooplankton) use their mobility to maintain or change position within the environment. At fine temporal scale (diurnal) euphausiids often exhibit diel migration, moving down in the water column during the daytime and up at night (Fulton and LeBrasseur 1984), presumably to avoid predation during the daytime and to feed during nighttime and crepuscu-

lar periods. At larger scales fish migrate, presumably to utilize higher seasonal production, and may also orient themselves around such productive features as ocean fronts and eddies (Shinomiya and Tameishi 1988). To examine how effectively these strategies work for the fish and plankton would require observation through the water column at a spatial and temporal scale currently unattainable. We are left with either monitoring smaller areas more extensively or larger areas occasionally and not simultaneously (i.e., we cannot cover the entire study area synoptically and instantaneously). As such, we must be content with repeated three-dimensional snapshots of the same area at selected time periods and make brave assumptions. Such is the case with this study. Yet, I hope to demonstrate that the spatial proximity between feeding fish shoals and their plankton prey is remarkably consistent in the face of the spatial complexity of continental shelf ecosystems. Here I will use the large number of survey transects as pseudo-replicates to suggest certain patterns that repeat over given spatial areas in the California Current Ecosystem (CCE) through much of the summer, and some that do not.

Data

The data used in this study were collected by the National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) acoustics group during summer, from July 1 to September 1, 1995, and July 6 to August 27, 1998. A hull-mounted SIMRAD EK-500 split beam sonar system with BI500 software (Knudsen 1994) and with two transducers at 38 and 120 kHz was used along survey transects from Monterey, California, to Queen Charlotte Islands, British Columbia in both years (Fig. 1). Survey tracks were parallel, generally oriented east-west, and spaced at 10-nmi intervals. This study uses the data from the latitude of Cape Mendocino, California to the Washington-British Columbia border at the Strait of Juan de Fuca because there were almost identical transects within this region in both study years. Large-net midwater and bottom trawls (anchovy and otter trawls) were used to corroborate fish distribution in the backscatter, and smaller "plankton nets" (Methot trawls) were used for species composition and size composition of the fish and plankton. The 120 kHz acoustic system has a range of not more than 250 m and, as such, data on plankton abundance below 250 m were not available. The fish shoals and plankton patches identified using the methods described below were not compared with the fish catch data (scrutinized) to give information about species composition. However, the catch data were dominated by Pacific hake and euphausiids, respectively. The survey was conducted during the daytime hours.

Methods

Fish shoal identification used the 38 kHz echograms, while plankton patch identification used both the 38 and 120 kHz data. The identification algo-

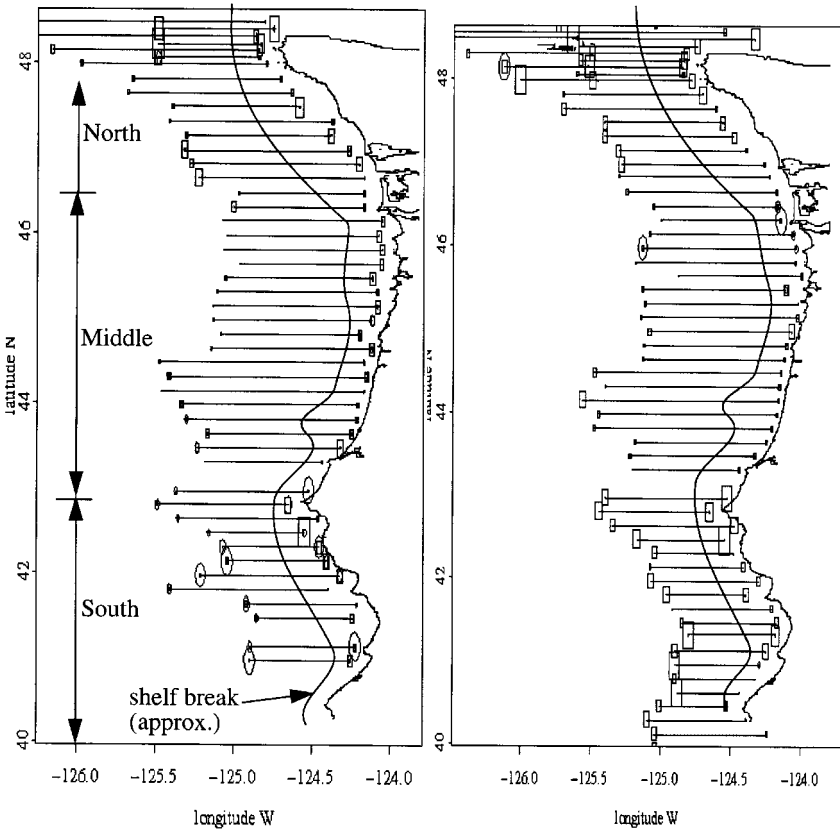


Figure 1. Shoal abundance (biomass per kilometer) shown by ovals and plankton abundance by rectangles for 1995 (left panel) and 1998 (right panel). Results for the offshore region (>250 m) are shown on the left side and shallow region results on the right side of each transect. Three coastal regions (North, Middle, and South) and the approximate location of the shelf break are identified.

gorithms required that patches comprise contiguous pixels in the echogram images, with a clearly defined boundary, and with a backscatter range indicative of the target group (e.g., greater than -51 dB for Pacific hake shoals [Swartzman 1997] and between -62 and -45 dB for euphausiid patches). (The threshold levels for euphausiids were obtained after trial and error tests on individual transects. The best thresholds to use may vary depending on the project objective.) After applying the appropriate threshold to the 38 kHz echograms a morphological filter using a 3×3 (horizontal \times vertical) binary structuring element was used according to methods from Swartzman et al. (1994, 1999).

Plankton patches were located by taking the difference between the 120 and 38 kHz images after the threshold filters for euphausiids were applied. A morphological closing followed by an opening (Haralick and Shapiro 1992) using a 3×2 structuring element was applied to the difference echogram after a $+2$ dB threshold was applied to it (Swartzman et al. 1999). This second threshold assured that all remaining pixels had backscatter at 120 kHz at least 2 dB higher than backscatter at 38 kHz, which is consonant with geometric backscatter models used for euphausiids (the bent cylinder model; Stanton et al. 1993). (The backscatter difference between 120 and 38 kHz for euphausiids may be higher than 2 dB. McKelvey (2000) found an average backscatter difference of about 10 dB for backscatter by euphausiids.) The resulting euphausiid patches and fish shoals were recorded in a table which describes parameters of the patches including shape, size, location, backscatter, and environmental parameters of the patches using a connected component algorithm to extract this information (Haralick and Shapiro 1992, Swartzman et al. 1999).

An index of abundance for fish shoals and plankton patches was derived from the processed images (Fig. 1). Because the shelf and offshore areas are so different bathymetrically and hydrodynamically in the CCE, we computed transect abundance (biomass per kilometer) separately for the shelf and offshore regions. We used the product of the patch area (in square meters) times the mean s_A (m^2/m^2) for the patch. This was converted to an index of transect abundance by summing the abundance indices for all the patches in the transect and dividing by the length of the transect (in kilometers). The index was applied separately to deep, off-shelf (offshore) regions (bottom > 250 m) and shelf regions (bottom < 250 m) within each transect (Fig. 1). The distance in the denominator was the part of the transect within each region (offshore and shelf). The study area was divided into three regions north to south (Fig. 1), to reflect differences in oceanographic conditions. These are the North region, from Cape Flattery to the Columbia River; the South region, from Cape Mendocino to Cape Blanco; and the Middle region, between these. Cape Blanco forms a natural oceanographic boundary, with a narrower shelf and more consistent wind-driven upwelling to the south (Hickey 1979, 1998). The Columbia River, the major river system along the U.S. West Coast, is used as another region boundary (Hickey et al. 1997). Having these regions gives us a way to sim-

plify broad spatial patterns in fish and plankton abundance. By assuming homogeneity within transects in a region we can treat the transects as replicates and quantify large-scale distribution patterns.

To examine the spatial proximity of fish shoals and plankton patches two complementary approaches were used. A nonparametric regression generalized additive model (GAM) approach was used to look at the relationship of several factors to shoal biomass, and a distance-based proximity index (Swartzman et al. 1999) to look at the proximity of fish shoals and plankton patches.

In the GAM model (Hastie and Tibshirani 1990) fish shoal abundance was modeled as an additive sum of smooths of shoal depth, bottom depth, and plankton abundance proximate to the fish shoals. This model was used on a transect-by-transect basis for both 1995 and 1998. To compute the plankton abundance proximate to each fish shoal we chose a distance range of 1 km, an estimate of the short-term fish feeding range. The GAM model, run in S-Plus software, used a spline smoother with a range set by cross-validation (Venables and Ripley 1994) and assumed the abundance data were normally distributed.

A distance-based proximity index, computed for 1995 and 1998, measured the plankton abundance index at different distances from each fish shoal from 0 m (i.e., the patch overlaps the shoal) to 1 km, in intervals of 100 m. The measure was compared with results obtained by randomly translating the plankton patches within the transect a large number of times (20) and recomputing the measure. This provided error bounds to determine the distance range over which the plankton were uniformly distributed around the fish shoals (the empirical proximity index was within the 95% error bounds), more regular than uniform (below the lower error bound), or clustered (above the upper error bound). The proximity measure is based on Ripley's K , used in spatial statistics to test for randomness of points in space (Diggle 1983). We modified Ripley's K to include the size of the fish shoal and the plankton patches, using distance from the edge (instead of from the center) of each shoal as the measure of distance and summing the plankton patch abundance within each distance range from each fish shoal instead of just counting the number of points (e.g., patch centers) within that range (Swartzman et al. 1999). The proximity index was calculated separately for each transect both for fish shoals over bottom depths less than 250 m (shelf shoals) and those over bottom depths greater than 250 m (offshore shoals).

These two indexes examined different aspects of proximity. The GAM model tested whether there was a significant change in the abundance of fish shoals with changes in the total abundance of plankton patches within 1 km of the edge of the shoals. The proximity index showed whether, for a given distance range from the edge of fish shoals, the plankton abundance was randomly distributed or whether it was more clustered (i.e., more plankton abundance than expected from a random distribution of plankton patches around the fish shoals at small distance ranges) or regularly dis-

tributed (i.e., less plankton abundance than expected from a random distribution of plankton patches around the fish shoals at small distance ranges). The GAM model looked at the effect on shoal abundance of plankton within a single distance range, while the proximity index was a multi-scale effect, but did not tell anything about the size of the shoals.

Results

The distribution of fish differed markedly between 1995 and 1998 over the study region. Hake abundance was greater further north in 1998 and over half the hake biomass in that year was in Canada (Wilson and Guttormsen 1997, 1998). Similarly the north-south distribution of euphausiids was different between the 2 years, with plankton highest offshore in the North in 1995 and the South in 1998 (Figs. 1 and 2, Tables 1 and 2).

Hake abundance in 1995 was highest in the South region (abundance $> 2 \times 10^{-2} \text{ m}^2/\text{km}$ for all transects), especially in offshore water ($> 250 \text{ m}$ depth) but also, somewhat along the shelf. This was accompanied by consistently low plankton abundance offshore over the same region (Figs. 1 and 2). In 1998, an El Niño year, fish abundance, especially over the shelf, was consistently low in the South (abundance $< 5 \times 10^{-3} \text{ m}^2/\text{km}$ for 11 of 12 transects; median abundance = $2 \times 10^{-3} \text{ m}^2/\text{km}$) while plankton tended to be elevated (Fig. 2).

Figures 3, 4, and 5 show fish shoal and plankton patch distributions along matching transects for 1995 and 1998 in the South, Middle, and North regions, respectively. In these figures the intensity of the shading is proportional to the biomass of the shoal or patch. The intensity scaling is on a per transect basis, so relative abundance can only be ascertained within, not between, transects. These transects are fairly typical of transects in each region. Some of the observable features of note are: (1) consistent overlap of large plankton patches and larger fish shoals in the neighborhood of the shelf break; (2) a consistent "layer" of plankton between 150 and 250 m depth in the shelf break and offshore regions, generally more pervasive in 1995 than in 1998; and (3) more variable plankton patch and fish shoal abundance from transect to transect along the shelf than offshore.

Results from the GAM regressions and the Ripley's proximity tests are summarized in Tables 1 and 2 for 1995 and 1998, respectively. The tables also give the median fish and plankton abundance for each region on the shelf and offshore. In some cases the Ripley's clustering test did not work, because there were insufficient fish or plankton in a region to give a result, which accounts for there being fewer tests reported in some regions than numbers of transects in that region.

Tables 1 and 2 show the number of transects in each region having significant clustering of plankton patches around fish shoals (i.e., the empirical mean of Ripley's K was above the upper 95% confidence limit for randomness for a distance range up to 1 km) for both the shelf and offshore

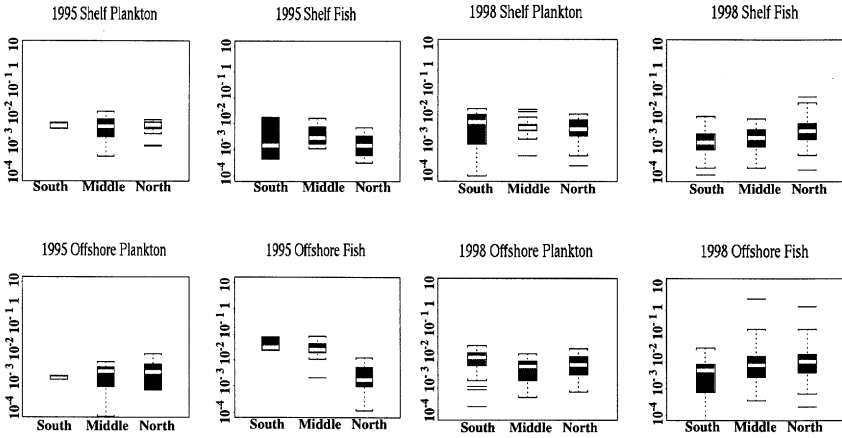


Figure 2. Box plots for relative abundance (m^2/km) of fish shoals and plankton patches on the shelf and offshore in the South, Middle, and North regions for 1995 and 1998.

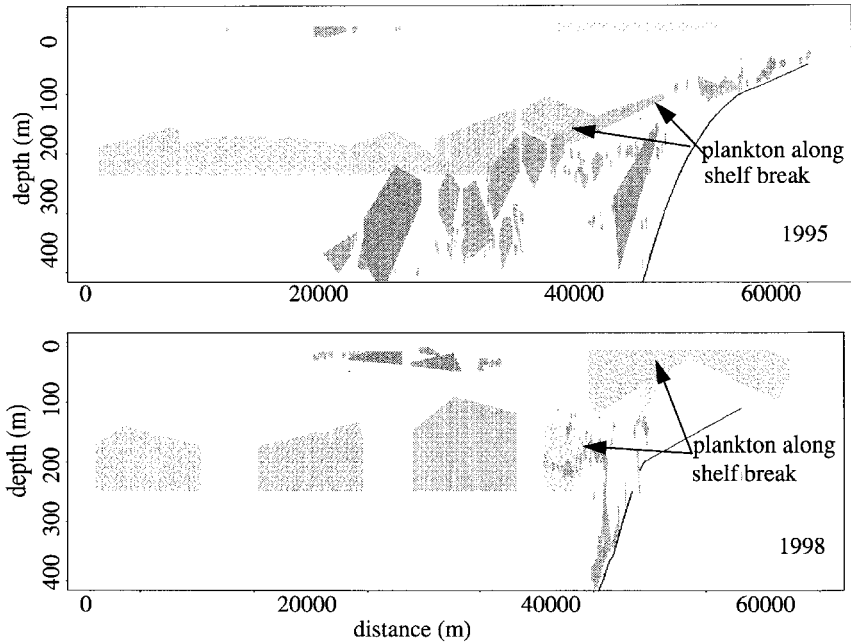


Figure 3. Distribution of plankton patches (light-shaded polygons) and fish shoals (dark-shaded polygons) for transects at 42.14°N in the South region. Shading is proportional to biomass. The bottom contour and plankton patches at the shelf break are also shown.

Table 1. Distribution in 1995 of shelf and offshore fish and plankton abundance (m^2/km) and results of proximity index and GAM tests.

Region	Tran-sects	Median shelf plankton	Median shelf fish	Median offshore plankton	Median offshore fish	Tran-sects showing offshore clusters	Tran-sects showing shelf clusters	Tran-sects with GAM signif.
South	16	9×10^{-3}	6×10^{-3}	2.5×10^{-3}	3.2×10^{-2}	5/16	4/11	14/16
Middle	14	8×10^{-3}	2×10^{-3}	3×10^{-3}	6×10^{-3}	7/13	12/14	9/14
North	20	9×10^{-3}	1×10^{-3}	5×10^{-3}	1.5×10^{-3}	5/16	15/16	6/20

Table 2. Distribution in 1998 of shelf and offshore fish and plankton abundance (m^2/km) and results of proximity index and GAM tests.

Region	Tran-sects	Median shelf plankton	Median shelf fish	Median offshore plankton	Median offshore fish	Tran-sects showing offshore clusters	Tran-sects showing shelf clusters	Tran-sects with GAM signif.
South	16	1×10^{-2}	2×10^{-3}	1.5×10^{-2}	5×10^{-3}	6/16	8/13	9/16
Middle	14	7×10^{-3}	3×10^{-3}	7×10^{-3}	8×10^{-3}	6/14	7/14	9/14
North	19	7×10^{-3}	3×10^{-3}	8×10^{-3}	1.1×10^{-2}	9/17	9/19	14/19

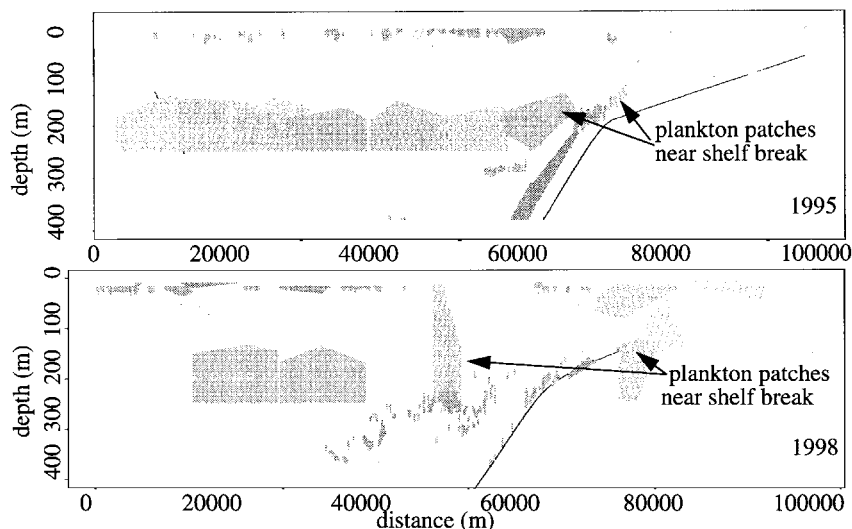


Figure 4. Distribution of fish shoals (dark-shaded polygons) and plankton patches (light-shaded polygons) for a transect in the Middle region at 43.8°N. Intensity of shading of the polygons is proportional to biomass.

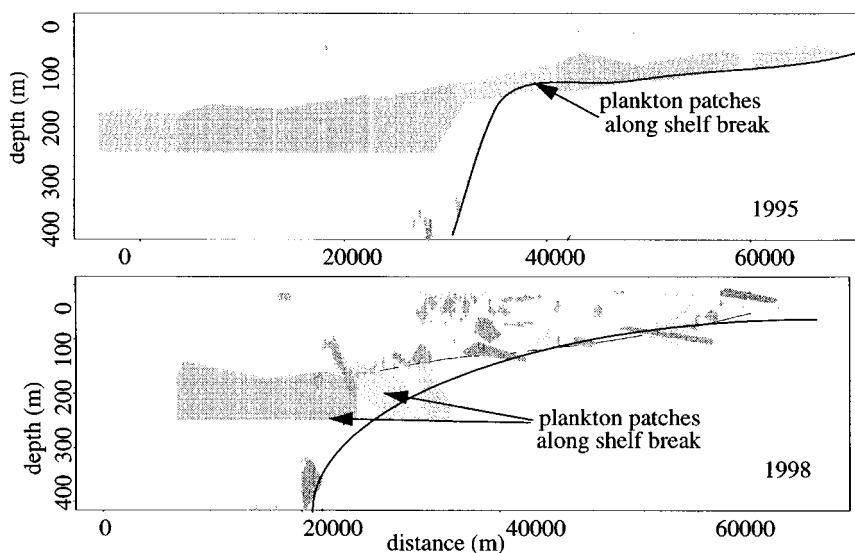


Figure 5. Fish shoal (dark-shaded polygons) and plankton patch (light-shaded polygons) distribution for a transect at 46.1°N latitude in the North region. Intensity of polygon shading is proportional to biomass.

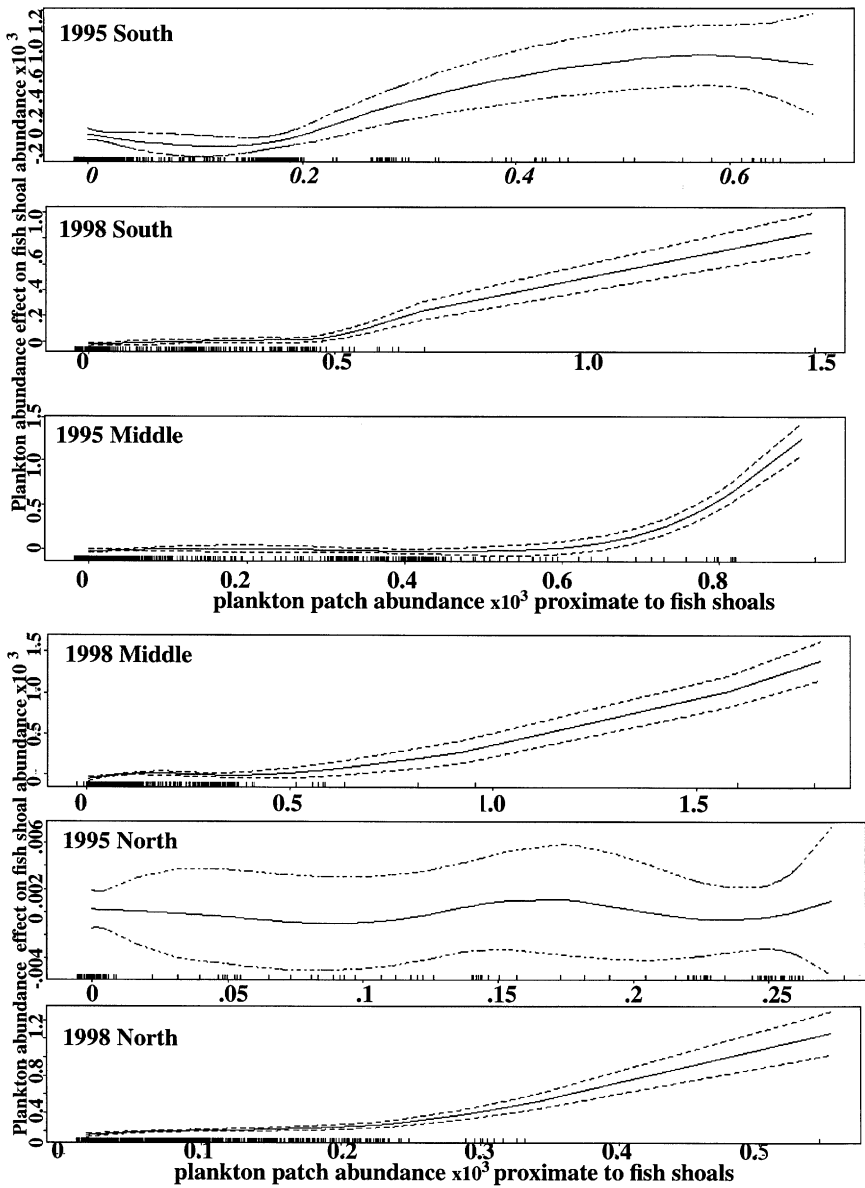


Figure 6. Results of GAM model for the effect of plankton patch abundance proximate to fish shoals on fish shoal abundance for transects in the South, Middle, and North regions.

regions. They also show the number of transects in each region having significant GAM relationships for the effect of plankton abundance within 1 km of fish shoals and the abundance (biomass) of the fish shoals.

In all regions GAM results (e.g., Fig. 6) indicate that, in every transect, the most significant covariate for fish shoal abundance was the abundance of plankton patches within 1 km of the fish shoal. The other covariates (shoal depth and bottom depth under the shoal) were rarely significant at $P < 0.05$. Figure 6 shows the effect of proximate plankton abundance on fish shoal abundance for the same transects in each region depicted in Figs. 3-5. Five of 6 cases shown gave significant results at $P < 0.01$. In all significant cases shown here fish shoal abundance increased with increasing proximate plankton abundance only for higher abundance of plankton. This is seen in the ascending right limb in all significant transects in Fig. 6. The tick marks along the x-axes in Fig. 6, termed the "rug," indicate where data points were located. The rugs show that the ascending right limb was based on a relatively small number of shoals.

Figure 6 shows the effect of plankton patch abundance on fish shoal abundance, conditional on the effects of other covariates (mostly insignificant) and with the overall mean shoal abundance subtracted. This accounts for the curves having negative as well as positive values on the y-axis. Examination of the plots of plankton and fish abundance as a function of distance along the transects in this region (e.g., Figs. 3-5 and other transects not shown here) suggests that for almost all transects where the GAM results were significant (e.g., 13 of the 14 significant transects in 1995 and all 9 significant transects in 1998 in the South region) there was clear visual evidence for proximity of high-abundance plankton patches near the shelf break with larger biomass fish shoals in the area. Furthermore, for transects in the South region, where there was no significant GAM effect of proximate plankton abundance on fish shoal abundance, there was generally no observable proximity of fish and large plankton patches near the shelf break (e.g., 1 of 2 transects in 1995 and 6 of 7 transects in 1998). This pattern also held for the other regions.

In the Middle region, the abundance of fish and plankton were at intermediate levels for both 1995 and 1998 (Fig. 2). However, for 9 of 14 transects in both years (Tables 1 and 2) the GAM model showed a significant effect of plankton abundance near fish shoals on fish shoal abundance, with the relationship being due to high-abundance fish shoals associated with high-abundance plankton patches (Fig. 4). All transects having significant GAMs in this region in both years had visual evidence of large fish shoal-plankton patch proximity near the shelf break (e.g., Fig. 6).

The North region had a plankton-fish relationship in the shelf region which differed between 1995 and 1998. In 1995 most transects had low fish abundance and relatively high plankton abundance (Figs. 1 and 2) along the shelf (median fish abundance was $1 \times 10^{-3} \text{ m}^2/\text{km}$ and plankton abundance was $9 \times 10^{-3} \text{ m}^2/\text{km}$; Table 1). In 1998, both fish and plankton abundance along the shelf were variable, with fish shoal abundance higher than

the overall region median and plankton abundance lower than the region median south of 47.3°N and vice versa north of this latitude (median plankton abundance = $4 \times 10^{-3} \text{ m}^2/\text{km}$ south and $1.1 \times 10^{-2} \text{ m}^2/\text{km}$ north of that latitude; median fish abundance = $1.8 \times 10^{-2} \text{ m}^2/\text{km}$ south and $4 \times 10^{-3} \text{ m}^2/\text{km}$ north of that latitude; Fig. 1). Offshore, both plankton and fish abundance were higher in 1998 than in 1995 in this region (Fig. 2).

The GAM relationship of large-abundance plankton patches and fish shoals in the North region also differed between 1995 and 1998. In 1995, when fish abundance was low both on the shelf and offshore, only 6 of 20 transects showed a significant GAM relationship between plankton abundance proximate to fish shoals and fish shoal abundance. In 1998, a year of higher fish and lower plankton abundance along the shelf in this region, 14 of 19 transects showed a significant effect of plankton abundance on fish abundance from the GAMs. The example transect shown in this region (Figs. 5 and 6) showed a significant GAM relationship for large plankton and fish in 1998, but not in 1995. In 1995, although high abundance plankton patches appeared near the shelf break, there were no high biomass fish shoals close by (e.g., Fig. 5).

Results from the proximity-index test for the possible clustering of plankton patches around fish shoals (irrespective of the biomass of the fish shoals) showed a strong clustering relationship on the shelf in 1995 for all transects in the Middle and North regions. In the shelf area, 27 of 30 transects showed significant clustering of plankton patch abundance around fish shoals. Offshore, there was less clustering of plankton patches around fish shoals, with somewhat less than half the transects showing clustering (somewhat more than half in the Middle region). The proximity picture was different in 1998. As in 1995, the number of transects showing clustering over the shelf area was higher than offshore (although only marginally so). There was significant clustering along the shelf in 16 of 33 transects in the Middle and North and in 8 of 13 transects in the South (Table 2). This was a much less striking contrast than in 1995, and, unlike 1995, clustering along the shelf was more prevalent in the South than in the Middle and North regions. In the offshore region there was significant clustering in 15 of 31 transects in the Middle and North and 6 of 16 transects in the South (Table 2). Clustering offshore in 1998 was about the same as in 1995 in all regions (12 of 29 transects showing significant clustering in the Middle and North and 5 of 13 transects in the South in 1995). Clustering on the shelf in the South was higher in 1998 than in 1995 (only 4 of 11 transects showed significant clustering in the South in 1995, while 8 of 13 did in 1998; Tables 1,2).

Discussion

The large number of transects having GAMs with a significant overlap between large-biomass fish shoals and higher levels of proximate plankton abundance and visual observation of these transects suggests that high-

abundance fish shoals were often close to the high-abundance plankton patches when the plankton patches were close to the shelf break and were, arguably, easier to locate by grazing hake shoals. This pattern occurred pervasively over the study region in both 1995 and 1998, and apparently independent of changes in the relative abundance of fish shoals and plankton patches. The only exception occurred in the North region in 1995, where fish abundance was, for most transects, exceptionally low (Fig. 5, Table 1). Perhaps the migration of hake did not go as far as the North region in 1995, or perhaps the high-biomass fish shoals in the North region were so patchy that they were not frequently encountered along the survey transects. Almost all transects in the North region in 1995 showed large patches of plankton near the shelf break, but few if any fish shoals along the transect (e.g., Fig. 5).

In the South region, irrespective of whether plankton abundance was high and fish abundance low (1998) or vice versa (1995), there was, for a majority of transects, a clear association between high-abundance fish shoals and high-abundance plankton patches. Furthermore high-abundance plankton patches were commonly found on the shelf break. In 1995, the proximity of high-abundance fish shoals to high-abundance plankton patches near the shelf break, despite the relatively low plankton abundance in this region, might reflect the effect of intense predation on euphausiids by Pacific hake such as to reduce the euphausiid abundance. The persistence of larger euphausiid patches near the shelf break in this region when plankton abundance was lower, as in 1995, suggests that these may be a favored habitat for euphausiids, maintained despite heavy predation. The shelf break might be a preferred euphausiid habitat because it provides a stable summer feeding environment and may also have hydrodynamic features that allow the euphausiids to remain in the area despite high alongshore currents (Mackas et al. 1997). While the spatial overlap of high-abundance fish shoals and plankton patches was marked in 1995, it was also apparent in the South (although not as prevalent) in 1998, a year when plankton were high and fish abundance low. However, in 1998, there was also consistent overlap of high-abundance fish shoals and plankton patches in the North region, where both shelf and offshore fish densities were higher than in 1995 (Table 2).

Because of the apparent importance of the shelf break, separation of this region from the offshore and shelf regions seems desirable. This was not done here, mainly because locating the boundaries of the shelf break by algorithm was difficult due to variability of shelf break bathymetry and the existence of bathymetric features (e.g., ocean rises and canyons) that can be confounded with the shelf break. This remains as future work.

The proximity measure examined how close shoals in general were to food resource patches without regard to the size of the fish shoals. Thus, although in the North in 1995 prey patches on the shelf were distributed around fish shoals in a nonrandom, clustered fashion in almost every transect (Table 1), the high-abundance shoals were not often associated

with high-abundance plankton patches over the entire transect. The major difference in fish-plankton proximity between 1995 and 1998 was in the shelf areas, which had more clustering in the Middle and North in 1995 (27 of 31 transects) but more clustering South in 1998 (8 of 13 transects). The high degree of clustering of plankton patches around fish shoals on the shelf in 1995 in the Middle and North regions may be due to the higher plankton abundance in this region than in the South and the effectiveness of hake in locating and grazing on plankton patches in this area. The lower (about 50% of transects) incidence of clustering of plankton patches around fish shoals in 1998 in the Middle and North regions over the shelf may be due to the hake being younger in this area in 1998 than in 1995 and therefore less effective grazers. For example, 95% of the Pacific hake caught in trawls off Washington in 1995 were above 42 cm fork length, while only 50% in 1998 were in this size category (Wilson and Guttormsen 1997, 1998).

Results from the GAM and cluster proximity tests frequently do not agree (Tables 1 and 2). Because the hake biomass is dominated by larger shoals, the GAM results give a more apt interpretation of what is happening for most of the fish in a region. However, for the shelf areas, where hake shoals tended to be smaller, the cluster results have provided additional insight into fish-plankton dynamics.

We have focused effort in this paper on fish-plankton relationships off the U.S. coast. In both years, the survey went farther north, to the neighborhood of the Queen Charlotte Islands, Canada (latitude 50°N). Significantly, large aggregations of Pacific hake were found off Vancouver Island in 1998, suggesting that one of the features of El Niño years was a northward shift of Pacific hake (Wilson and Guttormsen 1998). A similar pattern was found for acoustic surveys run during previous El Niño years (Dorn 1991, Dorn 1995).

It is unclear whether the higher than average northward migration in 1998 was driven primarily by physical factors, such as enhanced northward flowing current at depths between 150 and 400 m, where the hake were primarily found, or due to a lack of food resources farther south. This study showed regional reversals between 1995 and 1998 in fish and plankton abundance, with the South region having high fish abundance and low plankton abundance in 1995 and shifting to the reverse in 1998. Generally, fish abundance throughout the U.S. California Current Ecosystem (CCE) region was higher in 1995 than in 1998 and plankton was higher in 1998 than in 1995 (except for the region around the Columbia River; Fig. 1). That zooplankton abundance in 1998 was generally higher than in 1995, despite the expected reduction in primary production due to lowered wind-driven upwelling, which usually accompanies El Niño, leads to the hypothesis that movement of hake farther north during 1998 may not have been due to reduced food availability, but to enhanced northward flow. This can be investigated using ADCP data currently being processed (Pierce et al. 1999; M. Kosro, Oregon State University, pers. comm.) and also from current meters deployed during 1998 off Coos Bay, Oregon (B. Hickey,

University of Washington, unpubl. data). Because the zooplankton condition earlier in the summer, when many of the hake passed through the southern region, is not available, the question about the source of higher plankton abundance in 1998 remains unresolved. Does the larger euphausiid abundance in 1998 reflect reasonable food availability for and growth by euphausiids, or does it reflect the effects of reduced hake predation due to northward shift of the hake population in an El Niño year?

Another striking observation, which has not been further investigated, is the presence of large layers of plankton in the offshore region. The layers may be continuous or more patchy (Figs. 3-5). However, it is not clear how the plankton can remain in patches in the face of the large shear found offshore at a depth near the maximum northward flowing California undercurrent (Pierce et al. 1999). Perhaps the higher-production shelf break region is saturated and the plankton remain in the undercurrent until they encounter regions of higher food availability. Perhaps they remain offshore to avoid predation along the shelf break. Alternatively, they may be diel migrating such as to maintain position (surface waters in the summer CCE are generally southward flowing) in anticipation of higher production eddies or jets. Clearly, more work is waiting in this area.

The above discussion illustrates part of the difficulty in trying to ascertain patterns of grazing from the spatial configuration of predator and prey at a given time and place. We do not know the movement history of the animals prior to their observation and we do not know the production history of the euphausiids and their food resources. Nonetheless, some of the patterns are compelling and provide insight. Others serve to raise questions that may be addressed in the future through process studies.

Acknowledgments

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Spatial Patterns in Species Composition in the Northeast United States Continental Shelf Fish Community during 1966-1999

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Abstract

I evaluated spatial structure in the northeast United States continental shelf groundfish community based on a 30-year time series of bottom trawl survey data. Four major faunal regions were identified based on similarity in species composition. The faunal regions had consistent geographic boundaries across the time series. There were significant changes in species composition within faunal regions through time, reflecting changes in both species abundances and spatial patterns. Species that declined in abundance tended to contract their spatial range while those that increased tended to expand the total area covered by the population. However, the more general pattern in this community was a northward shift in spatial distribution observed in many exploited and unexploited species. The major changes in community structure and spatial distributions associated with both fishing pressure and climate variation have important implications for the trophic dynamics of this ecosystem.

Introduction

Fishery harvest and overexploitation have driven dramatic changes in ecosystem structure and dynamics in fish communities on a global scale (Jennings and Kaiser 1998). Predicting the response of fish communities to overexploitation requires a greater understanding of the ecosystem-wide effects of fishing on the interactions between species and the resulting

community dynamics (Fogarty and Murawski 1998, Jennings and Kaiser 1998). These “ecosystem” and multispecies approaches to fishery assessment and management require an improved understanding of the processes that regulate the strength of species interactions in fish communities.

The fish predators in continental shelf ecosystems are characterized by a high degree of dietary generalism and opportunistic feeding (Jennings and Kaiser 1998, Garrison and Link 2000). Selection of a given prey is largely determined by encounter rates and prey abundance, and high spatial overlap between predator and prey can significantly influence predation rates (Jennings and Kaiser 1998). The processes influencing spatial patterns in community structure therefore play an important role in driving variability in trophic interactions.

Fish spatial distributions are sensitive to environmental factors, particularly temperature and depth (Overholtz and Tyler 1985, Mountain and Murawski 1992), and species with similar habitat preferences have high spatial overlap (Murawski and Finn 1988, Garrison 2000). Environmental gradients drive the formation of species assemblages at regional scales in continental shelf fish communities (Gabriel 1992, Gomes et al. 1995). These associations are typically stable through time, and the species within them typically show a similar response to interannual variations in temperature (Gabriel 1992).

Exploitation patterns may also influence fish spatial distributions and species composition. There is a general relationship between population size and the spatial range of fish species. As population abundance declines, spatial ranges generally decrease and the species is concentrated into smaller areas (Atkinson et al. 1997). Alternatively, management restrictions on fishing effort, such as marine protected areas, or refugia from fishing gear may alter species distributions and concentrate fish in localized areas. Changes in spatial distributions associated with variations in population size, fishing pressure, and climate variability influence the spatial associations between species and therefore the strength of trophic interactions.

In the northeast United States continental shelf fish community, there have been significant changes in the population sizes of both over- and underexploited stocks. Over the last three decades, there has been a general decline in the abundance of heavily exploited species including gadids and flatfish. There has been a concomitant increase in less-utilized species including elasmobranchs and small pelagic fish (Fogarty and Murawski 1998, NEFSC 1998). In the current study, I examine temporal variability in the spatial structure of the northeast United States continental shelf fish community associated with these changes in population size. I document decadal-scale changes in the spatial pattern of species composition and identify major changes in spatial distributions associated with both fishery exploitation and environmental variability. I discuss the implications of observed changes in spatial structure and species composition for the trophic dynamics of this system.

Methods

The data for this study were drawn from seasonal bottom trawl surveys conducted by the Northeast Fisheries Science Center (NEFSC). The surveys employ a stratified random sampling design with strata defined by depth and latitude. Sample depths ranged between 8 and 400 m on the North American continental shelf between Cape Hatteras, North Carolina and Nova Scotia (Fig. 1). Typically 300-400 stations are occupied during each seasonal survey. At each station, a 36-Yankee or similar bottom trawl is towed for 30 min at a speed of 6.5 km per hr. All species within the sample are identified, weighed (kg), and subsampled to determine catch in numbers per 1-cm size classes. Catch correction factors were applied to account for changes in vessels and gears across the time series. Details of the survey sampling design, execution, and efficiency are available in NEFC (1988).

The current study included trawl tows from the northwest Atlantic continental shelf between 39° and 45° north latitude including areas of southern New England, Georges Bank, the Gulf of Maine, and the southwest Nova Scotian shelf (Fig. 1). The analyses were conducted using data from autumn (September-October) bottom trawl surveys conducted from 1966 to 1999. Patterns in spatial structure were evaluated in 5-year time blocks, and species abundance and distribution patterns were generally homogenous within 5-year blocks. Data from alternating time blocks are presented for brevity including the periods 1966-1970 (1,016 stations), 1976-1980 (1,455 stations), 1986-1990 (925 stations), and 1996-1999 (837 stations). The spatial pattern of sampling has remained consistent throughout the time series with the exception of reduced sampling in the Scotian shelf region in recent years (Fig. 1). Twenty-seven predator species were included in the study, including two squids (Table 1). These are numerical and biomass dominants, commercially valuable, and/or ecologically important species in the northwest Atlantic.

Species abundance data were aggregated into 0.5°-square grid cells for each time block to quantify spatial patterns. The average catch (in kilograms per square kilometer) of each species was calculated across tows collected within each grid cell. A swept-area biomass estimate was then calculated by multiplying catch per square kilometer by the total area of the cell (2,275 km²) and the proportion of the cell area available to the survey (e.g., proportion of cell not covered by land). This level of spatial and temporal resolution captured the major features of the spatial patterns in species distributions (Garrison, unpubl. data). Because I have not accounted for the catch efficiency of the gear in these calculations, the swept-area biomass should be considered an index of relative abundance rather than an absolute biomass value.

The 0.5° cells were clustered based upon their similarity in species composition. The biomass estimate in each cell (tons) was transformed by taking the fourth root to reduce the influence of highly abundant species (Pielou 1984). The proportional similarity in species composition between

Figure 1. Bottom trawl survey strata on the northeast United States continental shelf and sample locations during four time periods: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Inset map shows the eastern coast of North America and the study area.

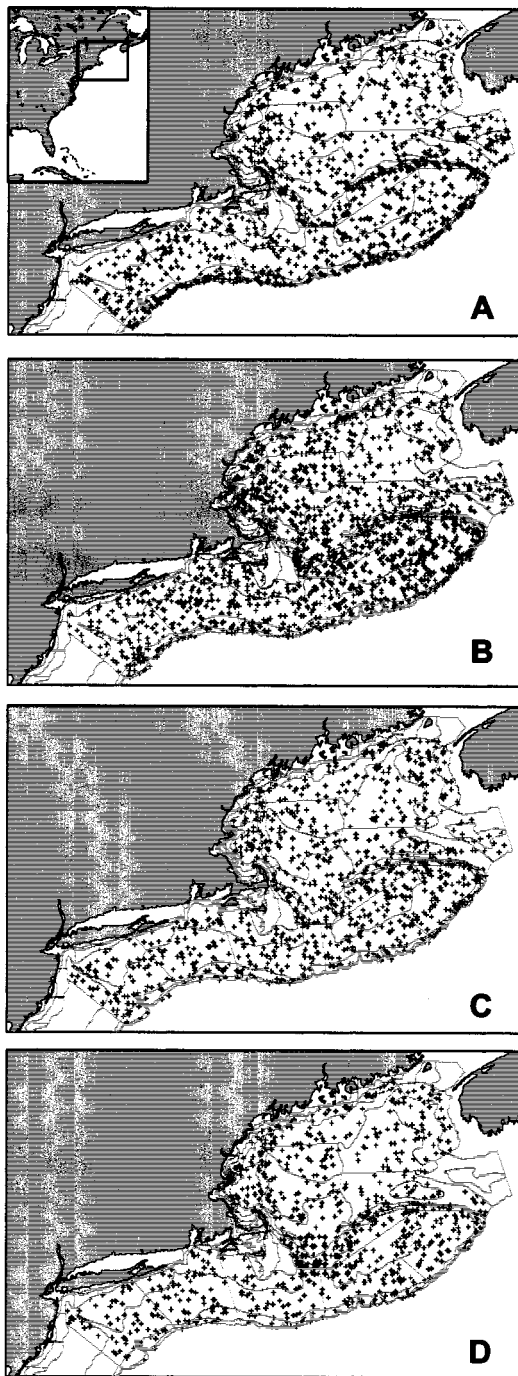


Table 1. Fish and squid species included in the current study.

Common name	Scientific name
Smooth dogfish	<i>Mustelus canis</i>
Spiny dogfish	<i>Squalus acanthias</i>
Winter skate	<i>Raja ocellata</i>
Little skate	<i>Raja erinacea</i>
Atlantic cod	<i>Gadus morhua</i>
Haddock	<i>Melanogrammus aeglefinus</i>
Pollock	<i>Pollachius virens</i>
Offshore hake	<i>Merluccius albidus</i>
Silver hake	<i>Merluccius bilinearis</i>
White hake	<i>Urophycis tenuis</i>
Red hake	<i>Urophycis chuss</i>
Yellowtail flounder	<i>Limanda ferruginea</i>
Winter flounder	<i>Pseudopleuronectes americanus</i>
Summer flounder	<i>Paralichthys dentatus</i>
Four-spot flounder	<i>Paralichthys oblongus</i>
Witch flounder	<i>Glyptocephalus cynoglossus</i>
Windowpane	<i>Scophthalmus aquosus</i>
Redfish	<i>Sebastes fasciatus</i>
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i>
Sea raven	<i>Hemitripterus americanus</i>
Ocean pout	<i>Macrozoarces americanus</i>
Goosefish	<i>Lophius americanus</i>
Atlantic herring	<i>Clupea harengus</i>
Atlantic mackerel	<i>Scomber scombrus</i>
Butterfish	<i>Peprillus tricanthus</i>
Shortfin squid	<i>Illex illecebrosus</i>
Longfin squid	<i>Loligo pealeii</i>

grid cells was calculated using the Bray-Curtis (Bray and Curtis 1957) similarity index,

$$S_{ij} = 1 - \frac{\sum_{k=1}^N |n_{ik} - n_{jk}|}{\sum_{k=1}^N (n_{ik} + n_{jk})}, \quad (1)$$

where N is the total number of species and n_{ik} and n_{jk} are the transformed biomass of species k in cells i and j respectively. Based upon this similarity index, grid cells were clustered with a hierarchical agglomerative clustering algorithm using unweighted group average clustering (Pielou 1984). The resulting dendrograms and the identified spatial clusters were not sensitive to different data transformations or clustering methods. Spatial gradients in species composition were also quantified using a detrended correspondence analysis (DCA, Hill and Gauch 1980). Based upon these analyses, in each time block I identified "faunal regions" defined as geographic areas with similar species composition in that time period. I examined changes in the species composition within these faunal regions through time.

In addition, I present example maps of changes in species distributions across time and discuss three types of spatial distribution shifts that occurred in this community: range contraction, range expansion, and range shifts. To further elucidate general patterns of latitudinal shifts in species distributions, I calculated the weighted mean latitude of occurrence for 18 example species in each 5-year time block from 1966 to 1999. The biomass data was lognormally distributed, and was therefore transformed ($\ln[y+1]$) prior to calculating the mean latitude to prevent large values from skewing the mean. For each species, the mean latitude of occurrence was calculated,

$$\bar{X} = \frac{\sum_{i=1}^N y_i x_i}{\sum_{i=1}^N y_i}, \quad (2)$$

where y_i is the log-transformed biomass of the species in latitude x_i for each of N 0.5° latitude cells. The variance was then calculated as,

$$s_{lat}^2 = \frac{\sum_{i=1}^N y_i (x_i - \bar{X})^2}{\sum_{i=1}^N y_i}. \quad (3)$$

The mean latitude is interpreted as a “center of mass” for the population being considered, and trends (with 95% CI) through time were evaluated to assess decadal scale shifts in species distributions.

Results

Faunal Regions

In all four time blocks examined, there were clear geographic patterns in species composition based on both the cluster analysis and the DCA ordination. The grid cells clustered into faunal regions at similarity levels ranging between 45% and 60%. The faunal regions were geographically contiguous and were generally consistent through time (Fig. 2). Grid cells clustered into four major faunal regions based upon their similarity in species composition in all four time blocks: Offshore, Georges Bank/Southern New England, Gulf of Maine, and Scotian Shelf (Fig. 2). During the 1976-1980 and 1986-1990 periods an additional faunal region was identified: Inshore Southern New England (Fig. 2b,c).

The DCA analysis also indicated important gradients in species composition, and cell groups in the ordination space defined by the first two DCA axes were similar to those identified in the cluster analysis (Fig. 3). The first two axes explained 50-53% of the total variation in the species data. The first axis organized locations along a latitudinal gradient. Cells in the southern portion of the sampling area had low scores on this axis, while those in the Gulf of Maine and Scotian Shelf regions had higher scores (Figs. 2 and 3). Species abundant in southern habitats such as smooth dogfish, summer flounder, butterfly, and longfin squid had low scores on this axis while those abundant in northern habitats including redfish, witch flounder, haddock, and pollock had higher scores. The second axis organized locations along a depth gradient. The deepwater, offshore locations had lower scores while those in shallower habitats on Georges Bank and the Scotian Shelf area had higher scores (Figs. 2 and 3). Species abundant in deep water, including offshore hake, shortfin squid, and goosefish, had low scores on this axis while species abundant in shallower water, including summer flounder, winter skate, and windowpane, had higher scores.

The offshore faunal region was characterized by a high biomass of longfin and shortfin squids during the early portion of the time series (Fig. 4a,b). During these periods, these two species accounted for over 50% of the biomass, and butterfly, silver hake, and white hake were also important components in offshore habitats. However, during the 1986-1990 and 1996-1999 periods, the relative importance of the squid species declined to total approximately 30% of the biomass while that of spiny dogfish increased to 24% and 27% in 1986-1990 and 1996-1999, respectively (Fig. 4c,d). In addition, silver hake was an important component of the biomass (22%) during the 1986-1990 time period.

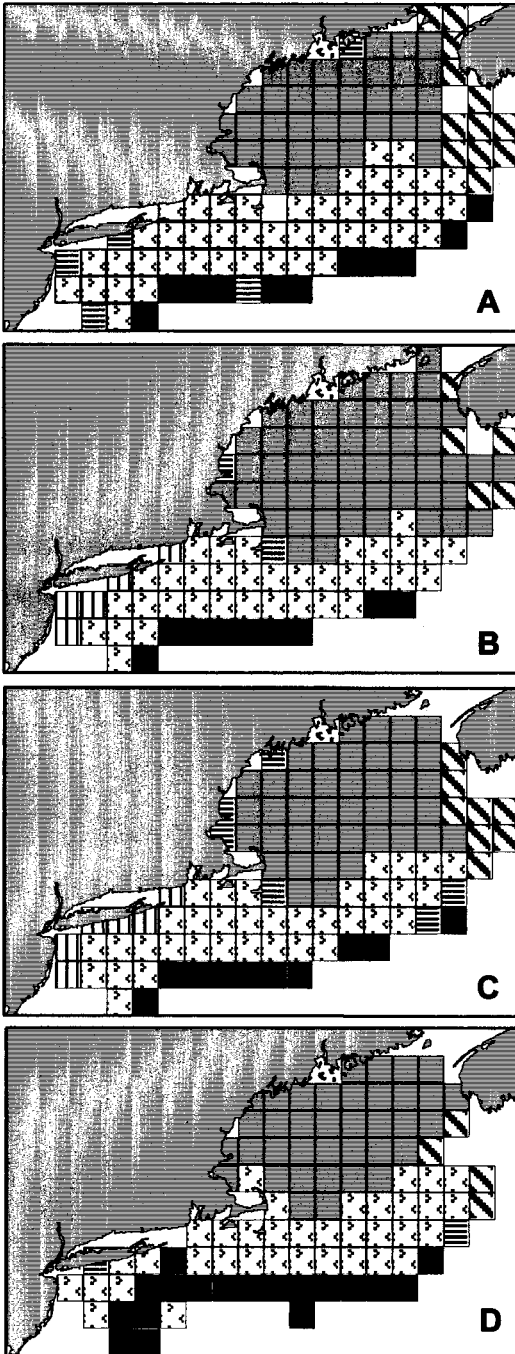


Figure 2. Faunal region maps based on cluster analyses for four time periods: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Grid cells that were not members of a cluster were identified as outliers. Blank cells indicate areas where no samples were collected.



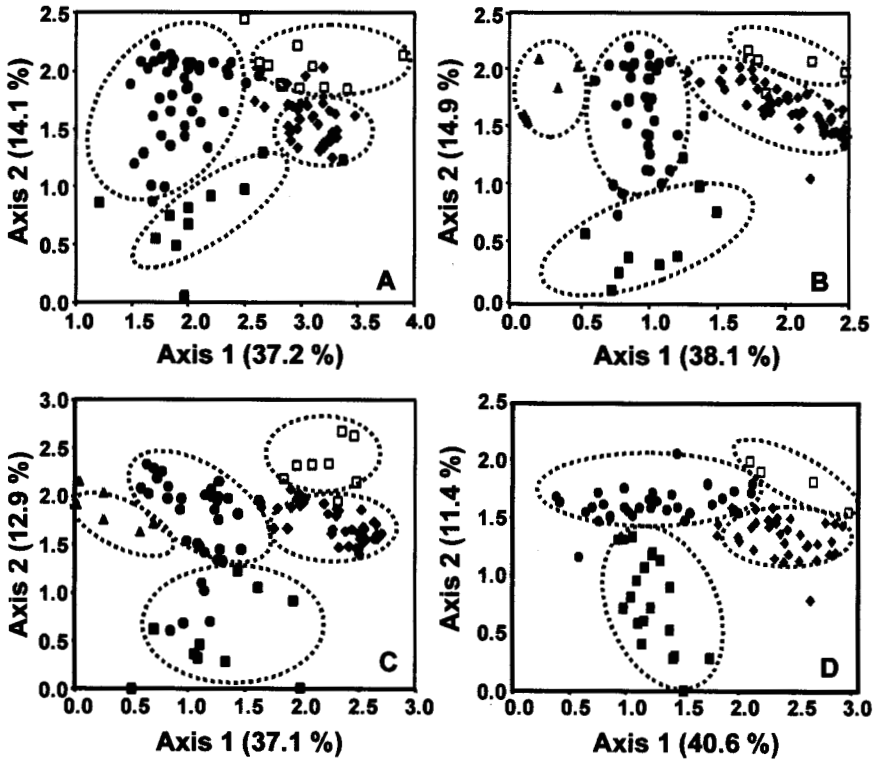


Figure 3. DCA ordination plots showing the distribution of grid cells in the ordination space defined by the first two axes in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Percentage of total inertia in species data explained by each axis is indicated in parentheses. Dashed circles enclose grid cells within the faunal regions identified in Fig. 2: ■ Offshore, ▲ Inshore SNE, ● Georges Bank/Southern New England, ◆ Gulf of Maine, □ Scotian Shelf.

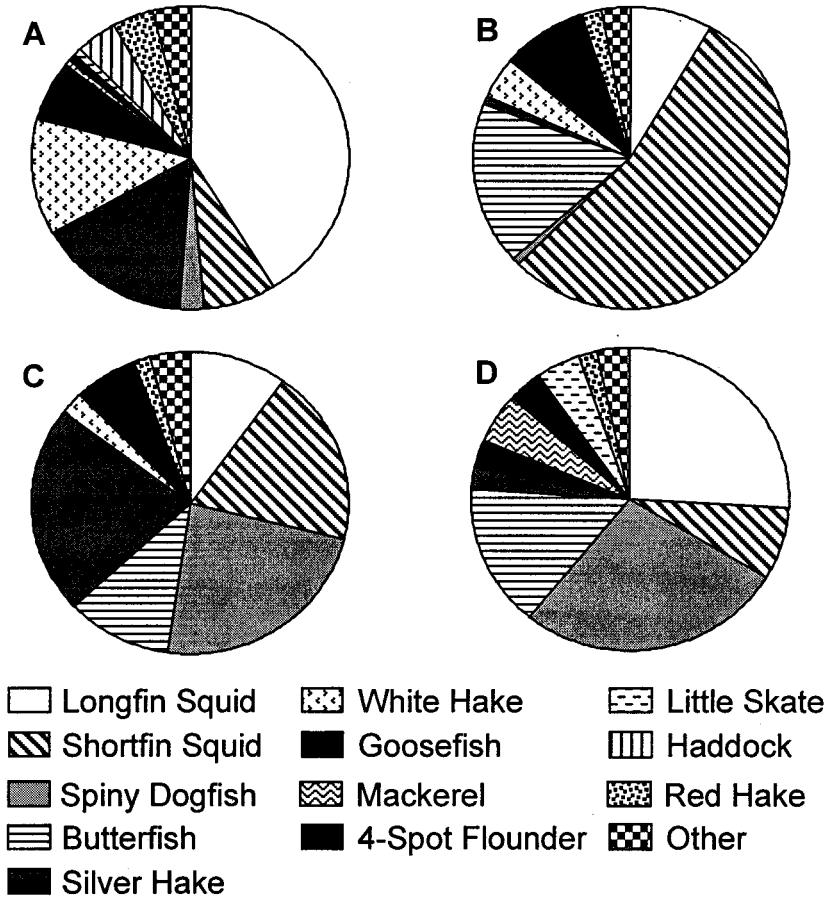


Figure 4. Proportion of total fish biomass by species in grid cells in the Offshore faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.

The Inshore Southern New England faunal region was only identified during the 1976-1980 and the 1986-1990 time periods. During the earlier time block, the region was dominated by spiny dogfish (49% of biomass) along with longfin squid (25%) and smooth dogfish (8%, Fig. 5a). The importance of spiny dogfish was much lower (4%) during the later time period, and the region was dominated by longfin squid (42%), smooth dogfish (19%), and butterfish (19%, Fig. 5b).

The Georges Bank/Southern New England faunal region was characterized by a greater number of species than other assemblages. Spiny dogfish was the dominant biomass component throughout the time series (Fig. 6). During the two earlier time periods, spiny dogfish accounted for 48% and 40% of the biomass in this region (Fig. 6a,b). In the 1966-1970 time block, haddock (7%), yellowtail flounder (8%), and cod (4%) were also important biomass components (Fig. 6a). In the 1976-1980 time period, the importance of these gadids and flatfish declined and winter skate (8%), little skate (7%), longfin squid (7%), and butterfish (11%) became more important (Fig. 6b). During the 1986-1990 period, spiny dogfish declined to 27%, while the importance of winter skate (22%) and longfin squid (11%) increased (Fig. 6c). In the most recent period, spiny dogfish was again the dominant species in this region (54%), winter skate remained important (8%), and haddock also increased (7%, Fig. 6d).

The Gulf of Maine region was dominated by redfish, haddock, cod, and pollock during the 1966-1970 and 1976-1980 time periods (Fig. 7a,b). Spiny dogfish accounted for a relatively small proportion of the biomass during these time periods (12% and 11% respectively), and both silver hake and white hake were also important species (Fig. 7a,b). During the 1986-1990 period, spiny dogfish was much more important and accounted for 44% of the biomass in the region (Fig. 7c). Redfish, haddock, cod, and pollock were each <8% of the biomass during this period, and silver hake (8%), white hake (8%), and winter skate (6%) were also important (Fig. 7c). During the 1996-1999 period, spiny dogfish declined to 31% of the biomass while redfish increased to 27% (Fig. 7d). Silver hake (12%) and white hake (6%) remained important while haddock, cod, and pollock each accounted for <6% of the regional biomass (Fig. 7d).

The southwest Scotian Shelf was characterized by a high proportion of haddock throughout the time series (Fig. 8). During the 1966-1970 and 1976-1980 periods, haddock accounted for 47% and 75% of the biomass in this region, and cod (24%) and pollock (13%) were the other important species during the 1966-1970 period (Fig. 8a,b). During the 1986-1990 period, haddock remained important (35%), but spiny dogfish became the biomass dominant (42%) and both cod (7%) and pollock (2%) were less important (Fig. 8c). In the 1996-1999 period, the proportion of spiny dogfish declined (9%), haddock (41%) and pollock (14%) were the dominant species, and winter flounder and redfish were also important species (Fig. 8d).

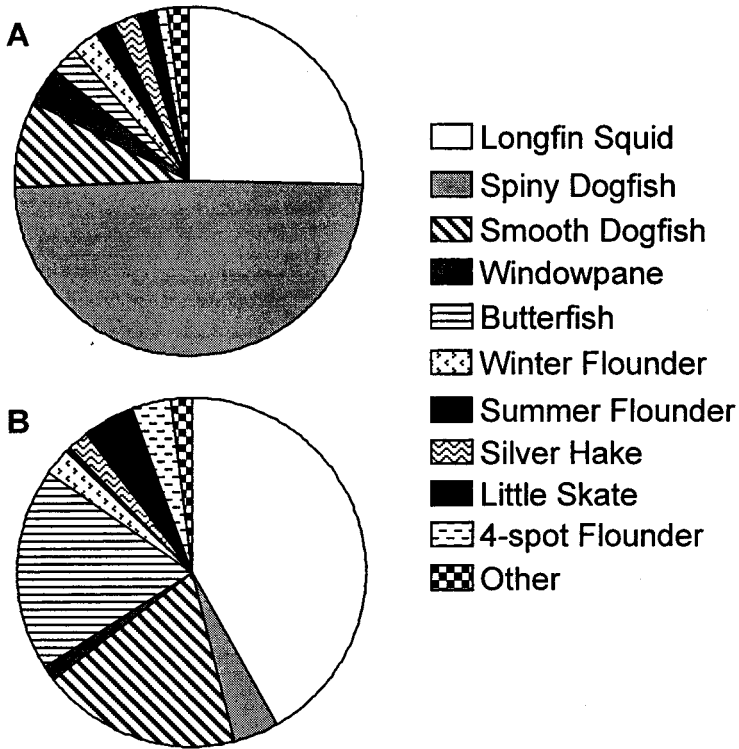


Figure 5. Proportion of total fish biomass by species in grid cells in the Inshore Southern New England faunal region in (A) 1976-1980 and (B) 1986-1990. Other is the sum of all species accounting for <1% of the biomass.

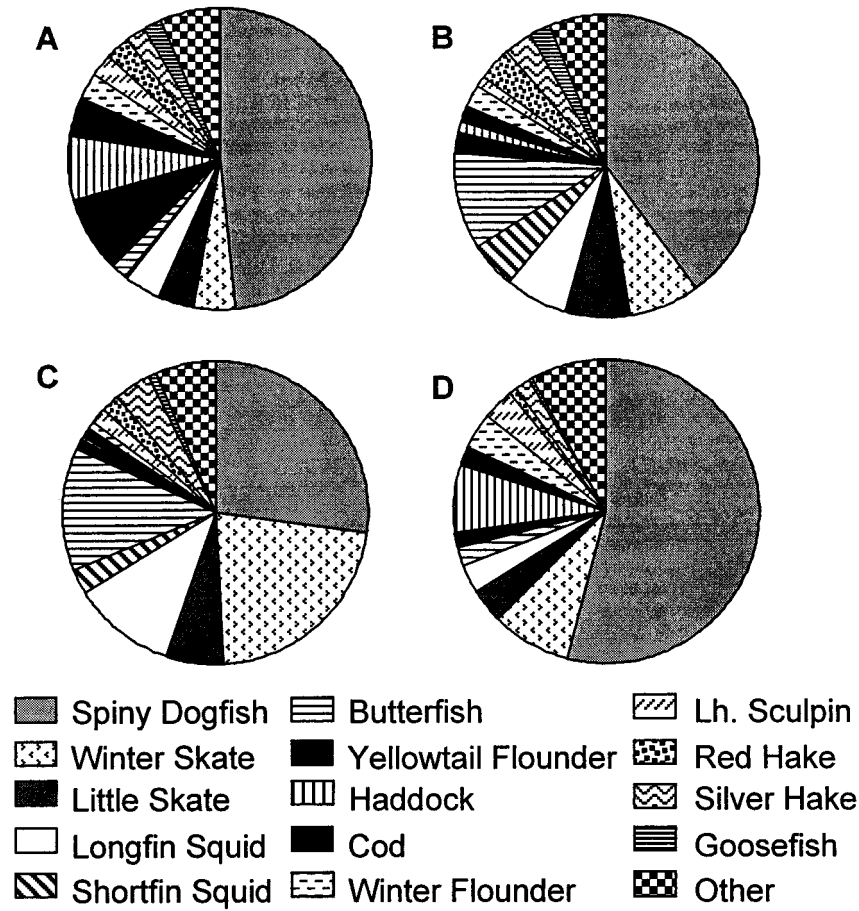


Figure 6. Proportion of total fish biomass by species in grid cells in the Georges Bank/Southern New England faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.

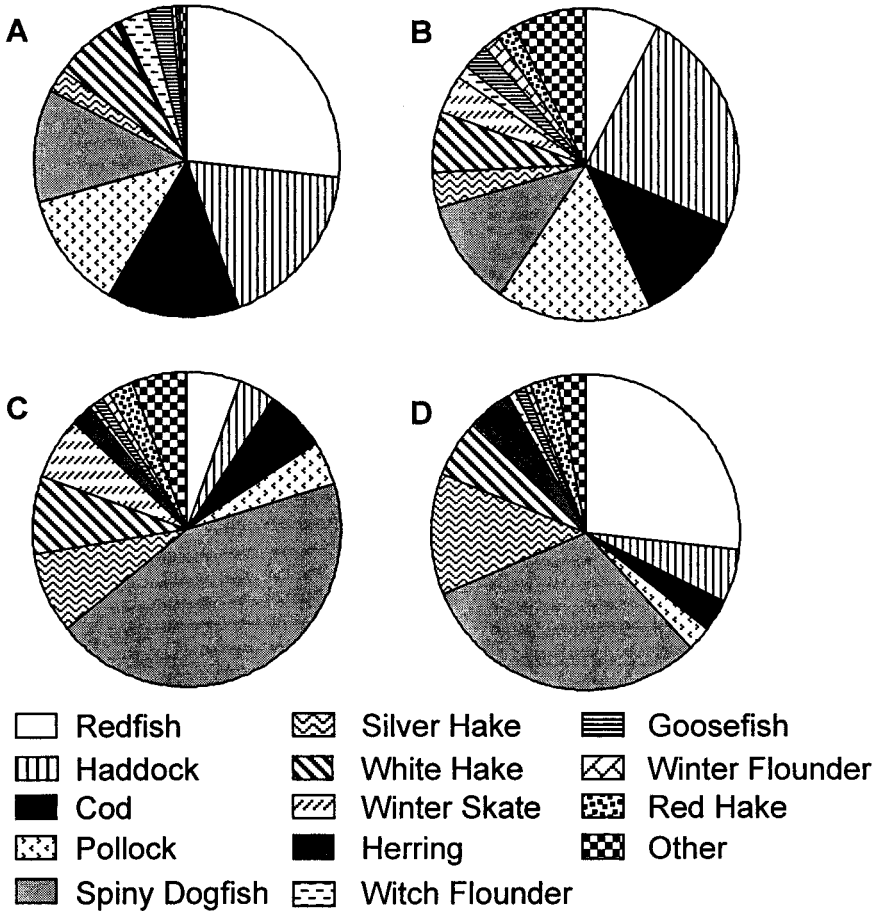


Figure 7. Proportion of total fish biomass by species in grid cells in the Gulf of Maine faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.

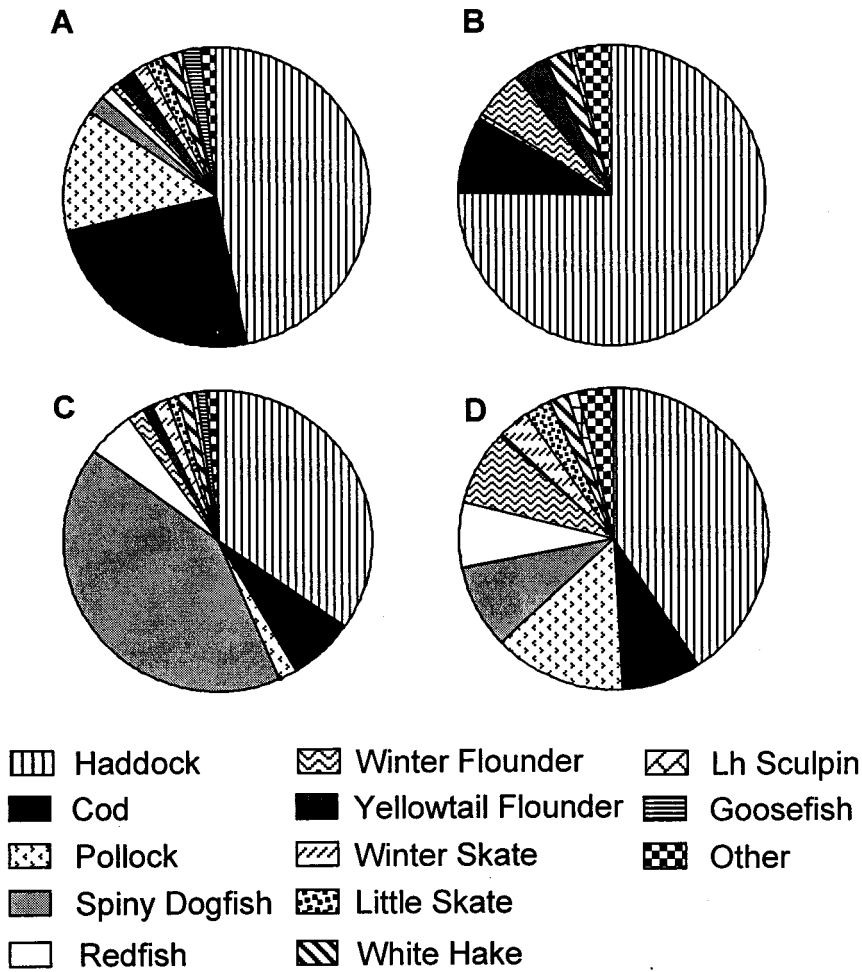


Figure 8. Proportion of total fish biomass by species in grid cells in the Scotian Shelf faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.

Temporal Changes in Species Distribution

The changes in species composition within faunal regions reflect changes in both species biomass and spatial distribution across time. There were three general patterns of changes in spatial distribution in the northwest Atlantic fish community. First, as population sizes declined, there was a reduction in the total area covered by a species, defined as a “range contraction.” As an example, during the 1960s, haddock were abundant throughout Georges Bank, the Gulf of Maine, and the Scotian Shelf (Fig. 9a), and the total estimated biomass of haddock was 2.9×10^5 tons. The haddock biomass index declined to 0.9×10^5 tons in the 1986-1990 time period, and haddock distributions were restricted to the Scotian Shelf and the Great South Channel on Georges Bank during this period (Fig. 9c). Haddock estimated biomass has recently increased to 1.4×10^5 tons, and their range has expanded slightly in recent years (Fig. 9d). Similar contraction of ranges occurred in many species that experienced declines in biomass including cod, pollock, and yellowtail flounder.

Conversely, species whose population sizes increased through time have increased their spatial range, termed a “range expansion.” For example, the estimated biomass of Atlantic herring during the 1966-1970 was 4.5×10^3 tons and declined to only 0.5×10^3 tons during the 1976-1980 period. During this period, their range contracted and became restricted to small areas of the Gulf of Maine (Fig. 10a,b). The herring biomass index increased during the 1986-1990 period and increased to 61×10^3 tons during the 1996-1990 period. Their range expanded during the 1990s to cover the majority of the Gulf of Maine (Fig. 10c,d). A similar pattern of range expansion occurred in Atlantic mackerel and butterfish as their estimated biomass increased through time.

Finally, many species have exhibited significant “range shifts” through time and have become relatively more abundant in northern habitats. For example, spiny dogfish was abundant primarily in southern New England during the 1966-1970 time period (Fig. 11a). The spiny dogfish population shifted north through time, and their estimated biomass declined in southern regions and increased in northern regions including the Gulf of Maine and the Scotian Shelf through the 1976-1980 and 1986-1990 time periods (Fig. 11b,c). During the 1996-1999 period, the spiny dogfish population has again shifted south, becoming less abundant in the Scotian Shelf area and more abundant in southern regions (Fig. 11d).

Across decadal time scales, many species have exhibited northward distribution shifts, and these were indicated by trends in their mean latitude of occurrence across the time series (Fig. 12). Northward shifts of 0.5° – 1.0° of latitude occurred in fourspot flounder, butterfish, winter skate, yellowtail flounder, herring, mackerel, red hake, silver hake, spiny dogfish, ocean pout, longhorn sculpin, and sea raven (Fig. 12). This reflects a very significant shift in spatial distribution. For example, during 1966-1970 81% of the total estimated spiny dogfish biomass occurred in the Offshore and

Figure 9. Estimated biomass of haddock in 0.5° cells in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999.

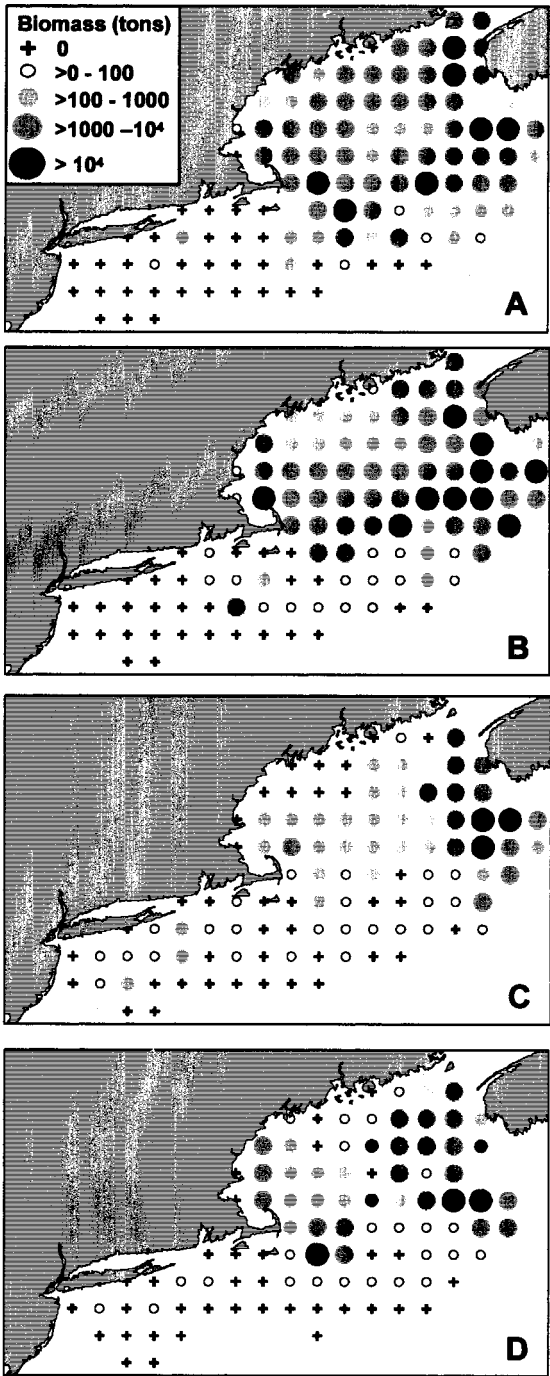


Figure 10. Estimated biomass of Atlantic herring in 0.5° cells in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999.

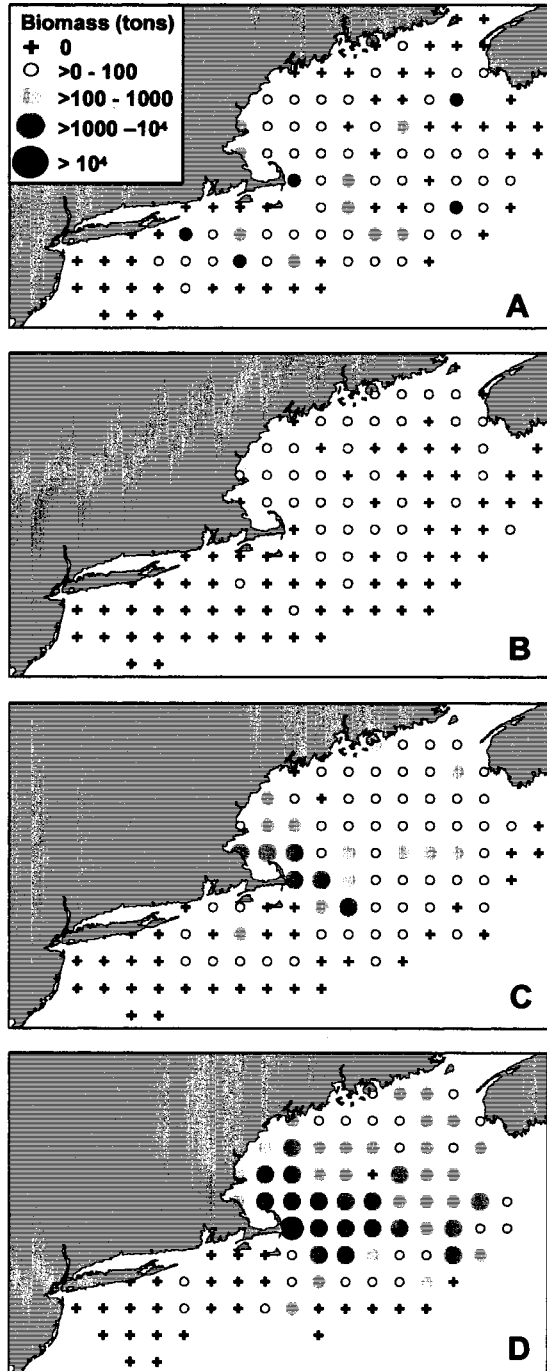
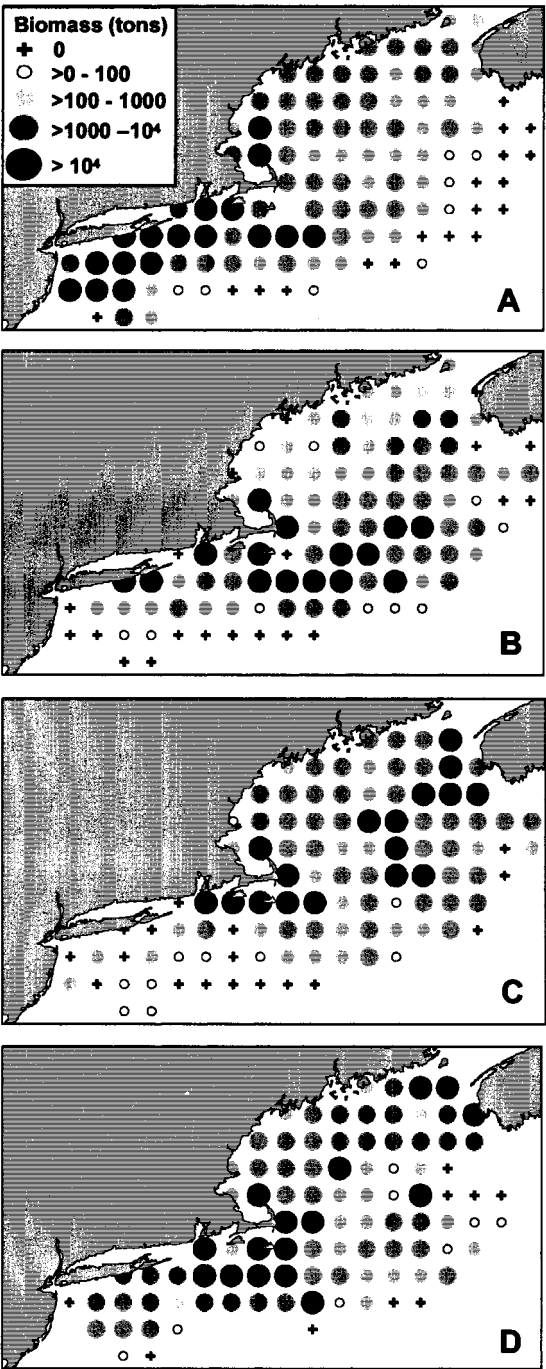


Figure 11. Estimated biomass of spiny dogfish in 0.5° cells in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999.



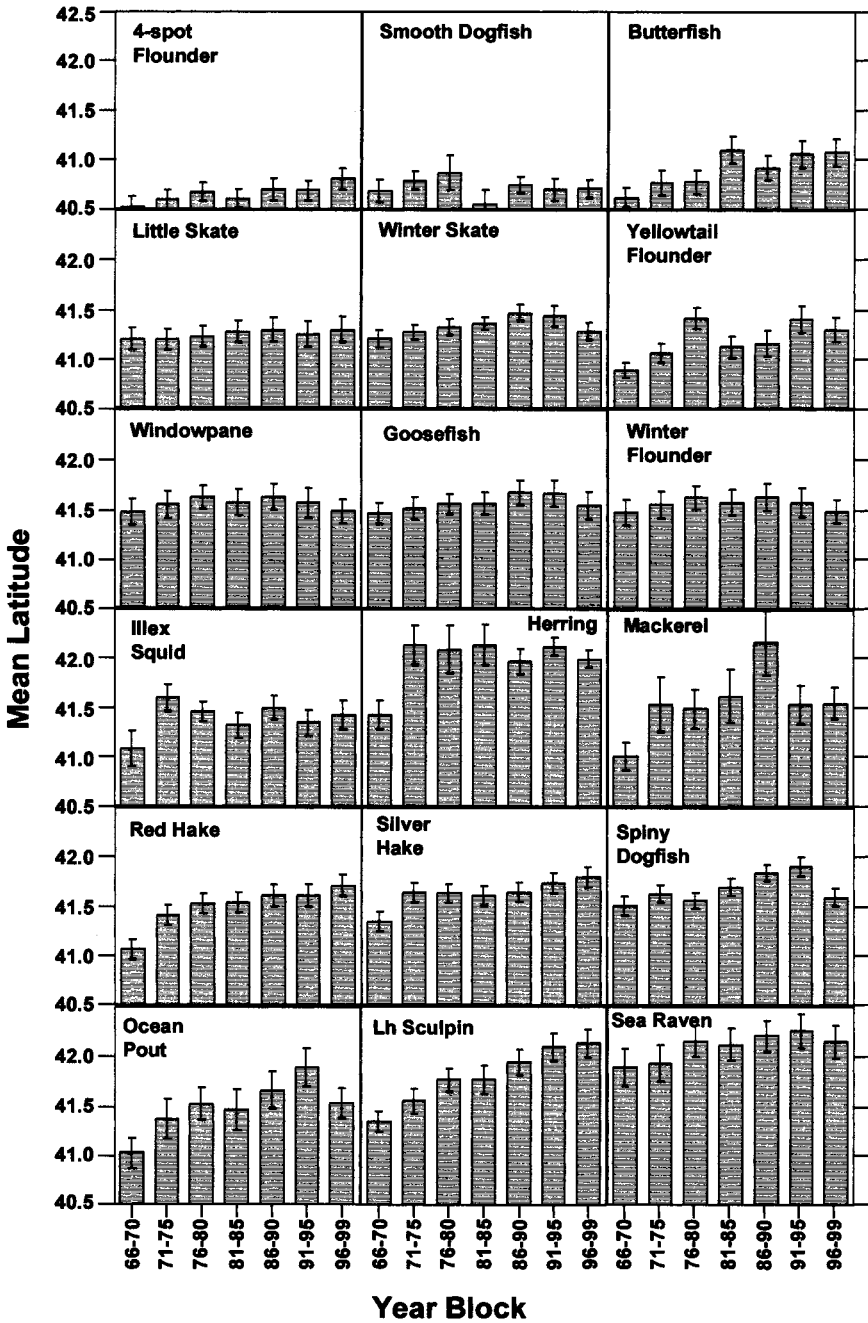


Figure 12. Mean latitude of occurrence for 18 species of fish across 5-year time blocks from 1966 to 1999. Error bars indicate 95% CI.

Georges Bank/Southern New England faunal regions while during 1986-1990 only 21% of the spiny dogfish biomass was in the southern regions and 79% of the biomass occurred in the Gulf of Maine and Scotian Shelf regions. This shift was manifested in a change of 0.5° of mean latitude (Fig. 12). Similar latitudinal shifts were not observed in many southern species (e.g., smooth dogfish, little skate, windowpane; Fig. 12) and did not occur in primarily northern and deep-water species including redfish, haddock, cod, witch flounder, and white hake (not shown).

Discussion

The spatial patterns and faunal regions in this community have remained generally stable over the last three decades despite major changes in species composition. These patterns are consistent with previous studies both within this community (Overholtz and Tyler 1985, Gabriel 1992) and in the groundfish community of the Canadian Atlantic continental shelf (Gomes et al. 1995). These generally stable patterns are related to similarities in habitat preferences among species. Spatial overlap between species on Georges Bank was strongly related to similarities in habitat preferences, particularly preferred depth and temperature ranges (Murawski and Finn 1988, Garrison 2000). As habitat characteristics, primarily temperature, change on an interannual basis, species with similar habitat preferences alter their spatial distributions in similar ways (Mountain and Murawski 1992). The distinct regional geographic boundaries in species composition observed in the current study therefore reflect spatial boundaries in habitat characteristics.

The most notable change in the northwest Atlantic groundfish community over the last three decades is the general decline in the abundance of heavily exploited species including gadids and flatfish and an increase in the abundance of less-exploited elasmobranchs, in particular spiny dogfish (Fogarty and Murawski 1998). In recent years, a large fishery for adult female spiny dogfish developed, and the stock has experienced severe declines in biomass over the last 5 years (NEFSC 1998). The changes in the biomass of spiny dogfish through time are reflected in changes its spatial distribution and the species composition within faunal regions observed in the current study. Prior to 1980, spiny dogfish was a dominant component of the biomass only in the Georges Bank/Southern New England region, and the majority of its biomass was concentrated in southern and offshore habitats. During the 1980s and early 1990s, spiny dogfish became a biomass dominant in all of the faunal regions on the northwest Atlantic continental shelf. The increase of spiny dogfish populations and its movement north into Scotian Shelf and Gulf of Maine habitats represents a major change in the trophic dynamics of this system. Spiny dogfish is a pelagic predator feeding on ctenophores and shrimp taxa in smaller size classes and pelagic fish and squids in larger sizes (Garrison and Link 2000). Spiny dogfish is among the major predators of pelagic fish biomass

in the northwest Atlantic (Overholtz et al. 1999), and it exerts a major influence on community dynamics due to its high abundance and predatory nature.

Concomitant with the increases in spiny dogfish biomass, there has been a decline in the populations of heavily exploited species, including Atlantic cod, yellowtail flounder, and haddock. These species have experienced a contraction of ranges, associated with their overall decline in abundance and have become only minor components of the fish biomass in the Georges Bank and Gulf of Maine faunal regions. Similar declines in species area with declines in population size are well documented in other fish communities (Atkinson et al. 1997). During the early 1960s, prior to the time-frame of the current study, these species were biomass and numerical dominants on Georges Bank and throughout the northwest Atlantic (Overholtz and Tyler 1985, Fogarty and Murawski 1998). Both yellowtail flounder and haddock are benthivorous species feeding upon polychaetes, amphipods, and echinoderms while Atlantic cod is a generalist predator feeding upon both pelagic and benthic invertebrates and fish in larger size classes (Garrison and Link 2000). The change from dominance by these primarily demersal species to the more pelagic spiny dogfish represents a major change in the structure of this ecosystem. In addition, spiny dogfish has replaced large Atlantic cod as the major piscivore in this community (Link and Garrison 2001).

In the last decade, the biomass estimates for small pelagic species, including Atlantic herring and mackerel, increased by nearly an order of magnitude, and this increase in biomass was accompanied by an expansion of ranges for these species. The dramatic increase in pelagic biomass influences the trophic dynamics of this community in two ways. First, small pelagic species are important prey items for the many piscivores in this community. During the period of depressed abundance of small pelagic fish, the diets of piscivores including silver hake, cod, and spiny dogfish were composed of other species and squids. As herring populations have increased and expanded into the Gulf of Maine, the diets of major piscivores have included higher proportions of herring (Link and Garrison 2001). The increase in herring biomass significantly alters the prey field available to piscivores in this system. Second, these small pelagic fish are important consumers of zooplankton, and their increased abundance may result in a greater removal of water column secondary production prior to its export to benthic communities. Herring is also a potentially important predator of larval fish, particularly haddock and cod on Georges Bank (Garrison et al. 2000). The impact of elevated pelagic biomass on the recovery of demersal fish stocks remains an important area for continuing research.

The most general change in the spatial distributions of fish species was an increase in the mean latitude of occurrence for a large number of species. These included both exploited and unexploited species, suggesting that directed fishery removals are not the major cause of this pattern. The observed northward distribution shifts suggest a community-wide re-

sponse to increases in temperature (Mountain and Murawski 1992, Murawski 1993). There has been a notable increase in bottom temperatures in the northwest Atlantic over the last three decades; the 1990s were significantly warmer than the 1960s. The majority of this temperature change occurred during the early portion of the time series (Holzwarth and Mountain 1990), and the majority of the northward shift in species distributions observed in the current study also occurred during the earlier period. While the broad changes in spatial distribution are consistent with a community-wide response to temperature change, changes in population size, geographic patterns in fishing effort, and changes in the survey sampling intensity through time may also influence the observed patterns of biomass distribution (Murawski 1993). Assessing the importance of climate variations in altering spatial distributions and the underlying mechanisms remain important areas for further investigation.

The major changes in community structure and spatial distributions associated with both fishing pressure and climate variation have important implications for the trophic dynamics in this ecosystem. This community has generally shifted from one dominated by demersal species to one dominated by more pelagic predators and planktivores (Link 1999). In addition, the changes in spatial patterns documented in the current study will influence the strength of species interactions. The northward shift observed in many species in this community along with the range expansion observed in small pelagic species influences predator and prey fields and potential competitive interactions. Continuing efforts will directly evaluate the impact of observed spatial patterns on species interactions by using spatial overlap and selectivity models to assess trophic interactions between species and compare them across the time series.

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An Empirical Analysis of Fishing Strategies Derived from Trawl Logbooks

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Extended Abstract

During a fishing trip a fisher must make a series of decisions regarding where to fish and how long to operate at each fishing location. The problem of organizing fishing operations during a trip is extremely complicated, especially in a multispecies fishery. This paper presented preliminary results from an ongoing Oregon Sea Grant project that is developing quantitative measures of fishing strategies for the Oregon trawl fishery for groundfish and evaluating intra- and interannual changes in fishing strategies with respect to fish prices and fishing regulations. The term "fishing strategy" here means the fishing gear and sequence of fishing locations selected by a fisher during a fishing trip.

Principal components analysis (PCA) was applied to trip-by-trip summary statistics derived from logbooks from a set of 28 trawlers that operated every year during 1987-1997. These boats made 9,556 of the 30,455 fishing trips (from 245 different boats) for which logbook data are available during 1987-1997. For simplicity the analysis was limited to data from these 28 trawlers for 1988, 1991, 1994, and 1997, a total of 3,635 trips. The logbook data files and corresponding landings information were provided by the Oregon Department of Fish and Wildlife, whose port agents collected logbooks each year from 77% to 85% of all groundfish trawl trips and landings receipts for all trawl landings. The logbook data were subjected to preliminary screening to identify fishing trips with incomplete information. For the data set used in this study 30 trips (0.8%) were excluded from the analysis because the logbook data had no information on tow locations, bottom depths, or durations, or because the logbooks were missing from the database. The data were also screened to identify infeasible tow starting locations (ones that were on land or that had bottom depths that were inconsistent with the reported latitude and longitude).

For the 23,581 tows from the 3,635 trips used in this study there were 337 tows (1.4%) with missing or infeasible tow starting locations.

PCA was used to transform the 23 attributes associated with each fishing trip into a set of two scores that were then examined graphically and with standard statistical methods. The PCA scores have the property that trips with similar scores have similar attributes and vice versa. The set of trip attributes were: the number of days at sea, the number of tows, the average and range of the tow durations, the average and range of bottom depths at the tow starting locations, the proportion of the tow time spent at four depth classes (1-99, 100-199, 200-299, and >300 fathoms), the proportion of tows made with bottom versus midwater trawl, the proportion of tows starting north of the return port, the proportion of tow hours that were during daylight, the distance of the first tow from the starting port, the distance of the last tow from the return port, the maximum distance from the return port, the average distance between tow starts, the proportion of tow starting locations on the current trip that also had been occupied during the most recent previous trip, and the proportion of tow starting locations occupied on trips during the previous 90, 180, 270, and 360 days. Also tabulated for each trip were auxiliary data: boat identifier, year, month, return port, and the landings of 20 species or species groups (Pacific hake, Dover sole, thornyheads, sablefish, arrowtooth flounder, Pacific ocean perch, widow rockfish, yellowtail rockfish, large rockfish, small rockfish, lingcod, petrale sole, English sole, rex sole, Pacific sanddab, miscellaneous flatfish, Pacific cod, Pacific mackerel, jack mackerel, and other). The auxiliary data were not included in the PCA of the trip attributes but were used to help interpret the PCA scores.

For the 3,635 trips examined the boats on average were at sea for 3.0 days and made 6.5 tows that lasted 3.9 hours. On average the bottom depth at the tow starting locations was 172 fathoms, 70% of the tows were made with bottom trawl gear, and 75% of the tow time was during daylight. The starting location of the first tow on a trip on average was 31 nautical miles from the departure port, the last tow was 34 nmi from the return port, and the maximum distance from the return port was 45 nmi. The average distance between tow starting locations was 8.6 nmi. On average only 18% of tow starting locations on a trip were within 5 nmi and within 5 fathoms by depth of one of the tow starting locations made by that boat during the most recent previous trip. Boats usually returned to tow starting locations that they had occupied previously. On average 47% of tows started at locations that had been occupied during the past 90 days, 54% of tows were at locations occupied during the past 180 days, 58% of tows were at locations occupied during the past 270 days, and 64% of tows were at locations occupied during the past 360 days.

PCA was applied initially to the data set for all 3,635 trips. The first and second principal components accounted for 31.4% and 17.5% of the variability in the trip attributes. Plots of the PCA scores for the first two components indicated two distinct groupings of trips. Examination of the

attribute and auxiliary data indicated that one group was composed almost entirely of trips that used midwater trawl gear, which caught widow rockfish during 1988 (86% of the trip landings by weight) and Pacific hake during 1991, 1994, and 1997 (95-99% of the trip landings by weight). A second PCA was applied to the subset of trips that used bottom trawl gear on at least one tow of each trip (2,574 trips that made 21,835 tows). For this PCA the first and second components accounted for 32.4% and 11.2% of the variability in the trip attributes. The first axis was highly negatively correlated with the proportion of tows made at locations occupied during the past 180, 270, and 360 days ($r^2 > 0.58$) and with the proportion of tow time in the 1-99 fathom depth class ($r = -0.758$). The second axis was highly correlated with the number of tows ($r = -0.674$), the maximum distance from port ($r = -0.630$), and the average tow duration ($r = 0.527$). The PCA scores in general were not strongly correlated with the auxiliary landings data. The axis 1 scores were moderately correlated with landings of the deepwater species: thornyheads ($r = 0.578$); sablefish ($r = 0.504$); and Dover sole ($r = 0.343$). The axis 2 scores were moderately correlated with the landings of Pacific ocean perch ($r = -0.431$) and Pacific cod ($r = -0.310$).

The first and second axis scores (PCA1 and PCA2) from the second PCA were analyzed using a generalized linear model (GLM) to gauge the importance as explanatory factors of the auxiliary variables boat, year, month, and port and their two-way interactions. With both sets of PCA scores the GLM analyses showed that all main effects were highly significant ($P < 0.001$). In the GLM with PCA1 the factor boat had a particularly large mean squared error and all two-way interactions were significant ($P < 0.05$), except for boat with port and month with port. In the GLM with PCA2 the factors boat and port had large mean squared errors and all two-way interactions were significant ($P < 0.05$).

Scatterplots of the PCA scores (PCA2 versus PCA1) were examined for each of the main effects in the GLM. There was a positive linear trend in the scores averaged on an annual basis, with trips from 1997 associated with larger values of PCA1 and PCA2. There was an almost-linear trend in the scores averaged by port, with trips from Coos Bay and Brookings (on the south coast of Oregon) associated with larger values of PCA1 and PCA2, and trips from Astoria (at the northern border of Oregon with Washington) associated with smaller values. Also, there was a distinct seasonal component to PCA1: trips during the winter months were associated with larger PCA1 values.

Additional analyses are planned that will examine whether changes in fish prices or trip limit regulations have had detectable effects on fishing strategies. PCA scores will be derived using the fishing trip attributes from a more complete set of the available logbook data. Also planned are analyses to identify fishing strategies that generate the greatest revenue flows for a given class of fishing boat and to determine whether boats that leave the fishery after a few years use different fishing strategies from those that remain.

Distributing Fishing Mortality in Time and Space to Prevent Overfishing

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Abstract

In this paper we describe a method for measuring the spatial and temporal distribution of fish school densities and exploitation rates. A herring purse-seiner, fishing on nonspawning feeding aggregations, and a herring gillnetter fishing on smaller, highly dense spawning aggregations, in the southern Gulf of St. Lawrence, Canada, collected the data used in this study. Four statistical methods were tested to determine the most appropriate method for density estimation from these data: inverse distance weighting, Voronoi-nearest neighborhood, arithmetic, and kriging. No differences in density estimate trends were found among the four methods and the Voronoi-nearest neighborhood method was chosen. The relationship between gillnet catch rates (kilograms per net) estimated for assessment of this stock reaches asymptotic values at lower than expected densities and was not useful for tracking daily trends in school density. Gillnet and purse-seine catch per meter searched were linearly related to density, and are likely suitable abundance indices for stock assessment estimates. An individual boat with data collected in this manner was found to be representative of the entire fleet. There was a threshold density beyond which exploitation rates remained low. This threshold provides managers with a method for identifying and eliminating spatial and temporal trends in high exploitation rates and preventing overfishing. Catch

rates, which use searching as the unit of effort, and density were found to be good indicators of high exploitation rates in the gillnet fishery.

Introduction

Two principal goals of stock assessment are to determine if fishing mortality is within conservation target levels and to maintain the spatial and temporal integrity of spawning components. A first step in achieving these goals is to provide managers with tools that would allow them to distribute fishing mortality in time and space, relative to the size of schools being harvested. For example, we may expect the spatial and temporal structure of a spawning component to be compromised if all the fishing mortality comes from one area and time, even if the overall fishing mortality is within conservation limits. If, however, the overall fishing mortality is kept within conservation limits and is distributed in proportion to the relative abundance of the various spatial and temporal components, we may expect to meet our goals. To make these relative distributions in fishing mortality, information on the spatial and temporal distribution of fish biomass in the fishing area, as well as exploitation rates on those schools, is required.

In this paper we describe a method for measuring the spatial and temporal distribution of fish school densities. This method is developed using acoustic data collected during regular fishing activity from two herring fishing fleets in the southern Gulf of St. Lawrence, Canada. Fishery information commonly used in assessments includes catch and effort information provided through logbooks, dockside monitoring, and purchase slips (Claytor and LeBlanc 1999). These sources provide indirect measures of density only on areas where fish are caught. The method we describe improves on these data sources because it provides information on densities of fish throughout the entire fishing and searching area of the fleet and not just on where fish were caught. It also enables us to test the assumptions required of these indirect measures when they are used to estimate population biomass and to determine the effect of current fishing mortality on the population. For example, scientists are often concerned that catch rates have remained high in spite of population density declines because of efficient search methods available to modern fishing fleets (Hilborn and Walters 1992). Alternatively, concerns among industry are that catch rates have been lowered because of management or market restrictions on daily catches, interference from other gear, and weather (Claytor et al. 1998). In this fishery and many others (see examples in this volume) there is increasing demand for local area assessment and management. For this to occur, knowledge of the spatial and temporal distribution of fish densities in each area is essential.

As a first step in this direction, we set the following objectives for this paper. First, determine the appropriate density estimation method for these data. Second, determine the relationship between catch per unit of effort, kilograms per net, and kilograms per meter of searching on the fishing

grounds, and density observed by boats collecting acoustic data. Third, determine the spatial and temporal distributions of exploitation rate indices and determine if they would provide managers with the necessary tools for adjusting fishing mortality in these fisheries. Fourth, determine if density and catch rates are useful indirect measures of the temporal and spatial distribution of exploitation indices.

Materials and Methods

Fishery and Fleets

The data analyzed in this paper come from two of the herring fleets participating in the fall southern Gulf of St. Lawrence herring fishery. This fishery consists of several gillnet fleets with a total of about 1,500 licenses of which about 600-1,000 are active, and a purse-seine fleet with six active boats. The gillnet fleets fish inshore on spawning aggregations in five areas of the southern Gulf of St. Lawrence. Their allocation is about 80% of the total quota for the area and recent average landings range from 30,000 to 60,000 t. Data from the gillnet fleet were collected from 7 September to 30 September 1997 from the Pictou, Nova Scotia area, by a commercial boat, the *Broke Again* (Fig. 1A). In this area, the fleet consists of about 120 boats. The purse-seine fleet fall fishery occurs on nonspawning feeding aggregations in the Chaleur Bay area and recent average landings have ranged from 6,000 to 16,000 t. Data from the purse-seine fleet were collected from 23 August to 20 October 1995 by a commercial boat, the *Gemini* (Fig. 1B).

Acoustic Data Collection and Calibration

The acoustic system employed on the gillnet boat *Broke Again* consisted of a 120-kHz transducer with a 14° beam angle, a transceiver (Femto DE9320 digital echo sounder), and a computer for logging data. The digitizing system (Femto) used on the purse-seiner was identical to that used during acoustic research surveys in the southern Gulf of St. Lawrence (Claytor and LeBlanc 1999) and was attached to a 50-kHz Furuno FCV120 sounder. These systems are analogous to a black box on an airplane in that the captain of the vessel turns the unit on when leaving port and off when returning and digital acoustic data are continually recorded during the fishing trip (Claytor et al. 1999). The software used to process and collect the acoustic data was the Hydroacoustic Data Processing System (HDPS, Femto Electronics). Calibration of the acoustic hardware consisted of a ball and time varied gain calibration and proceeded as described by Clay and Claytor (1998).

Acoustic Data Preparation

The fishing track was identified by recording latitude and longitude once per second using Garmin 45XL portable GPS units. The acoustic signal at every fourth navigational position fix was retained to determine biomass

density along the fishing track. Selection at every fourth fix was done to reduce the size of the data set and to remove small fluctuations in the fishing track because of errors in GPS satellite signals. Latitude and longitude coordinates for each remaining fix were converted to distances (meters) from a common reference (45° latitude, 67° longitude) taking into account the curvature of the earth.

The activities along each fishing track were then identified as traversing (traveling to or from port to the fishing grounds), searching which included looking for fish and setting the net on the fishing grounds, hauling the net, and other activities that were not part of the directed fishing, such as waiting in port and unloading the catch.

Once these activities were identified the fishing track was divided into equal 100-m increments by activity. The area backscatter coefficients at each of these positions were linearized and a distance weighted average of these linearized coefficients along each 100-m increment was calculated. This calculation was made by multiplying the distance traveled associated with each coefficient times the value of the coefficient. The sum of these values was then divided by the length of the interval, which was 100 m. The center of each increment became the data point for subsequent analyses. Increments at the end of an activity were less than 100 m and their weighted average and center was based on the length of these increments to the nearest meter.

The next step in the analysis was to estimate target strength of the acoustic signals during each night of data collection so that biomass abundance indices could be estimated. Samples for estimating length and weight of the acoustically recorded herring for gillnet fishing trips were collected from experimental gillnets fished in the Nova Scotia area of the southern Gulf of St. Lawrence on 11 and 18 September 1997. Net construction and sampling protocols are described in Claytor et al. (1998). Samples for estimating length and weight of the acoustically recorded herring for purse-seine fishing trips came from daily sampling from the *Gemini* by shipboard observers (Claytor et al. 1996). The length-weight relationship from these samples estimated the target strength using Foote's (1987) formula:

$$\text{Target Strength} = (20 \times \log_{10} \text{length [cm]} - 71.9) - 10 \times \log_{10} \text{weight (kg)}$$

The density was estimated by dividing the linearized backscatter coefficient by the linearized target strength (Claytor et al. 1998).

Spatial Analysis

Only the portion of the fishing track associated with searching and setting the net (see above) was selected for spatial analysis. Searching was generally triggered at densities ≥ 0.0625 kg per m² or about 1/4 herring per m² and setting the net occurred only in areas that had been searched. Hauling the net was always associated with setting the net, but this activity created a lot of debris in the water and these data were not suitable for biomass

estimation and were eliminated. A polygon drawn around the boundary of the searching and setting data points defined the area for spatial analysis and biomass estimation (Fig. 1C). The density estimate used in all analyses was the biomass estimate within the polygon divided by the area of the polygon.

The next step in preparing the data for biomass estimation was to aggregate identical data points. This aggregation was done by averaging all points that were within 1 m of each other to form a new data point. All mapping, data selection, and aggregation were done using Mapinfo (1997) and Vertical Mapper (1998) routines.

Inverse Distance Weighting

Inverse distance weighting (IDW) is an interpolation method that gives more weight to the closest samples and decreasing weight as samples become further from the estimation point. Vertical Mapper was used to estimate biomass by this method. The cell size was 10 m and search and display distances were the defaults, based on a percentage of the total map area, provided by the software. The exponent which described the decay of influence between points was kept at the default of 2. A maximum of 25 points were analyzed for each grid node. The number of zones and the minimum number of points were kept at 1. Inverse distance weighting provides maximum estimates below and minimum estimates above those observed.

Voronoi-Nearest Neighbor Analysis

Nearest neighborhood interpolation forms a region around each point so that the boundary of the region is the perpendicular bisector between a point and each of its nearest neighbors. Vertical Mapper builds these regions around data points using Delaunay triangulation. The network of polygons generated is called a Voronoi diagram. The area of the region or polygon is then the weight for the point. The Voronoi-nearest neighborhood method maintains observed maximum and minimum values.

Arithmetic

The arithmetic method assumes that all points have equal weight in the estimation and is simply the arithmetic average of all the points within the polygon.

Kriging

The spatial structure of the distribution in each group was examined using variograms as described by Isaaks and Srivastava (1989). A set of eight variograms was calculated from 0° to 157.5° at 22.5° intervals. Initially the lag distance was set to the average distance between the data points. In some cases, this assumption about the initial lag distance produced variograms with little or no spatial structure. These cases were easily rec-

ognized because the nugget value was equal to or similar to the sill and the model showed no improvement from using the mean. When this situation occurred, the lag distance was reduced or increased until variograms that identified a spatial structure were obtained. Lag tolerances were set to 50% of the lag spacing. Angular tolerance was generally at 45° but in some cases it was reduced to 30° to produce variograms that provided a better spatial description. The variogram for each angle was plotted and the highest variogram value that occurred was identified for each angle. The distance corresponding to this value at each angle was then plotted on a compass plot to determine the spatial orientation of the data points. This plot was analogous to the rose diagrams discussed in Isaaks and Srivastava (1989). When there was no overall directionality identified or all the distances were similar, isotropy was assumed and an omnidirectional variogram was modeled for kriging. When directionality was indicated, an anisotropic variogram was modeled. These analyses were performed using Variowin (Pannatier 1996). A geometric variogram, with a common sill but differing ranges, was assumed for all anisotropic analyses.

The final variogram modeling and kriging were as described by Hébert et al. (2000). The direction of the variogram determined above was imposed on the variogram model assuming a spherical model of the form:

$$\text{Variogram} = Co + C \times [(1.5 \times (h/a) - (0.5 \times (h/a)^3)] \text{ (Cressie 1991),}$$

where Co = nugget; C = sill; h = distance; and a = range

The results of the variogram modeling were used to obtain ordinary kriging estimates for each region and school structure analyzed. Kriging is a method of estimating spatial data such that points nearest the point of interest receive the highest weight and those most distant receive the least weight. These weights are linear combinations of the available data. The parameters of the variogram are used to assign these weights. Kriging has the advantage over the other methods described above because it is a best linear unbiased estimator and confidence intervals are readily estimated (Isaaks and Srivastava 1989).

Stock Assessment Parameters

The stock assessment parameters estimated for analysis were: density of the schools on the fishing grounds as defined above, gillnet catch per unit of effort (CPUE) defined as kilograms per net, gillnet and purse-seine catch per meter searched with searching as defined above, and an exploitation rate index (ER) defined as the reported catch per biomass estimate from the school as defined above.

The source of catch data for the gillnet fleet was the 100% dockside monitoring program in place in the gillnet fishery in 1997. The number of nets used each night by the *Broke Again*, as reported to us each night by the captain, was always 5. The average number of nets used by all other gillnetters in the area was also 5 as estimated by a phone survey conducted

each year for the annual assessment of this stock (Claytor and LeBlanc 1999). The source of catch data for the purse-seiner was the purchase slip sales recorded at dockside.

Statistical Analyses

Linear and nonlinear regression techniques, using SAS (1999) procedures, were used to examine the relationships among the four estimation methods, between density and distance searched, and between catch rate indices and density. A P -value < 0.05 was considered significant.

The relationship between CPUE and density was examined using a von Bertalanffy type function and a standard linear regression. A zero intercept was forced in each case because at zero density the catch must also be zero. The von Bertalanffy function followed the additive error structure as defined by Quinn and Deriso (1999) as:

$$CPUE_i = CPUE_{inf} \{1 - \exp(-k N_i)\} + e_i$$

In this form, $CPUE_{inf}$ is an asymptotic value, k describes the rate at which the asymptote is reached, and N_i is density at each observed density i .

The linear regression model was defined simply as:

$$CPUE_i = b N_i + e_i$$

Parameters were estimated with and without logarithmic transformation.

A nonlinear exponential model (Exp) and linear reciprocal model were used to determine the relationship between density and distance searched on the fishing grounds. The exponential model was :

$$N_i = b_0 \exp(b_1 \times \text{Distance}) + e_i$$

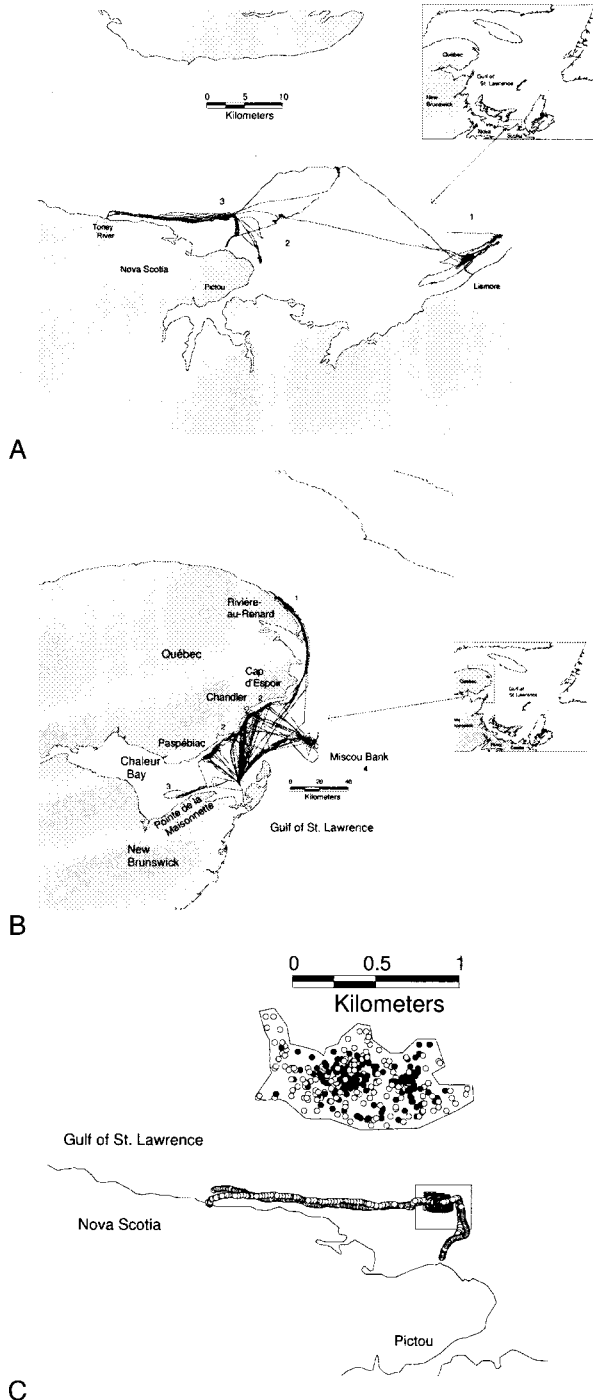
The reciprocal model was:

$$N_i = b_0 + b_1 1/\text{Distance} + e_i$$

The von Bertalanffy and linear models were used to determine the relationship between catch per meter and density as described above for purse-seine and gillnet boats.

In these analyses, the density estimated from the data collected by the *Broke Again* and the *Gemini* were compared to their individual landings as well as to those of all the boats participating in each of their fleets. Regions for the gillnet fishery are defined as: 1, easternmost zone; 2, midzone; and 3, the westernmost zone of the Pictou, Nova Scotia fishing area (Fig. 1A). Regions for the purse-seine fishery are defined as: 1, Rivière-au-Renard; 2, Gaspé side of Chaleur Bay; 3, Pointe de la Maisonnnette; and 4, Miscou Bank (Fig. 1B).

Figure 1. (A) Fishing and searching tracks for Pictou area gillnetter, Broke Again, collecting acoustic data from 7 September to 30 September 1997. Key to map regions: 1, Eastern area; 2, Mid-zone; 3, Western area. (B) Fishing and searching tracks for Chaleur Bay area purse-seiner, Gemini, collecting acoustic data from 23 August to 20 October 1995. Key to map regions: 1, Rivière-au-Renard; 2, Gaspé side of Chaleur Bay; 3, Pointe de la Maisonnette; and 4, Miscou Bank. (C) An example of an identified herring school from Pictou area gillnetter data collection, 26 September 1997. Solid squares are fish densities ≥ 0.0625 kg per m^2 , open squares are fish densities < 0.0625 kg per m^2 . School is outlined by polygon used to delineate school area.



Results

Biomass estimates made by each of the four estimation methods were all significantly correlated ($P < 0.001$, $r^2 > 0.96$). Differences in estimates were the least between the IDW and Voronoi-nearest neighbor methods. Differences were greatest for all comparisons with the arithmetic method.

In the results, "Gillnet Boat" refers to catch and effort data only from the *Broke Again*, the gillnetter boat used to collect the acoustic data. "All Gillnet Boats" refers to catch and effort data from all the boats participating in the Pictou, Nova Scotia fishery. "Purse-Seine Boat" refers to catch and effort data from the *Gemini*, the purse-seiner used to collect the acoustic data. "Purse-Seine Fleet" refers to all six purse-seine boats participating in this fishery. In each of these cases, the distances searched and the estimated density of schools applies only to the boats collecting the acoustic data.

The $CPUE_{inf}$ value for the Gillnet Boat was larger than the $CPUE_{inf}$ value for All Gillnet Boats. The Gillnet Boat also reached its $CPUE_{inf}$ asymptote before All Gillnet Boats (Fig. 2A).

There was a significant curvilinear relationship ($P < 0.005$) between density and distance searched on the fishing grounds for the Gillnet Boat and Purse-Seine Boat. The fits for the exponential and reciprocal models were similar for each data set (Table 1, Fig. 2B,C).

Linear and von Bertalanffy models significantly explained the relationship between catch per meter and density ($P < 0.001$) for Purse-Seine and Gillnet Boat models. The linear model provided the best fit for the Purse-Seine Boat data and the von Bertalanffy model for the Gillnet data and purse-seine fleet data (Table 1, Fig. 2D,E).

The reciprocal model significantly explained the relationship between exploitation rate (ER) and density for each of the purse-seine and gillnet fleets ($P < 0.001$) (Table 1, Fig. 2F). These results indicate that ER increases as density decreases.

All above-average exploitation rates for the Purse-Seine Fleet occurred after 13 September 1995 (Fig. 3A,B). All high exploitation rates in the gillnet fishery occurred at the beginning and end of the season when densities were lowest (Fig. 3C,D).

Discussion

In this study we sought to determine the relative trends and relationships between density and key stock assessment parameters such as catch rates and exploitation rates. The high correlation among the estimation methods indicates that the method used to estimate density will not affect conclusions regarding these relative relationships. One reason for this high correlation may be the ratio of distance surveyed to survey area compared to other survey methods. For example, during acoustic surveys of the southern Gulf of St. Lawrence the maximum sampling rate does not exceed 0.50 km

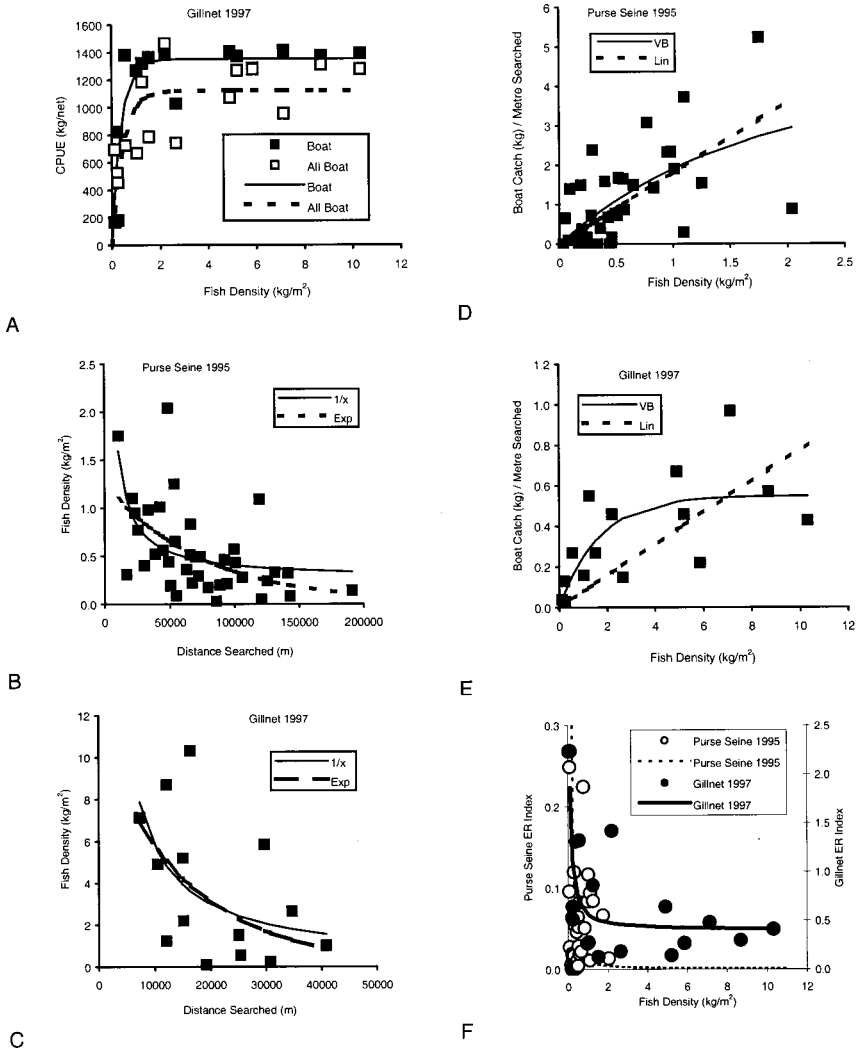


Figure 2. (A) Scatterplots and regression lines for relationship between gillnetter catch rates (CPUE, kg per net) from boat collecting acoustic data and all boats in the Pictou gillnet fishery. (B, C) Scatterplot and regression lines for relationship between fish density and distance searched for fish schools by (B) purse-seine and (C) gillnet boat collecting acoustic data. (D, E) Scatterplots and regression lines for relationship between catch rates (kg per meter searched) and fish density for (D) purse-seine and (E) gillnet boat collecting acoustic data. (F) Scatterplots and regression lines for relationship between exploitation rate index (ER) and fish density for purse-seine and gillnet boat collecting acoustic data.

Table 1. Sum of squared residual (SSR) values for indicated regression models.

Relationship	Model	Gillnet Boat	All Gill-net Boats	Purse-Seine Boat	Purse-Seine Fleet
Density-Distance	Exponential	114		5.52	
	Reciprocal	113		5.48	
	Figure reference	Fig. 2C		Fig. 2B	
Density-Cat/Met	von Bertalanffy	0.51	3,770	33	1,090
	Linear	0.85	4,480	31	1,210
	Figure reference	Fig. 2E		Fig. 2D	
Density-ER	Exponential		3,700,000		0.17
	Reciprocal		4,200,000		0.16
	Figure reference		Fig. 2F		Fig. 2F

Figure references are provided. Cat/Met is catch per meter searched, ER is exploitation rate.

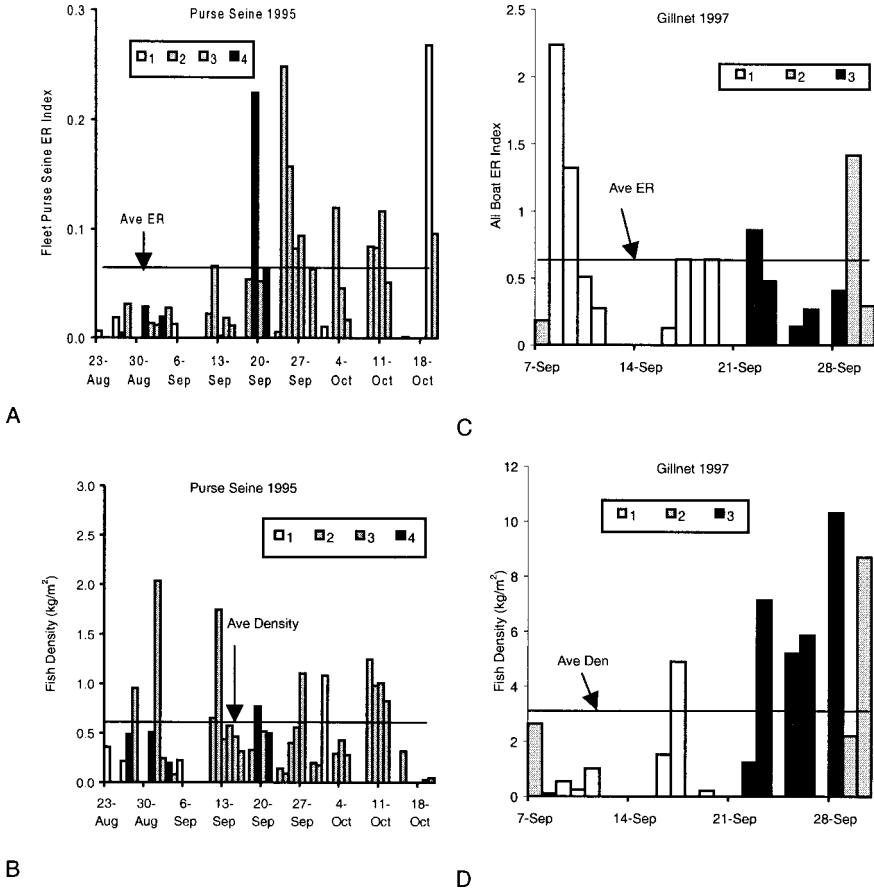


Figure 3. Distribution over time by region of ER and fish density for (A, B) purse-seiner and (C, D) gillnet collected data. Regions are those defined in Fig. 1A, B.

of transect surveyed per km² of survey area (Claytor and LeBlanc 1999). In this study, 2.4 km were surveyed per km² of fishing area for the purse-seine boat, and 55 km per km² of fishing area for the gillnet boat. This comparison of survey length is important because each 100 m is a data point. Transects for acoustic and trawl surveys in the southern Gulf of St. Lawrence are typically several kilometers apart (Claytor and LeBlanc 1999). This high sampling rate means that there is less interpolation among the points than has been encountered in other investigations .

An important consideration in the selection of an estimation method is that it accounts for the clustering of data samples. Samples which are close together must have their influence reduced in the overall estimate because they do not represent as large an area as samples that are more distant from one another. The Voronoi, kriging, and IDW methods account for distances between samples. The arithmetic method, which is the unweighted average of all the points, does not take clustering effects into account and it is the reason why this method differs the most from each of the other methods (Isaaks and Srivastava 1989). For these data and for the purposes of our investigation, any of the three declustering methods would be sufficient and the Voronoi method was chosen primarily for convenience of implementation.

The nightly limit imposed on each boat in the gillnet fishery is similar to the estimated asymptotic CPUE of 1,353 kg per net for the gillnet boat model (Fig. 2A). The boat collecting the acoustic data used 5 nets per night. The 7,000 kg nightly fishing limit then corresponds to a CPUE of 1,400 kg per net. The maximum CPUE was reached at a density of about 1 kg per m² while the densities observed during the fishing season ranged up to 10 kg per m² (Fig. 2A). The maximum CPUE for the entire fleet was lower than for the individual collecting the acoustic data but was still reached at a density of about 1 kg per m² (Fig. 2A). These results indicate there is little change in these CPUE over most of the densities observed during the fishing season and they would be of limited use in tracking daily abundance trends in this fishery. Many fisheries depend upon voluntary logbook programs to obtain these types of catch rate information and it is often the individuals with the highest interest and highest catch rates that participate in these programs. If they are able to consistently catch their nightly limits regardless of density, then relatively little information is being obtained from such logbook CPUE for the assessment of the stock. As a result, the effects of nightly limits whether because of boat capacity, management, or market quotas, must be considered in interpreting fluctuation in CPUE for assessment purposes.

Other problems in using these types of data in assessment models may result from nonlinear relationships between CPUE and abundance. Many assessment models require a linear relationship (Hilborn and Walters 1992) and logarithmic transformations are often used to meet this requirement. In our results, no linear relationship was obtained for the gillnet CPUE, even after log-transformation.

The purse-seine CPUE (catch per set) shows no relationship with density. This may be explained by the importance of search, effort, and catching efficiency for this type of gear, which results generally in poor relationships between CPUE and abundance. Consequently, CPUE indices, defined as catch per net in the gillnet fishery or catch per set in the purse-seine fishery, are not useful indices for tracking daily population trends and exploitation rates.

A principal objective of this study has been to provide managers with a tool for identifying and eliminating high exploitation rates as a step in preventing overfishing. The relationship between exploitation rate and density implies there is a threshold density beyond which there will be no change in exploitation rate. The threshold may be a function of the boat limit and may be different if there were no nightly limits, but we have not tested this hypothesis. Nevertheless, exploitation rates that are considerably above average occur only at low densities for both types of fleets. If these exploitation rates are restricted in time and space, they could be eliminated by reduced or reallocation of effort by managers. For example, the gillnet fishery in 1997 was scheduled to open on 1 September. The individuals fishing in the area voluntarily delayed their season because of low densities observed during acoustic surveys conducted during the first week of September. This delay no doubt had the effect of eliminating other high exploitation rates from this fishery during 1997.

This type of acoustic data may not be easy to collect and analyze for all laboratories. Thus, we investigated whether CPUE, kg per net, or catch per meter would be useful indirect measures of temporal trends in exploitation rates. There was a significant relationship between catch per meter and density for both fleets. As a result, where trends in density and exploitation rate occurred it would be expected that catch per meter could be used as an indirect measure of temporal trends in exploitation rate. Gillnet CPUE (kg per net) was below average at the beginning of the season, but there was little contrast between early and late season kg per net CPUE and they are unlikely to be a useful tool for managers to identify high in-season exploitation rates.

Throughout this paper we have restricted our interpretations of acoustic biomass estimates to those of relative rather than absolute estimates. Some of the factors that preclude an absolute biomass interpretation are: the variability of backscattering in high target concentrations, the relationship between target strength and fish size, vessel avoidance, and acoustic extinction from near-surface reverberation (MacLennan and Simmonds 1992, Clay and Claytor 1998, Fréon and Misund 1999). The fisheries we examined occur over a short period of time and on a single species in particular phases of its life history, either as spawning or feeding aggregations. As a result, our estimates are likely to be relatively consistent and while we cannot claim that we have estimates of absolute biomass of the schools, spatial and temporal changes in exploitation rate in these fisheries may be identified from changes in relative indices.

Herring fisheries in the southern Gulf of St. Lawrence occur on several spawning beds at the same time. The simultaneous occurrence of these fisheries makes it impractical, with current resources, to use these trends for making in-season adjustments in management plans. Thus, we view the identification of spatial and temporal trends in exploitation rates as part of an annual stock assessment process. This process would be used to derive decision rules that govern the fishery during the season (Claytor 2000). The success of these rules in distributing exploitation rates, relative to the size of schools being fished, would be evaluated at the end of the season. This evaluation would subsequently form the basis for advising on changes in decision rules. We expect that the greatest potential for using these analyses for in-season management occurs where a single fleet sequentially harvests a series of stock components in time and space.

Collecting acoustic data and information on searching effort has several advantages over more traditional forms of data collection for fisheries stock assessments. They provide marked improvement over kg per net indices, particularly when there are daily or trip limits on catches resulting from regulatory, market, boat capacity, or environmental sources. These techniques apply to a wide variety of fisheries where the species of interest is detectable by acoustic methods either as schools or individuals and are particularly suitable for single species pelagic fisheries.

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In-Season Spatial Modeling of the Chesapeake Bay Blue Crab Fishery

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Abstract

The Chesapeake Bay blue crab resource is characterized by a high degree of natural variability, which masks structural relationships between harvests and populations when considered on an annual basis. However, within a fishing season there appears to be statistically detectable relationships between harvests of different market classes of crabs in both a spatial and temporal dimension. These relationships are statistically modeled and the parameter estimates are used as input to an optimization model of harvest. By adjusting effort and landings by time and area, fishermen can achieve higher revenues from the same biomass and level of effort. The lack of sufficiently long time series data containing appropriate spatial information is the major constraint to applying this approach.

Introduction

Blue crab (*Callinectes sapidus*) is currently the most valuable product harvested from the Chesapeake Bay. In 1998, the total reported Chesapeake Bay harvest was 65.5 million pounds, with an ex-vessel value of \$70.7 million. The states of Maryland and Virginia attempt to manage the harvest with a complex set of regulations which include size limits, cull rings in crab pots, restrictions on fishing days, hours, amount of gear that can be used, where gear can be placed, license limitation, etc. There is little, if any, published evidence to demonstrate that this set of rules contributes to the stated management goals of optimizing long-term use of the resource (CBP 1997).

Recent concerns have focused on the health of the Chesapeake Bay crab population. To address this, a major stock assessment was undertaken of the blue crab resource to determine the status of the stock, and determine whether additional harvest restrictions are necessary (Rugolo

et al. 1997). The results of the stock assessment have generated a good deal of controversy regarding their interpretation. Part of the controversy stems from the sensitivity of model results to parameterization of the stock assessment model. For example, the estimates of natural mortality used in the Rugolo model require an assumption regarding the theoretical maximum age it is assumed crabs can live to. The current range being debated, 4-8 years, yields very different results in the model about whether or not the resource is currently biologically overfished. The issue is not easily resolved because of the difficulty in aging and tagging blue crabs, or using other methods to estimate natural mortality.

Focus on this level of detail about the stock assessment model ignores a major factor in crab population dynamics, which is that random climatic and oceanographic factors dominate the population dynamics of the resource and obscure the population relationships that are explicit in the stock assessment modeling. Consequently, when compared with actual data, the models do a poor job of predicting how regulations change current harvest and the ultimate impact on future populations of blue crabs and their harvest from the bay. Recruitment to the blue crab fishery, which occurs throughout the year in the Chesapeake Bay, is a random variable that up to this point cannot be accurately predicted from year to year using standard stock assessment techniques that rely only on stock-recruitment relationships. When faced with an inability to link recruitment to spawning stock biomass, the standard approach for fishery biologists is to explore yield-per-recruit relationships (Thompson and Bell 1934, Beverton and Holt 1957). The focus is therefore on in-season management, obtaining the greatest value from the given availability of crabs. However, yield-per-recruit models still require estimates of population parameters such as natural mortality, growth, and gear selectivity, which can have a large degree of uncertainty. For example, in trying to characterize crab growth Smith (1997) developed a complex model of crab molting related to temperature exposure over time (degree days). Despite this level of uncertainty, Miller and Houde (1998) recently estimated a deterministic yield-per-recruit model for Chesapeake Bay blue crab.

As an alternative to the numerical modeling approaches discussed above, this study acknowledges the inherent random nature of blue crab abundance throughout its life cycle in Chesapeake Bay. By taking a more statistically oriented approach, we address the inability to adequately capture the structural relationships that exist in the blue crab population and thus rely on a reduced form approach to help predict consequences of regulatory changes. The approach also reflects the heterogeneous nature of the crab fishery, which results from the differential migration of crabs throughout the bay during the harvest season, and the distribution of fishing and processing industries that have developed around this migration pattern. Spatial allocation of fishing effort is guided by the spatial distribution of fish abundance, and this appears to be the case in the Chesapeake Bay blue crab fishery.

Similar economic approaches to in-season fisheries management issues were studied by Önal (1996), who used multilevel optimization techniques to study sequential exploitation in the Gulf of Mexico shrimp fishery, and Criddle (1996), who simulated Yukon River salmon fisheries as a Markov process. Sequential exploitation refers to the fact that in these species, as in blue crab, exploitation at a particular time and place interacts with exploitation of the same stock at another time and place. The present study more closely resembles Criddle's approach but differs from both previous studies in that it relies on statistical modeling of the production relationships. Another major difference with the Önal and Criddle studies is that the sequential nature of the shrimp and salmon fisheries is essentially unidirectional. For example, salmon swim upstream and a negative relationship is expected between downstream harvest and upstream availability of fish. Blue crab migration is more complex than these species during the fishing season and differs for males and females.

The basic approach in this paper is to statistically relate harvest of different classes of crabs in a given segment of Chesapeake Bay in a given month to harvests of related classes of crabs in other parts of the bay in later months. Classes of crabs refer to the different market categories reported in the Maryland landings data: #1 males; #2 males; females; mixed; and soft and peeler. For example, the harvest of #2 male crabs in the mainstem portion of the bay is postulated to have a negative effect on the harvest of #1 male crabs in a tributary of the bay in future months, since the #2 crabs that are not harvested or do not succumb to natural mortality eventually molt to become #1 crabs. Since we can observe the harvests of the different size of crabs at different times, it is possible to model this relationship statistically without knowing the explicit underlying biological relationships, such as the specific mortality, growth (molting), or migration components. Since the different crab classes have different market demands and the demand varies by season, the profitability of harvest will differ depending on the harvest pattern. Once these production relationships and market demands are estimated, it is possible to optimize the system by controlling harvest of crab classes during the season. The challenge is to utilize the time series and spatial nature of the crab harvest data to improve the efficiency of estimates of the production relationships between an area at one period of time to another area at another period of time. In particular, the portion of the variability that is correlated across time and space is expected to contain much of the information explaining variability in catches.

In the following section, the general framework for an in-season harvest model is developed. This is followed by development of a model that is estimatable given current data limitations. Some discussion of the econometric issues that may arise in performing the model estimation is provided. Since this is a work in progress, an empirical example is included to demonstrate the utility of the approach, but more work is needed to obtain a working model that can be used for management purposes.

An Econometric In-Season Harvest Model

Traditionally, the approach to modeling the blue crab fishery would assume some fishery production function:

$$H_{t,i,j} = f(E_{t,i}, X_{t,i,j}) \quad (1)$$

where $H_{t,i,j}$ is the harvest in time period t , i indexes the area of harvest, and j is the market class of crab. $E_{t,i}$ is a measure of fishing effort such as number of crab pots fished and $X_{t,i,j}$ is the fishable population size.

The dynamics of the population are implicit in the relationship between current population size and the population in the previous time period (Conrad and Clark 1987):

$$X_{t,i,j,k} = g(X_{t-1,i,j,k}, H_{t-1,i,j,k}) \quad (2)$$

The $g()$ function would typically be related to natural mortality, growth, migration, and recruitment patterns. However, because of the predominance of random factors that affect mortality and recruitment in the crab population, the function should contain an error term making population at time a random variable. For the Chesapeake Bay blue crab fishery, when the time step is annual the error term is very large relative to the non-stochastic part of the function, so that the large error tends to mask whatever structural relationship is present. When it is concluded that for Chesapeake Bay blue crab there is no stock recruitment relationship (Miller and Houde 1998), it is this large error term that is being observed. In contrast, if the time step being modeled is less than a year, it may be that the error term is smaller relative to the structural dynamics. Thus, it may be possible to detect the influence of harvest at a particular area and time period on subsequent population and harvest levels in the same and other areas. We will be testing to see if that is the case in the empirical section of this paper.

In addition to the statistical approach mentioned above, another difference in the approach taken in this paper with typical fisheries models is the inclusion of the area index (i) for the stock. Stocks are usually managed as a unit, and the spatial distribution of the population is typically not a major factor in allocation of harvest under a management regime unless the stock crosses state or international boundaries. In our model, where the harvest takes place has important ramifications because it may have an effect on the relative abundance of crabs in other market categories in other areas, and also due to the fact that different segments of the crab processing industry have located around traditional harvest areas. Shifting harvest patterns spatially, will affect the costs of these operations that will be reflected in their derived demands for different market categories of crabs.

Developing an Estimatable Econometric Model of Crab Harvest

A biological model of in-season blue crab harvest would attempt to estimate crab growth, molting, mortality, and net migration. Given the lack of quantification of most of these factors for Chesapeake Bay blue crab, we attempt to develop a reduced form econometric model that can be estimated with only existing data on crab harvests, effort, and estimates of beginning season crab stock size. Although the data is available with greater geographic resolution, to keep the model relatively simple, we divide the Maryland portion of Chesapeake Bay and its tributaries into 6 areas, indexed as $i = 1-6$ (Fig. 1). The mainstem of the bay is made up of areas 1, 2, and 3, going generally from north to south. The tributaries to each of the mainstem areas are labeled 4-6, going from north to south. An additional area, 7, represents the southern boundary of the area, the Virginia portion of Chesapeake Bay. Because of a lack of corresponding spatial and market class specific harvest data for the Virginia portion of the Chesapeake Bay, only Maryland areas are included in our model even though the blue crab in the Chesapeake is considered a single stock. In the initial wintertime preharvest period $t = 0$, there are crabs in all areas. We model three subsequent periods: spring, summer, and fall ($t = 1-3$). Harvest data are available on a monthly basis, but combining into seasons reduces the number of parameters we must estimate.

Ideally, we would like to represent harvests as a nonlinear function of effort and stocks. However, given the short time periods involved, a linear approximation of a more complicated function may fit reasonably well. Therefore, for each time period, t , and each area, i , the harvest function is approximated as follows:

$$H_{t,i} = \alpha_0 + \alpha_1 E_{t,i} + \alpha_2 X_{t-1,i} + \varepsilon_{t,i}. \quad (3)$$

At this point, we ignore crab market categories to keep the notation simple. Harvests and effort are observable, but the stock of crabs at time t in area i is not observable, so we can not yet estimate this harvest equation. However, we do have data on initial stocks of crabs by area ($X_{0,i}$) from a winter dredge crab survey. Since we can expect that crab stocks in various areas will be related over time, we can use this information to transform equation 3 so that it only contains observable variables.

For example, in period 1 and area 1:

$$X_{1,1} = \sum_{s=1}^6 \gamma_{1,1,s} X_{0,s} - \beta H_{1,1} + \eta_{1,1}. \quad (4)$$

Harvests in period 1 and area 1 ($H_{1,1}$) result in a decrease in the stock, where we would expect the coefficient β to be equal to 1. However, we allow for the possibility that β is other than 1 due to misreporting of har-

vests and/or incidental mortality proportional to the actual harvest. Reductions also occur because of migration out of the area and because of natural mortality, while stock in area 1 increases because of migrations into the area from other areas and recruitment into the fishery due to molting. In the above, $\gamma_{1,1,s}$ is the transition parameter that captures the net effect of these unknown population processes, where the subscript s indexes the fishing area of interaction. Finally, η is a stochastic term indexed by time period and area, capturing the fact that the relationship is not perfectly specified.

Expressions for the stock size in periods 1 and 2 are more complicated because multiple period substitutions need to be made to represent the current stock being fished as a function of only the stock in period 0 and harvests in previous time periods. Once these substitutions are made, the new expressions for stock can then be substituted back into equation 3 to yield:

$$H_{1,i} = \alpha_0 + \alpha_1 E_{1,i} + \alpha_2 X_{0,i} + \varepsilon_{1,i};$$

$$H_{2,i} = \alpha_0 + \alpha_1 E_{2,i} - \alpha_2 \beta H_{1,i} + \alpha_2 \sum_{s=1}^6 \gamma_{1,i,s} X_{0,i} + \tilde{\varepsilon}_{3,i}; \quad (5)$$

$$H_{3,i} = \alpha_0 + \alpha_1 E_{3,i} - \alpha_2 \beta H_{2,i} + \alpha_2 \sum_{r=1}^6 \gamma_{2,r,s} H_{1,r} + \alpha_2 \sum_{r=1}^6 \sum_{s=1}^6 \gamma_{1,r,s} \gamma_{2,i,s} X_{0,r} + \tilde{\varepsilon}_{3,i}.$$

where $\tilde{\varepsilon}(2,i) = \alpha_2 \eta(1,i) + \varepsilon(2,i)$ and $\tilde{\varepsilon}(3,i) = \alpha_2 \tilde{\eta}(2,i) + \varepsilon(2,i)$.

Now, each equation is a function only of observable variables: effort, previous harvests, and period 0 stocks.

Estimating the equations in (5) above involves several econometric difficulties. One is that effort, although observable, may be an endogenous variable in the system. Using an instrumental variables approach, effort, $E_{t,p}$ can be represented as a function of previous prices and previous yields in area i . The latter can be proxied by $X_{t-1,i}$, so:

$$E_{t,i} = \lambda_0 + \lambda_1 P_{t-1} + \lambda_2 X_{t-1,i} + \mu_{t,i} \quad (6)$$

where we would need to substitute as in equation 4 to restate the $X_{t-1,i}$ in terms of observable variables. Alternatively, we could assume that effort is exogenous, predetermined by regulation and the fact that the fishery is considered highly overcapitalized with no alternative use for the fishing effort. This latter assumption is the one that we maintain in the estimation below.

Another econometric issue is the number of parameters to be estimated relative to the length of the available data series (see discussion on data below). A way to address that problem is to set some of the parameters to zero based on a priori knowledge or assumptions about the crab

resource. For example, we can assume that the transition parameters are zero for all non-adjacent areas. This may be a reasonable assumption based on the little information that is available about crab migration and residence times in different river systems (Hines et al. 1995).

Another econometric issue that we do not deal with within the scope of this paper has to do with the error structure. We have written the errors as if they were simple errors in (5) above, but they are functions of other errors and raise issues of spatial autocorrelation that need to be accounted for (Anselin 1988).

Blue Crab Demand

In addition to the harvest prediction equations, we must be able to predict how relative prices of different crab market classes will be affected by changes in landings, as this will ultimately influence crabber profits. To capture these price differences, we estimated a simple inverse demand equation for each crab class:

$$P_j = \varphi_0[1 + \varphi_1(D)] + \sum_{j=1}^4 \varphi_j H_j \quad (7)$$

where P_j is the price of market class j crab, D equals 1 during the peak demand summer months and 0 in other periods.

Optimization

In developing our estimatable model, we have ignored to this point consideration of the crab market categories. Accounting for categories results in having to estimate 90 equations since there are 18 equations for each of the 5 market classifications. Each equation will also have additional transition parameters to estimate since harvests of some market categories will depend on previous harvests of both the same market category as well as others. For example, #1 male harvests will depend on previous harvests of #1 males as well as previous harvests of #2 males, and perhaps mixed crabs and soft and peeler landings as well. These harvests of other market categories may be from the same area or adjacent areas, thus greatly increasing the number of transition parameters that need to be estimated.

Once we have estimated the full suite of equations, the next step is to take this system of harvest prediction equations and use an optimization approach to determine harvest levels that yield the greatest profit to crabbers. For this purpose a stochastic simulation/optimization program is employed, RISKOptimizer (Palisade Corporation 1998). The program is based on a combination of Monte Carlo simulations and genetic algorithms to find the optimum solution to the crabber profit maximization problem. The stochastic portion arises from using the distribution of parameter estimates from the statistical model. Model constraints are also stochastic and are determined from the distribution of landings and effort from the data.

At this time, preliminary model results are demonstrated using the Solver function in Excel, a standard optimization routine. This routine does not handle the stochastic simulation so results shown below are deterministic. The optimization is configured to maximize revenue over two periods for the harvest of #1 and #2 male crabs. Overall fishing effort is constrained to be at or below the average effort being employed in the fishery, although effort may be shifted into different areas. The total crab harvest allowed is constrained to be at or below the average for the period for the areas being studied (7,600 t).

Data

Data on Maryland monthly fishing effort by gear type and blue crab harvest by market category and NOAA water area were made available from the Maryland Department of Natural Resources (DNR) survey of crab license holders for the period 1985-1998. Landings by area in Maryland were reported using NOAA water codes which were aggregated into the six geographic areas shown in Fig. 1. Maryland DNR was also the source of monthly crab prices by market category.

The blue crab winter dredge survey described in Rugolo et al. (1997) has been conducted since the winter of 1989-1990, and is designed to develop an index of the winter crab population in Chesapeake Bay. Data from the survey are used to develop our initial stock estimates. At this time we are exploring other possible estimates of initial stock size, since the dredge survey only provides us with 10 years of data, whereas we have 14 years of spatially explicit harvest data.

Results

Since we are reporting on ongoing research, the purpose of this application of the model is to demonstrate its utility for informing future management actions. For purposes of illustration we only provide results for a simple two-period, two-area model for male crabs. The area chosen is area 1 from Fig. 1 with harvest interactions allowed with areas 2 and 4, the adjacent areas. Thus, we are assuming that harvests of male crabs from the areas not included have no impact on subsequent male crab harvests from the included areas.

Results of the inverse demand estimations for #1 and #2 male crabs are given in Table 1. For both classes of crab, the intercept, #2 male crabs and female crab landings were significant and had the expected downward effect on price.

At this time we have not completed determining the appropriate maximum likelihood estimator for the harvest prediction equations. To perform the simulations we used results from ordinary least squares regression to estimate model parameters, recognizing that we have not accounted for spatial autocorrelation. The results from one of the estimations are given

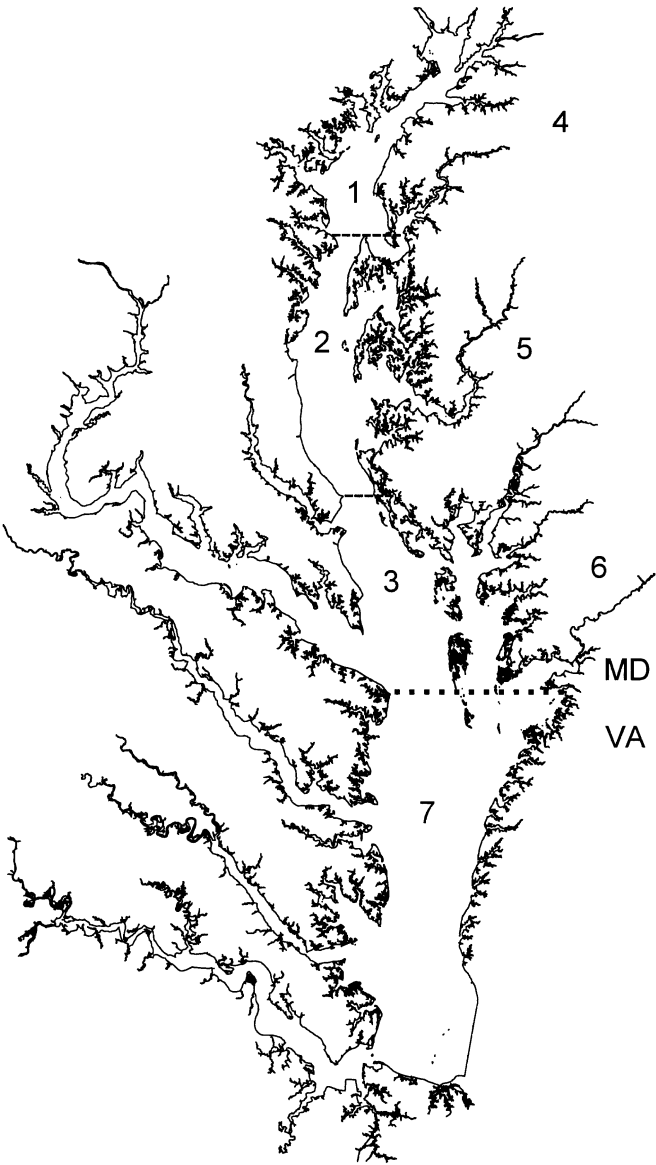


Figure 1. Crab harvesting areas in Chesapeake Bay used in spatial modeling of harvest.

Table 1. Estimates of inverse demand for #1 and #2 male crabs.

Variable	#1 male crabs		#2 male crabs	
	Value	S.E.	Value	S.E.
Intercept	1.293046	0.167310 ^a	0.756415	0.101340 ^a
Summer	0.230403	0.177617	0.168947	0.107583
#1 male	-1.09×10^{-7}	2.525×10^{-6}	-9.92×10^{-7}	1.53×10^{-6}
#2 male	-8.615×10^{-6}	4.966×10^{-6a}	-6.415×10^{-6}	3.008×10^{-6a}
Female	-3.801×10^{-6}	1.087×10^{-6a}	-1.774×10^{-6}	6.59×10^{-7a}
Mixed	2.285×10^{-6}	5.769×10^{-6}	1.235×10^{-6}	3.494×10^{-6}
R ²	0.58		0.60	
Observations	100		100	
Durbin-Watson	1.66		1.59	

^a Indicates significant at the 90% confidence level.

Table 2. Ordinary least square regression results for #1 male crab harvest from area 1 in period 2.

Variable	Value	S.E.
#1 male, area 1, per. 1	0.526901	0.618276
#1 male, area 4, per. 1	2.625823	1.789554
#1 male, area 2, per. 1	-1.783567	0.353342 ^a
#2 male, area 1, per. 1	1.168945	1.011647
#2 male, area 2, per. 1	4.288769	0.658698 ^a
Pots fished	9.271472	0.772598 ^a
Population index	-20,032	6303.0 ^a
R ²	0.98	
Observations	12	

^a Indicates significant at the 90% confidence level.

Table 3. Comparison of key variables between base scenario and optimum.

Variable	Baseline	Optimum
Revenue	\$6,848,761	\$8,334,949
#1 male harvest	2,318 t	3,285 t
#2 male harvest	1,143 t	0.177 t

in Table 2, and a complete set of results is available from the authors. The results not shown here consist of five similar equations that include predictions of #2 male crab landings and include model predictions for the adjacent areas to the target area. The explanatory power of these equations is quite high ranging from an R^2 of 0.86-0.99; however, this is probably explained by multicollinearity in right-hand-side variables that will be adjusted for in the future maximum likelihood estimation. We have no *a priori* assumptions about the signs on the model parameters for harvest levels since these are combinations of the effects of natural and fishing mortality as well as migration and recruitment. The sign on effort is, as expected, positive, and the parameter is significant. For the reported equation, the parameter on initial population is significant but is unexpectedly negative. This may be due to the fact that we have not disaggregated the winter dredge survey data by size and sex.

The optimization results showed that by changing the first period harvest and redistributing effort in period 2, crabbers could increase their total revenue from \$6.8 million to \$8.3 million, a 22% increase. A comparison of the base scenario and the optimization for key variables is given in Table 3. Although harvest is constrained to be the same in the base and optimal scenario, effort is redistributed toward the first period and toward the harvest of #1 male crabs with a major cutback in the harvest of #2 crabs in both periods. These preliminary results should be viewed with caution both because model parameters have yet to be estimated appropriately, and the partial model results may be different in the full model.

Discussion

To be useful for management it is important that fisheries models reflect the major characteristics of the resource being managed. In the case of Chesapeake Bay blue crab, the high degree of year-to-year variability in recruitment and the spatial composition of the stock are important components of the fishery. A yield-per-recruit analysis addresses the concern about variability in recruitment, but a spatially explicit yield-per-recruit analysis has not been conducted for this fishery. Such an analysis will be difficult because of the large number of parameters that would need to be estimated. These models would require detailed structural information on spatial variation and dependence in recruitment, growth, migration, and mortality. In our reduced form approach, these factors are subsumed in the transition parameters.

Although our results are very preliminary, the approach of a spatial statistical analysis of the Chesapeake Bay blue crab fishery in conjunction with more conventional yield-per-recruit models appears to be a promising tool for examining management options. The primary constraint to the success of the statistical approach is the limited length of time series data with spatial information. This problem will diminish with time in the Maryland portion of the Chesapeake Bay fishery, but it will continue in Virginia

where they have yet to institute a harvest data collection system with spatial information.

We have also demonstrated that spatial management, controlling when and where a fish population can be harvested, may lead to significant improvements in fishermen incomes. It is not possible to capture the spatial component of harvest in the existing non-spatially explicit yield-per-recruit models. The tradeoff is that the statistical approach requires long time series of data and presents a number of spatial econometric issues that must be addressed. In the long run, the two methods can converge to develop a statistically estimated, spatially explicit yield-per-recruit model. More practically, a hybrid approach may emerge that includes statistically estimated parameters in combination with numerical estimates from experimental studies.

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Territorial Use Rights: A Rights Based Approach to Spatial Management

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Abstract

The advantages of increasingly fine scale management of fisheries may be offset by increased enforcement and management costs, reduced catch per unit of effort and increased running costs for harvesters, and by an intensification of the race for fish. An alternative to regulated open access would be to lease, or permanently transfer, spatially defined harvest privileges. Exclusive spatial use privileges have been used to control grazing on public rangelands, and the exploitation of forest, petroleum, and mineral resources on state and federal lands and on the submerged lands of the outer continental shelf. Individual and community based spatial use privileges have been used to stint access to fish and shellfish resources. This paper explores the potential economic and management consequences of transferable and nontransferable, individual and community based spatial use privileges in the context of the Aleutian Islands golden king crab (*Lithodes aequispinus*) fishery.

Introduction

Participants in the Aleutian Islands golden king crab (*Lithodes aequispinus*) fishery have adopted a pattern of spatial dispersion that reduces conflict and gear loss and has avoided excessive capitalization. Currently, with

relatively few participants and a large geographic region, it has been in each harvester's interest to recognize informal claims of others to exclusive rights to fish particular sites. However, recent declines in the abundance of other regional crab stocks, expansion of pot fisheries for Pacific cod (*Gadus macrocephalus*), the advent of pollock (*Theragra chalcogramma*) fishing cooperatives, and the imposition of pot limits could increase the number of participants in the Aleutian Islands golden king crab fishery, resulting in the collapse of informal agreements and an economically and ecologically wasteful race for fish. This study provides an initial examination of the possible pitfalls and benefits of implementing a more formal system of spatial-rights based management of the Aleutian Islands golden king crab fishery.

Spatial controls have long been a part of the management of living marine resources and have been exercised over a wide range of scales. For example, coastal nations reserve to themselves authority over access to marine resources within their territorial waters and extended jurisdictions. Although these territorial claims are not coincident with the distribution of target species biomass where the claims overlap or abut one another, nor are they for highly migratory species, they have provided coastal nations the possibility of controlling harvest effort and technology over much of the distribution of some stocks. Spatial controls have often been applied at a fine scale for sessile stocks, and to address concerns about grounds congestion and localized depletion.

Spatial use privileges have been used to regulate utilization of a variety of publicly owned resources, including timber production, grazing, and petroleum and other mineral extraction on state and federal lands and on the outer continental shelf. The nature of the spatial use privilege has varied from seasonal or annual use permits to long-term leases and even to fee simple title. For example, concessionaires may be awarded seasonal, annual, or multiannual permits to supply campground, lodging, guiding, or other services on public lands; 50- to 100-year leases are not uncommon for timber and grazing rights; and, under certain conditions, fee simple title is granted to lands claimed for homesteading or mineral production. In general, the spatial use privilege has been an exclusive authorization to utilize a specific resource in a specific region and has not been a right to exclude or block other resource uses. For example, ranchers with federal grazing permits cannot control camping or hunting on leased lands. Similarly, outer continental shelf petroleum leaseholders cannot control commercial or recreational fishing in the waters above their leasehold. The extent to which spatial leaseholders husband their resources and consider the effect of their actions on others depends on the security, duration, and comprehensiveness of the right and the productivity of the resource.

Territorial Use Rights in Fisheries (TURFs)

TURFs assign exclusive use privileges defined in terms of target fishery and location to an individual or group (Christy 1982). They are a special

case of spatial harvest restrictions and have often been applied in less industrialized and smaller-scale coastal fisheries where management has been based on restricting participation to a localized population in a limited geographical area. Abalone (*Haliotis* sp.) and other nearshore fisheries in Japan are managed as spatially defined commons (Ruddle 1989). Some nearshore and fjord fisheries for Atlantic cod (*Gadus morhua*) in northwest Norway reserve exclusive territorial rights to littoral communities (Jentoft and Mikalsen 1994). Similar rights have been documented in Brazil (Cordell and McKean 1992), Chile (Gonzalez 1996), Mesopotamia (Berkes 1986), and the Caribbean (Berkes 1987). In some South Pacific cultures, the rights to fish specific locations have been further defined in terms of permissible fishing technology, target species, tide condition, and season or time of day, with different rights in the same space being held by different individuals, families, or social groups (Goodenough 1951, 1963; Johannes 1978; Carrier 1987; Lieber 1994). Exclusive use rights to fishing sites and species were held by clans, tribes, and family groups in the Pacific Northwest and Canada (Higgs 1982, McEvoy 1986, Bay-Hansen 1991, Newell 1993). Spatial rights to oyster (*Crassostrea virginica*) beds have been subject to leasing in some states since the 18th century (Agnello and Donnelley 1975, McCay 1998). Acheson (1988) describes community based social structures that defend customary harvest areas for Maine lobster (*Homarus americanus*). Alaska's salmon (*Oncorhynchus* sp.) and Pacific herring (*Clupea pallasii*) limited entry programs are managed under a system of spatial-use privileges that have failed to eliminate the economically wasteful race for fish (Schelle and Muse 1986). The local area management plan (LAMP) for Pacific halibut (*Hippoglossus stenolepis*) in Sitka Sound, Alaska (NPFMC 1997) represents a common property TURF with access restricted according to season, vessel size, and fishing purpose (commercial, charter, sport).

Recent Economic Studies of the Bering Sea and Aleutian Islands Crab Fisheries

The traditional management approach for conserving stocks of Alaska's king (*Paralithodes* sp., *Lithodes* sp.), Tanner (*Chionoecetes bairdi*), and snow crabs (*C. opilio*) has been to limit catch through the "three S's": season, size, and sex. These instruments are used to achieve a target harvest rate set by management. Other common controls used by management include restrictions on gear configuration, area fished, gear deployed (e.g., pot limits), and adoption of population thresholds, which must be maintained for the fishery to remain open. More recently, exclusive fishing zones, license limitations, and vessel buybacks are being discussed and/or implemented. Several recent studies have examined the effectiveness and efficiency of North Pacific crab management measures.

Greenberg and Herrmann (1994) examine the distributional consequence of pot limits in the Bristol Bay red king (*P. camtschaticus*) crab fishery. They find that fixed pot limits (an upper limit on pots per vessel) are

relatively more disadvantageous to larger vessels with the result being a reallocation of harvest and revenues from larger to smaller vessels. Moreover, because pot limits reduce entry costs, they may induce additional vessels to enter the fishery. Greenberg et al. (1994) explore the potential economic benefits of introducing a system of individual transferable pot quotas (ITPQs) in the Bristol Bay red king crab and the Bering Sea snow crab fisheries. ITPQs are transferable rights to individual units of fishing gear. Although restrictions on inputs only constrain output to the extent that there are few close input substitutes, ITPQs enhance fishing effectiveness by allowing vessel operators to determine the optimal number of pots that they fish. More efficient operators would buy pots from less efficient operators. Harvesters who wished to exit the fishery, or to downsize, would receive compensation from those wanting to enter the fishery or expand harvest, in other words, through voluntary market exchange. However, because the total number of ITPQs would need to vary in response to population cycles, an ITPQ system could involve considerable management costs for releasing additional ITPQs in times of high abundance and retiring ITPQs in times of low abundance.

As an alternative to input controls, Lynch et al. (1996) explore the potential efficiency gains from individual transferable quota (ITQ) management of the Bristol Bay red king crab fishery. In contrast to ITPQs and other input control measures that indirectly influence output, ITQs restrict output directly. The harvestable abundance of red king crab stocks is highly variable over time. Limited confidence in stock models has led managers to favor a strategy of setting a preseason guideline harvest level (GHL) while retaining the option of imposing an early closure if catch per unit of effort (CPUE) declines. Similar circumstances might arise in any fishery where management is highly dependent on fishery performance data. Lynch et al. (1996) find that the presence of stock uncertainty reduces the potential efficiency gains to ITQ management.

Natcher et al. (1996) examine the economic impacts of superexclusive vessel registration management as applied to the Norton Sound red king crab fishery. Vessels that participate in superexclusive crab fisheries are precluded from participating in other crab fisheries. Superexclusive registration was adopted by the North Pacific Fishery Management Council in 1993, overturned by the Secretary of Commerce, modified, readopted, and approved in 1994. Because participants in superexclusive area registration fisheries must forgo participating in other (more lucrative) crab fisheries during the same season, few large vessel operators choose to participate, effectively reserving the superexclusive registration area for a local, small vessel fleet. Consequently, superexclusive area registration is a form of common property TURF.

Herrmann et al. (1998) explore the potential consequences of applying pot limits to the Aleutian Islands golden king crab fishery. They note that fishery participants have adopted a pattern of spatial dispersion that reduces conflict and gear loss and has avoided excessive capitalization. How-

ever, they find that imposition of pot limits could stimulate entry and collapse the informal TURFs, triggering an economically and ecologically wasteful race for fish.

Aleutian Islands Golden King Crab Fishery

The Aleutian Islands golden king crab fishery is jointly managed by the state and federal governments through a cooperative fishery management plan (NPFMC 1989). The Bering Sea and Aleutian Islands FMP (Fishery Management Plan) contains a general management goal to maximize the overall long-term benefit to the nation of Bering Sea and Aleutian Islands stocks of king and Tanner crab by coordinated federal and state management. Although the fishery occurs over an expansive geographic area (Fig. 1), fishing takes place on a limited set of narrow ledges and shelves (Fig. 2). Currents can be extreme throughout the fishing grounds and weather conditions are frequently severe.

Although hard-shell adult male golden king crabs tend to be stratified by depth, that depth varies throughout the year (Blau et al. 1996, ADF&G 1999). Nevertheless, experienced fisherman can largely avoid juveniles, females, and molting crabs. These conditions have led many participants to customize their gear and equipment. In contrast to other Bering Sea crab fisheries that use individual pots, participants in the longline Aleutian Islands golden king crab fishery typically use strings of 20-30 pots.

Fishery participants indicate that informal agreements exist among harvesters not to fish near each other or to fish in regions where others have repeatedly harvested in prior seasons. This facilitates harvesters being able to return seasonally to the same fishing grounds. The ability to retain and protect fishing grounds is improved when the number of participants is low and when most are repeat participants. The Aleutian Islands golden king crab fishery is small, both in terms of the number of fishery participants (23 vessels) and total harvest (1.6 million crab) from the 1990/1991 through 1997/1998 fishing seasons.

In contrast to many other Bering Sea and Aleutian Islands crab fisheries, fishery performance indicators suggest that the Aleutian Islands golden king crab stock is healthy and stable. The CPUE has averaged 8 crabs per potlift since the fishery's inception in 1981, with no statistically significant differences between east and west regions and a small (-0.214 crabs per potlift per year) albeit statistically significant (P -value = 0.0007) decline over time. The average weight of harvested crab has not declined significantly (P -value = 0.327) since 1985/1986 when the crab size limit was lowered from 6.5 to 6 inches (16.5-15.25 cm) carapace width. Similarly, in contrast to compressed seasons that characterize other Bering Sea crab fisheries, openings in the Aleutian Islands golden king crab fishery have increased to year-round in the western subarea and have averaged 106 days in the eastern region.

While we have not made an in-depth analysis of economic performance, a few features are prominent. First, the inflation adjusted ex-vessel price of

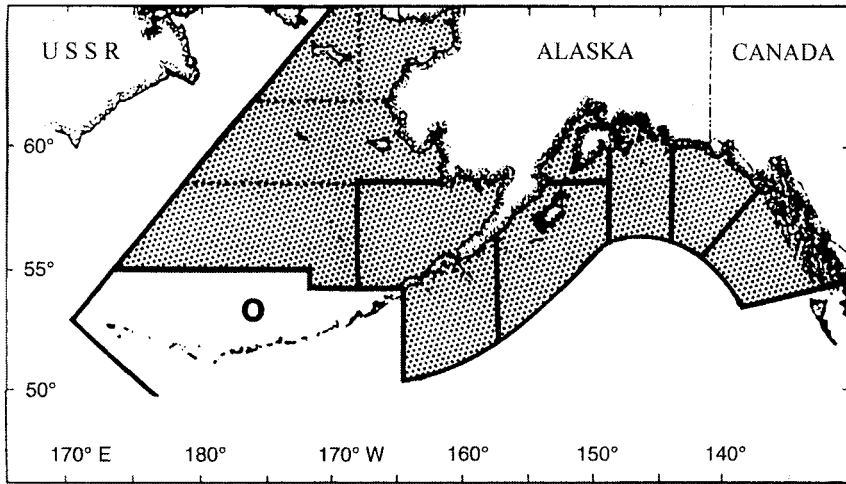


Figure 1. Aleutian Islands king crab management area "O" and other management areas.

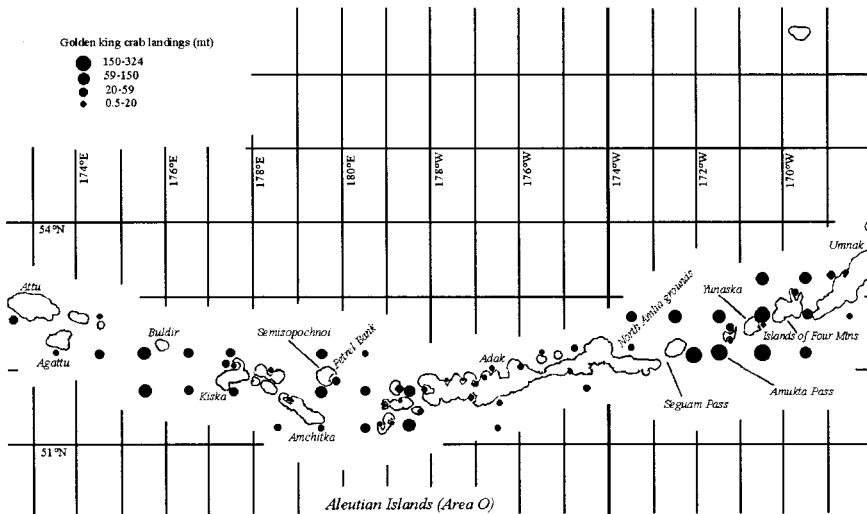


Figure 2. Distribution of Aleutian Islands golden king crab harvests, 1997/1998 season (ADF&G 1999). Areas to the east and west of 174°W are managed with separate seasons and guideline harvest limits. The boundary between east and west subregions has varied over time. The boundary was at 172°W from the 1981/1992 through 1983/1984 seasons, at 171°W from 1984/1985 through 1995/1996, and at 174°W since 1996/1997.

golden king crab has declined by an average of \$0.10 per lb per year (\$0.044 per kg per year). Second, the average number of potlifts per vessel has increased at a statistically significant (P -value = $1.4\text{E-}09$) rate of 499 lifts per year. As a consequence, the average real revenue per potlift has declined at a statistically significant rate of $-\$8.20$ per potlift per year (P -value < 0.0001) (Fig. 3). While variable cost data are unavailable, it seems reasonable to conjecture that variable costs are proportional to the number of potlifts. Consequently, it is likely that average real net revenue per potlift has declined.

The decrease in real ex-vessel revenue per potlift has been, in part, offset by an increase in the average number of potlifts per vessel; consequently, inflation adjusted average ex-vessel revenue per vessel has been relatively constant (Fig. 4). The lack of cost data prevents the determination of time trends in average real net revenues per vessel.

Because port and processing facilities lie eastward of the fishing grounds, running costs are higher for vessels that fish farther to the west. Moreover, because running costs are an important component of variable costs, it would be expected that average revenue per potlift would increase from east to west at a rate that approximately offsets the associated marginal increment to running costs. Consequently, in a fishery characterized by open access behavior, effort would be expected to disperse to the west only when average revenue per potlift declined in the easternmost fishing areas. That is, under open access, it is expected that average *net* revenue (ex-vessel revenue less variable costs) would be equated across fishing areas. The absence of a clear pattern of east-to-west increasing revenues per potlift (Fig. 5) suggests that participants in this fishery have, in part, avoided dissipation of net revenues.

Model

A simple discrete-time deterministic model can be used to characterize the bioeconomics of a system of privately owned transferable TURFs. These leases could be permanent or temporary, with an initial allocation based on participation history, lottery, or an auction. The objective of the i -th leaseholder can be characterized as the constrained maximization of net present value—discounted sum of net revenues—over the duration of the TURF:

$$NPV_i = \sum_{t=0}^T \left[\left(\frac{1}{1+r_i} \right)^t (p_t h_{t,i} - c_{t,i}^h - c_{t,i}^d) \right] \quad (1)$$

Net revenue in each period (t) is the difference between total revenue, the product of real ex-vessel price (P_t) and contemporaneous harvests ($h_{t,i}$), and total costs, here segregated into operating costs ($c_{t,i}^h$) and territorial defense costs ($c_{t,i}^d$). The private discount rate r_i reflects individual time preferences. Although theoretical models often consider values of $0 \leq r_i \leq \infty$,

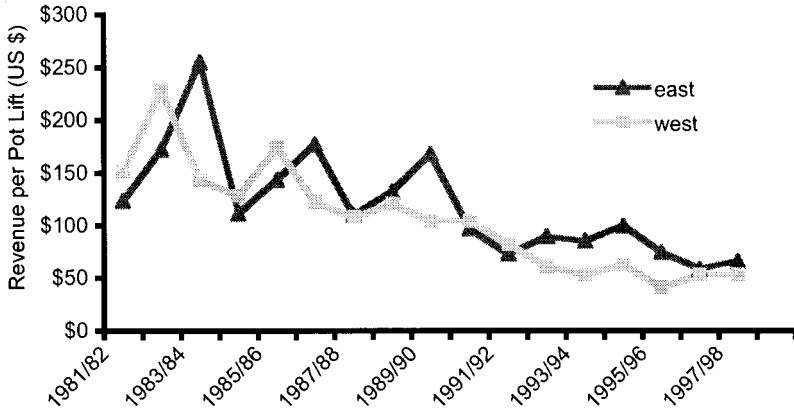


Figure 3. Average real ex-vessel revenue (\$1992 base) per potlift in the eastern and western subregions of the Aleutian Islands golden king crab fishery.

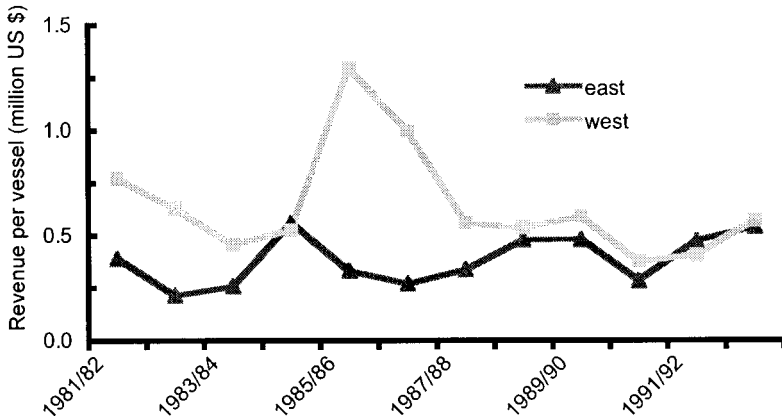


Figure 4. Average real ex-vessel revenue (\$1992 base) per vessel in the eastern and western subregions of the Aleutian Islands golden king crab fishery.

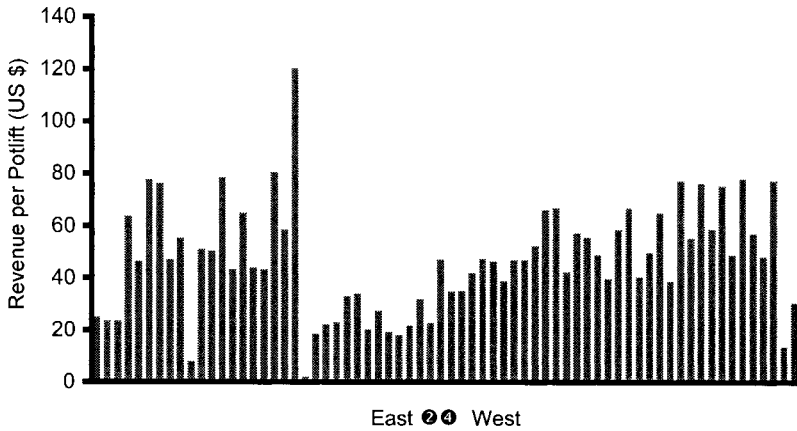


Figure 5. Average revenue (\$1992 base) per potlift by statistical reporting area in the Aleutian Islands golden king crab fishery during the 1997/1998 fishing season.

empirical evidence suggests that private discount rates are well approximated by the long-term corporate interest rate ($0.10 \leq r_i \leq 0.20$). The duration of the TURF is represented by $T - t_0$; permanent ownership is a special case of the general model where $T \rightarrow \infty$. Maximization of the objective function described in equation 1 is constrained by the inherent dynamics of golden king crab populations, and the interaction between supply and demand functions for golden king crab.

Aleutian Islands golden king crab stock dynamics can be described by a vector delay-difference equation:

$$x_t = f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k}) - h_{t-1}, \quad (2)$$

where x_t is the current abundance of Aleutian Island golden king crab, x_{t-k} is the lagged abundance of Aleutian Islands golden king crab, \mathbf{X}_{t-k} is a vector of the lagged abundance of species that are related to Aleutian Islands golden king crab through trophic or bycatch relationships in $t - k$, and \mathbf{Y}_{t-k} is a vector of lagged environmental variables. Aleutian Islands golden king crab abundance is assumed to be an increasing (at a decreasing rate) function of the previous year's abundance of Aleutian Islands golden king crab, a decreasing function of past harvests, and influenced by current and lagged environmental conditions and the current and lagged abundance of other species through trophic or bycatch relationships. That is,

$$\frac{\partial x_t}{\partial x_{t-1}} > 0, \frac{\partial^2 x_t}{\partial x_{t-1}^2} < 0, \text{ and } \frac{\partial x_t}{\partial h_{t-1}} < 0,$$

while

$$\frac{\partial x_t}{\partial \mathbf{X}_{t-k}}, \frac{\partial^2 x_t}{\partial x_{t-1} \partial \mathbf{X}_{t-k}}, \frac{\partial x_t}{\partial \mathbf{Y}_{t-k}}, \text{ and } \frac{\partial^2 x_t}{\partial x_{t-1} \partial \mathbf{Y}_{t-k}}$$

could be positive or negative depending on the particular combination of variables and lags.

The ex-vessel price formation process can be represented by:

$$P_t = f_p(h_t, W_t). \quad (3)$$

Ex-vessel price is inversely dependent on the magnitude of harvests,

$$\frac{\partial p_t}{\partial h_t} < 0,$$

and influenced by a vector of other factors, W_t , including inventories, exchange rates, income, and the price of substitutes. The influence of changes in W_t on P_t depends on the particular element of W_t .

Variable harvesting costs,

$$c_{t,i}^h = f_{c_h}(x_t, h_{t,i}, d_{t,i}, n_t) \quad (4)$$

are assumed to be a decreasing function of abundance, and an increasing function of the magnitude of harvests, the distance of the fishing area from port and processing facilities ($d_{t,i}$), and the number of participants (n_t). That is,

$$\frac{\partial c_{t,i}^h}{\partial x_t} < 0, \frac{\partial c_{t,i}^h}{\partial h_{t,i}} > 0, \frac{\partial c_{t,i}^h}{\partial d_{t,i}} > 0$$

and

$$\frac{\partial c_{t,i}^h}{\partial n_t} > 0.$$

The first of these assumptions is motivated by the observation that CPUE rises as abundance increases, thus the cost per crab caught declines as abundance rises. The second assumption states that catching more crab

costs more money for any given level of abundance. The third assumption reflects the contribution running costs make to harvest costs. Harvest costs are assumed to increase as the number of participants increases and results in more frequent gear interference, etc.

Territorial defense costs,

$$c_{t,i}^d = f_{c_d}(a_{t,i}, d_{t,i}, n_t), \quad (5)$$

depend on the size ($a_{t,i}$) and remoteness ($d_{t,i}$) of the TURF, and the number of fishery participants (n_t). These costs could be borne by government (as they are under traditional management structures) or by private individuals (as pollock and whiting allocations are enforced through private contracts within the pollock and whiting coops). Although technological advances such as vessel and gear transponders could change the structure these costs over time, it can be expected that enforcement costs are higher for large remote locations, particularly when there are a large number of participants (Anderson and Hill 1975). That is,

$$\frac{\partial c_{t,i}^d}{\partial a_{t,i}} > 0, \frac{\partial c_{t,i}^d}{\partial d_{t,i}} > 0,$$

and

$$\frac{\partial c_{t,i}^d}{\partial n_t} > 0.$$

In addition, maximization of the objective function (equation 1) is subject to non-negativity restrictions on r_t , P_t , $h_{t,i}$, $c_{t,i}^h$, $c_{t,i}^d$, $a_{t,i}$, $d_{t,i}$, n_t , x_t , and \mathbf{X}_t , and by policy limitations embodied in the Endangered Species and Magnuson-Stevens Fishery Conservation and Management Acts. These latter constrain the control variable, h_t (the sum of $h_{t,i}$ across i), to values that will not reduce the expected future abundance of Aleutian Island golden king crabs, $\mathbf{E}(x_{t+k})$, below threshold levels predicated on the concept of maximum sustained yield.

For a fishery manager charged with maximizing value to the nation, the objective includes a summation across individual fishers and the freedom to choose h_t and n_t . That is, the objective can be characterized as the maximization of

$$NPV = \sum_{t=t_0}^T \left[\left(\frac{1}{1+r} \right)^t \left(p_t h_t - \sum_{i=1}^n c_{t,i}^h - \sum_{i=1}^n c_{t,i}^d \right) \right] \quad (6)$$

subject to constraints 2 through 5. The social discount rate, r , reflects society's time preferences and is usually assumed to be somewhat lower than the private discount rate r_i .

Analytical Solution of the Model

While empirical data would be necessary to assess the magnitude of the net present value of alternative TURF specifications, analytical solution of the model can characterize the preferred number of fishers, harvest trajectory and corresponding stock, price, and cost trajectories under various conditions even without such data (see, e.g., Bjørndal 1988, Criddle 1993). The analytical solution is obtained from the system of first-order conditions of a Lagrangian function that is formed by augmenting the objective function (equation 1 or 6) with the constraints (equations 2 through 5). The Lagrangian function to be solved for the i -th leaseholder is:

$$L_i = \sum_{t=t_0}^T \left\{ \left[\left(\frac{1}{1+r_i} \right)^t (p_t h_{t,i} - c_{t,i}^h - c_{t,i}^d) \right] - \lambda_{t,i} [x_t - f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k}) + h_{t-1}] \right\} \quad (7)$$

Setting the derivatives of this Lagrangian functions with respect to the state (x_t) and control variables (h_t , n_t) and Lagrange multipliers (λ_t) equal to zero, yields a set of necessary conditions for an optimum. Combining these first order conditions and rearranging the arguments leads to

$$\lambda_{t+1,i} = \left(\frac{1}{1+r_i} \right)^t \frac{\partial \Pi_{t,i}}{\partial h_{t,i}} = \left(\frac{1}{1+r_i} \right)^t \left(p_t + \frac{\partial p_t}{\partial h_t} h_{t,i} - \frac{\partial c_{t,i}^h}{\partial h_{t,i}} \right), \quad (8)$$

$$\frac{\partial (\Pi_{t,i})}{\partial x_t} = (1+r_i) \frac{\partial p_t}{\partial h_{t-1}} h_{t,i} - \left(p_t + \frac{\partial p_t}{\partial h_t} h_{t,i} - \frac{\partial c_{t,i}^h}{\partial h_{t,i}} \right) \frac{\partial f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k})}{\partial x_t}, \quad (9)$$

and

$$\frac{\partial f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k})}{\partial x_t} = \frac{(1+r_i) \frac{\partial p_t}{\partial h_{t-1}} h_{t,i} + \frac{\partial c_{t,i}^h}{\partial x_t}}{p_t + \frac{\partial p_t}{\partial h_t} h_{t,i} - \frac{\partial c_{t,i}^h}{\partial h_{t,i}}} = \frac{(1+r_i) \frac{\partial \Pi_{t,i}}{\partial h_{t-1,i}} - \frac{\partial \Pi_{t,i}}{\partial x_t}}{\frac{\partial \Pi_{t,i}}{\partial h_{t,i}}}. \quad (10)$$

Equation 8 states that one characteristic of the optimal solution is that the shadow value ($\lambda_{t,i}$) of the resource to the i -th harvester in time t is equated to the discounted change in the i -th harvester's net revenue from an incre-

mental change in their catch. Similarly, equation 9 indicates that at the optimum, the change in net revenue to the i -th fisher from a marginal increase in stock abundance depends on the effect of previous harvests on the current ex-vessel price and the product of current marginal net revenues and the change in the rate of increase in abundance. Finally, equation 10 suggests that the optimal stock trajectory is a decreasing function of current stock levels, and depends on the marginal net revenue current and lagged harvests.

The related Lagrangian function to be solved by the fishery manager is:

$$L = \sum_{t=0}^T \left\{ \left[\left(\frac{1}{1+r} \right)^t \left(p_t h_t - \sum_{i=1}^n c_{t,i}^h - \sum_{i=1}^n c_{t,i}^d \right) \right] - \lambda_t [x_t - f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k}) + h_{t-1}] \right\} \quad (11)$$

The optimal solution to equation 11 can be characterized by:

$$\lambda_{t+1} = \left(\frac{1}{1+r} \right)^t \frac{\partial \Pi_t}{\partial h_t} = \left(\frac{1}{1+r} \right)^t \left(p_t + \frac{\partial p_t}{\partial h_t} h_t - \sum_{i=1}^n \frac{\partial c_{t,i}^h}{\partial h_t} \right), \quad (12)$$

$$\frac{\partial (\Pi_t)}{\partial x_t} = (1+r) \frac{\partial p_t}{\partial h_{t-1}} h_t - \left(p_t + \frac{\partial p_t}{\partial h_t} h_t - \sum_{i=1}^n \frac{\partial c_{t,i}^h}{\partial h_t} \right) \frac{\partial f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k})}{\partial x_t}, \quad (13)$$

and

$$\frac{\partial f_x(x_{t-k}, \mathbf{X}_{t-k}, \mathbf{Y}_{t-k})}{\partial x_t} = \frac{(1+r) \frac{\partial p_t}{\partial h_{t-1}} h_t + \sum_{i=1}^n \frac{\partial c_{t,i}^h}{\partial x_t}}{p_t + \frac{\partial p_t}{\partial h_t} h_t - \sum_{i=1}^n \frac{\partial c_{t,i}^h}{\partial h_t}} = \frac{(1+r) \frac{\partial \Pi_t}{\partial h_{t-1}} - \frac{\partial \Pi_t}{\partial x_t}}{\frac{\partial \Pi_t}{\partial h_t}}. \quad (14)$$

The individual leaseholder and fishery manager solutions differ in choice of discount rate, and because the number of leaseholders is a control variable for the manager and an exogenous condition for the individual leaseholder.

The leaseholder and manager solutions imply that as the discount rate increases, that is as $r_i \rightarrow \infty$, the net present value of future benefits and consequently the value of conserving the stock approaches zero. In other words, at high discount rates fishers will have an increased incentive to maximize current harvests at the expense of future harvests. This outcome holds even if the TURF is secure ($T \rightarrow \infty$) and the number of participants is low ($n_i \rightarrow l$). Because the social rate of discount, r , is generally assumed to be less than the private discount rate, r_p , private individuals

have a somewhat higher incentive to deplete the stock. That is, in conditions where $r_i \rightarrow \infty$, TURF-leaseholders cannot be relied on to voluntarily adhere to a sustainable harvest strategy.

In addition, short time horizons reduce the value of stock conservation to current TURF-leaseholders. Myopic conditions can arise when the TURF is temporary and the lease expiration date approaches, that is as $t \rightarrow T$, or even when $T \rightarrow \infty$ if the TURF is nontransferable and the leaseholder approaches retirement. The incentive to deplete the stock as $t \rightarrow T$ can be reduced if current leaseholders are given priority in the reallocation, particularly if the priority is conditional on the condition of the stock. Full transferability would preclude myopic tendencies. Zero-revenue auctions (Tietenberg 1995) and overlapping lease renewals (Young 1995) have been suggested as design criteria that offset myopia in fixed duration permit systems. Note that the effective duration of the TURF could be affected by the threat of fishery closure to provide marine protected areas, etc.

Another implication is that leaseholders have an incentive to exceed sustainable yields when the intrinsic rate of stock increase is below the discount rate, $\frac{\partial x_t}{\partial x_{t-1}} < r_i$, because the net present value of conserving the stock approaches zero. This result holds even if the TURF is secure ($T \rightarrow \infty$) and the number of participants is low ($n_t \rightarrow 1$). That is, TURF-leaseholders cannot be relied on to voluntarily adhere to a sustainable harvest strategy for a slow growing stock.

Where harvest decisions within one harvest area are affected by harvesting in other harvest areas, that is where there is significant larval dispersion or adult migration between TURFs, the abundance of crab in area i is a lagged function of the harvest of crab in area j , therefore the opportunity cost of foregoing current harvests is high and TURF-leaseholders have an increased incentive to exceed sustainable yields within their areas. Because larval dispersion and adult migration rates depend on area size and location, the incentive to overharvest is increased if the number of participants (n_i) is large and the average territory ($a_{i,p}$) is small.

Similarly, where territorial boundaries are insecure, for example, when the boundaries are customary and lack legal standing or where the cost of detecting border incursions are high, harvesters will have an incentive to increase their level of capitalization to maximize their share of the allowable catch. That is, there is a greater tendency toward overcapitalization in informal TURFs than in secure TURFs. Similarly, there is a greater tendency towards overcapitalization in communally held TURFs than in privately held TURFs. Alternatively, TURF-holders faced with porous territorial boundaries may choose to exceed sustainable yields in an effort to capture the maximum possible value before their rivals capture it. Measures that strengthen the delimitation of TURF boundaries, increase TURF size, restrict the number of participants, or reduce detection and enforcement costs will increase the benefits to adhering to sustained yield harvest limits and encourage a close matching of harvesting capacity with catch.

For stocks with highly stochastic recruitment, particularly where recruitment success is largely determined by exogenous environmental conditions, the expected value for risk averse leaseholders will be less than the mean harvest value. The effect is to increase r_p , thereby decreasing the present value of future harvests and providing an increased incentive to harvest beyond sustainable levels.

Finally, increases in the number of participants, particularly if the participants are heterogeneous, decreases the present value of future harvests because of the larval dispersion and adult crab migration effects described above, and because increased numbers of participants increase the cost of negotiating and enforcing formal or informal agreements (Schlager 1994).

Although actual behavior will differ from that implied by the theoretical model, the analytical results are indicative of inherent tendencies that could emerge if unchecked by social or regulatory constraints. The specific design characteristics of the TURF system and the social and regulatory structure within which it is embedded will determine the extent to which the following outcomes are realized.

Discussion

The underlying cause of problems in open-access fisheries has been attributed to incompletely specified property rights (Scott 1996). ITPQs define rights to units of gear and as such, provide indirect control of harvests. However, ITPQs fail to address the externalities associated with gear conflict or stock depletion. Moreover, while ITPQs block one avenue of overcapitalization, they leave open the possibility of capital stuffing in unconstrained input factors. ITQs define rights to specific quantities (shares of the total allowable catch) of fish. While the ITQ may reduce the need to race for fish and associated overcapitalization, there is still competition for preferred locations in the space-time commons. Moreover, unless individuals hold large catch shares, they gain little individual benefit from stock conservation because while they stand to reap immediate rewards from the sale of excessive catches, they share the resultant adverse stock effects with all other quota holders.

TURFs provide an alternative specification of rights. Under a secure TURF management structure with durable and transferable rights, harvesters will select efficient levels of capital investment, and, if the rates of larval dispersion and adult migration between areas are low, they will internalize the benefits of stock conservation. The ability to transfer spatial harvest use privileges ensures that those who wish to exit the fishery are compensated for stock husbandry. Efficient harvesters could optimize the size of their fishing operations by purchasing TURFs from less efficient operators and by adopting cost-minimizing technologies. Transferability would also allow operators to adjust to changes in stock abundance, and changes in product and input factor market equilibria. However, it may be

rational for TURF-leaseholders to deplete the target stock if the stock has low productivity or if there is a high level of uncertainty about future stock abundance, price, or costs. Moreover, if the boundaries of the TURF are porous, that is if it is difficult to control the number of participants, or if there is significant larval dispersion or adult migration, there will be an increased incentive to deplete the stock. Finally, it should be noted that there are ways to strengthen informal TURFs without creating formal property rights. For example, designating the Aleutian Islands golden king crab fishery as a superexclusive management area might reduce the threat of an influx of latent capacity, and thereby facilitate a continuation of the current informal arrangements regarding customary fishing areas. Similarly, restrictive license limitation schema for the Bering Sea and Aleutian Islands crab fleet would limit the pool of potential entrants into the Aleutian Islands area fishery.

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Sanctuary Roles in Population and Reproductive Dynamics of Caribbean Spiny Lobster

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Abstract

Located on the western edge of the Florida Keys, the Dry Tortugas National Park serves as a single large (190 km²) sanctuary for Caribbean spiny lobsters. During the breeding season (March to September), we surveyed the lobster population from 1996 to 1998 in the sanctuary and fishery. Lobsters in the sanctuary differed from those in exploited areas, both in size distribution and reproductive dynamics. Sanctuary lobsters were 20 mm larger in carapace length (CL) than lobsters in the fished population. The size differential between male and female lobsters was much greater in the sanctuary (19 mm CL) than in the fishery (4 mm CL). In the sanctuary, egg-bearing females produced approximately 2.6 times the number of eggs per clutch than those in the fishery. Fishable lobsters began producing eggs at a smaller size than those in the sanctuary. The breeding season of sanctuary lobsters was shorter than that of fishery lobsters, and a greater percentage of the sanctuary's egg-bearing sized population spawned at the height of the season.

Introduction

The Caribbean spiny lobster (*Panulirus argus*) population of south Florida has supported a commercial and recreational harvest of approximately 6 million pounds annually (Hunt 1994, Harper 1995) during the last 20 years. The bulk of the commercial harvest is taken with traps, whereas recreational fishers capture lobsters while diving and snorkeling. Within this fishery, one large sanctuary and many small ones have been established to protect part of this lobster population. The large sanctuary (190 km²) is Dry Tortugas National Park (Fig. 1). Along with Everglades National Park, it was established as a lobster sanctuary in 1974. Everglades National Park,

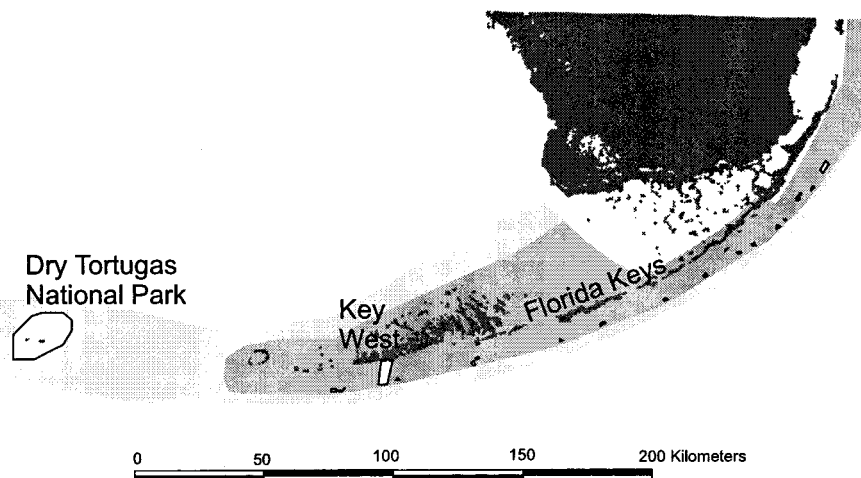


Figure 1. Locations of the Florida Keys and Dry Tortugas National Park. The darker-shaded areas around the Keys indicate where lobster fishing effort is greatest. The lighter shading indicates other areas that are fished. The small patches offshore of the Florida Keys are newly created (1998) Special Protection Areas.

while containing lobster nursery habitat, does not support an adult lobster population and therefore will not be discussed further in this paper. Dry Tortugas National Park supports both adult and juvenile lobsters within a wide variety of benthic habitats, including the following: emergent and shallow reef; reef rubble and sand flats; grass beds; deep (>20 m), muddy sand flats; rock outcroppings; and coral heads. The many small sanctuaries established in 1997 are located along the Florida Keys reef tract. The characteristics and lobster populations of these sanctuaries will be examined in a separate paper.

Herein we present findings from a 3-year study (1996-1998) in which we compared the characteristics and reproductive dynamics of Caribbean spiny lobsters in Dry Tortugas National Park with those of lobsters in the Florida Keys fishery. Specifically, we discuss differences in the size distributions of the sexes, in density of legal-sized lobsters in the closed and open seasons, in the size of egg clutches, and in the duration of the breeding season.

Methods

We used scuba, nets, tickle sticks, and snares to collect lobsters. Two hundred and forty-two 1-hour survey dives were made in the Dry Tortugas (75 dives) and Florida Keys (167 dives) from 1996 to 1998. With an extension

to the grant for the spring of 1999, an additional 24 dives were conducted in the Dry Tortugas to supplement the survey coverage of the early (March to April) breeding season. Surveys were conducted in the Dry Tortugas and at sites within fished areas in the upper Keys, middle Keys, lower Keys, and west of Key West. Within each of these regions, surveys were further made in three reef strata: (1) back reef (the relatively sheltered, typically shallow rubble zone behind the crest of the reef); (2) fore reef (the exposed-to-wave-surge, spur, and groove zone in front of the crest of the reef); and (3) deep reef (low-relief corals, 13-30 m deep, well in front of the crest or in the open ocean). Surveys within each stratum-site combination were completed at 6-week intervals between the months of March and September. Although six survey intervals were scheduled, poor weather, particularly in the early spring, prevented us from completing some surveys. In a typical survey, two dive teams searched for 30 minutes. To ensure that search times were consistent, the time spent capturing and handling lobsters was not included in the search. If a diver could not capture a lobster, the diver would note the observation of a lobster on a dive slate and if possible, record a size estimate. Captured lobsters were brought to the boat and carapace length (CL), molt condition, sex, and reproductive status of females (ovary condition, eggs, and spermatophore presence) were recorded. If present, eggs were shaved from the pleopods, placed in numbered sample bags, and stored on ice. Eggs were frozen upon return to the laboratory.

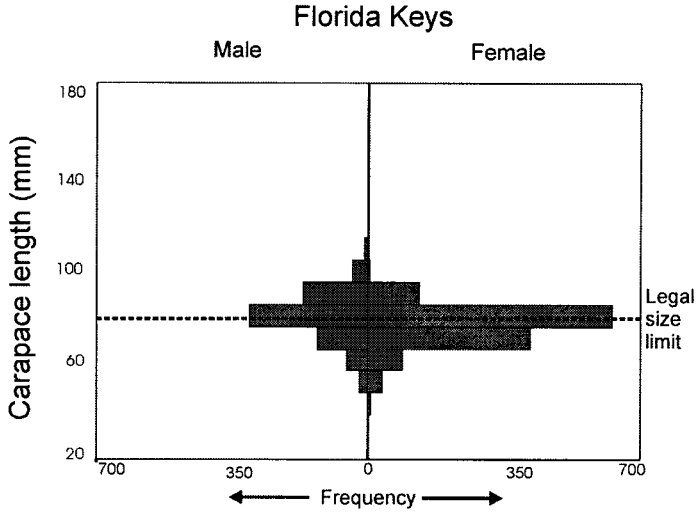
Egg clutch number was estimated in the laboratory by extrapolating the counts from three weighed (wet weight) subsamples to the wet weight of the entire egg mass, using the equation: Clutch size = (mean subsample egg count ÷ mean subsample wet weight) × (entire egg mass wet weight). Curve-fitting software (Table Curve 5.0) was used to model the relationship between clutch size and carapace length.

Results

Size

Overall, lobsters were an average of 20 mm CL larger in the Dry Tortugas than in the Florida Keys. Within the Florida Keys fishery, the frequencies of lobsters declined sharply just above the legal limit (76 mm CL) at which either sex can be harvested (Fig. 2). In the Dry Tortugas, the frequencies of females declined above 90-100 mm CL and for males above 150 mm CL (Fig. 2). Consequently, the difference in size between males and females was highly pronounced in the Dry Tortugas population and reduced in the Florida Keys population. Males averaged 19 mm CL larger than females in the Dry Tortugas and only 2-5 mm CL larger in the Florida Keys. Despite the much smaller differences in size between the sexes within the fishery, these differences are statistically significant in all areas except the upper Keys (Table 1). Geographically, the difference in the size between the sexes increased from east to west or from the upper Keys to west of Key West, then dramatically increased in the Dry Tortugas.

A



B

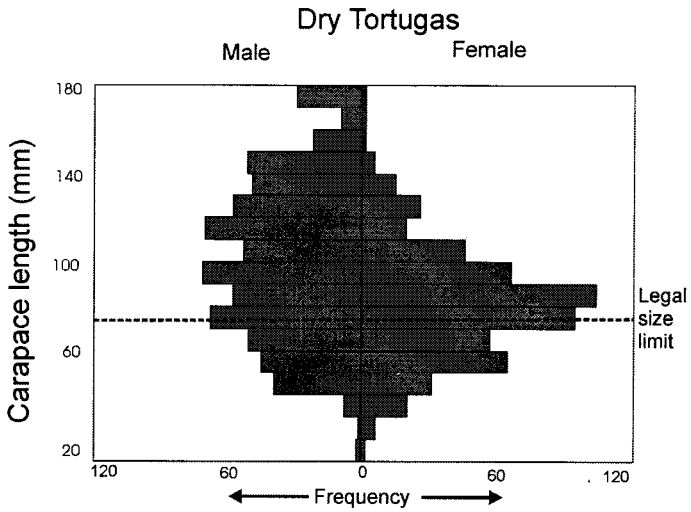


Figure 2. Size distribution of spiny lobsters by sex and area. The dashed line indicates the smallest size class that can be harvested in the fishery.

Table 1. The mean size of sexually mature male and female lobsters by region and size differential.

Region	Mean size (mm CL)		Size differential (mm CL) (significance) ^a
	Males	Females	
Upper Keys	79.4	77.2	2.2 (ns)
Middle Keys	77.6	74.2	3.4 (>0.001)
Lower Keys	80.0	75.5	4.5 (>0.001)
West of Key West	80.8	75.8	5.0 (>0.001)
Dry Tortugas	114.9	95.8	19.1 (>0.001)

^a One-tailed *t*-test for whether males are larger than females.

Density of Legal-sized Lobsters in Open and Closed Seasons

There were no statistically significant differences in density between the closed and open season for either males or females in the Florida Keys fishery or Dry Tortugas sanctuary. The median density of legal-sized lobsters in the Florida Keys fishery was between two and three lobsters per search hour for both males and females (Fig. 3). Although the median density estimate was virtually identical during both the closed and open seasons, the 75th percentile of density for legal-sized male density dropped from six lobsters per hour during the closed season to three during the open season. Thus the likelihood of finding a large concentration of male lobsters was lower during the open season than during the closed season. For females the decline in the 75th percentile was small (seven to six per hour). This was perhaps because at least 10% were still bearing eggs and protected from harvest (see below).

In the Dry Tortugas, the median density of legal-sized males was five lobsters per hour, whereas legal-sized female lobsters were less dense (two to three lobsters per hour). As in the Florida Keys fishery, median densities of sanctuary lobsters were similar during both the closed and open seasons. However, the likelihood of finding a large concentration of lobsters was higher during the open season than during the closed season. For example, the 75th percentile for male density increased from 9 lobsters to 15 lobsters during the open season and the 75th percentile for female density increased from 3 lobsters to 12 lobsters during the open season.

Eggs

In the Dry Tortugas, egg clutch sizes were much larger than in the Florida Keys. Clutch sizes ranged from 300,000 to 2,000,000 in the Dry Tortugas and 40,000 to 900,000 in the Florida Keys (Fig. 4). The mean clutch contained 800,000 eggs in the Dry Tortugas and 300,000 in the Florida Keys

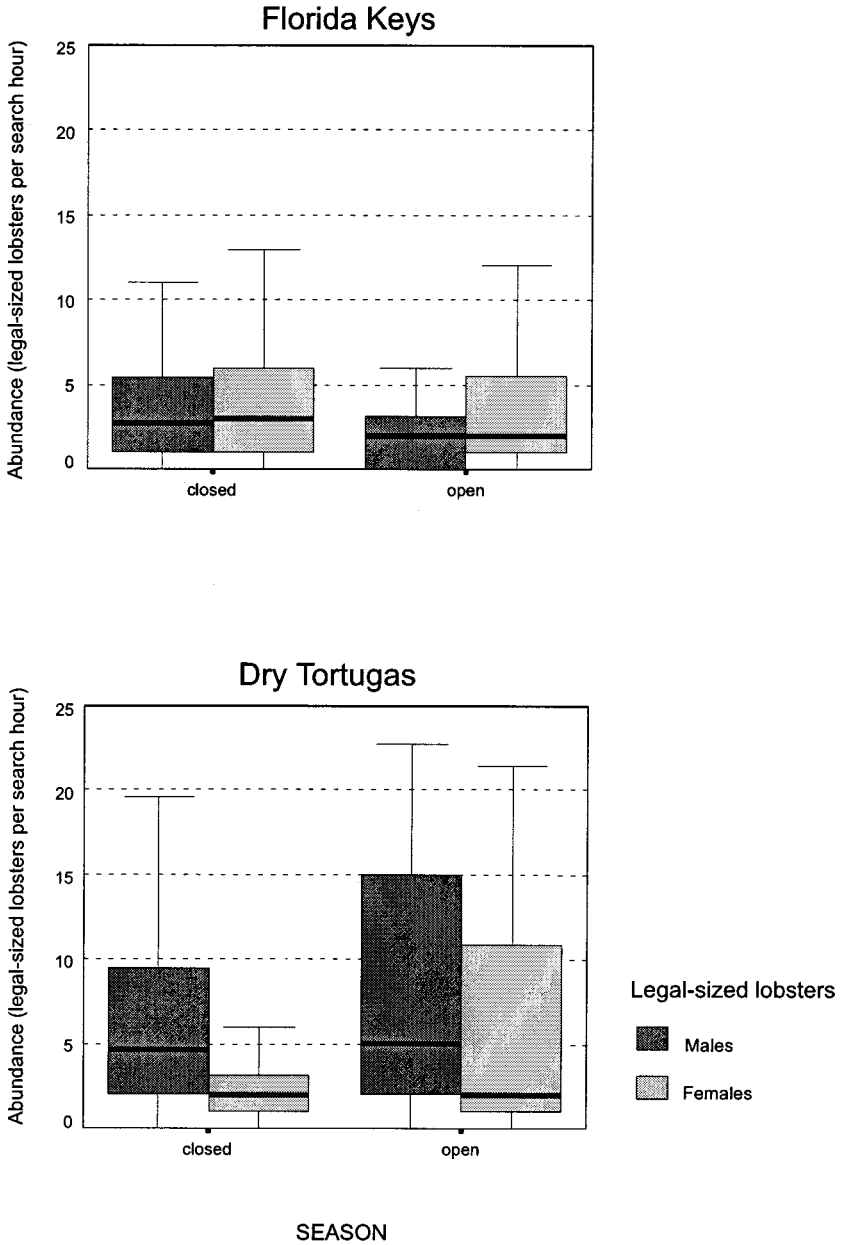


Figure 3. Box plots of the density of legal-sized (>76 mm CL) lobsters (lobsters observed per search hour) by area, sex, and season. The dark lines within the boxes indicate the median density; whereas the top and bottom of the boxes indicate the 75th and 25th percentiles of density.

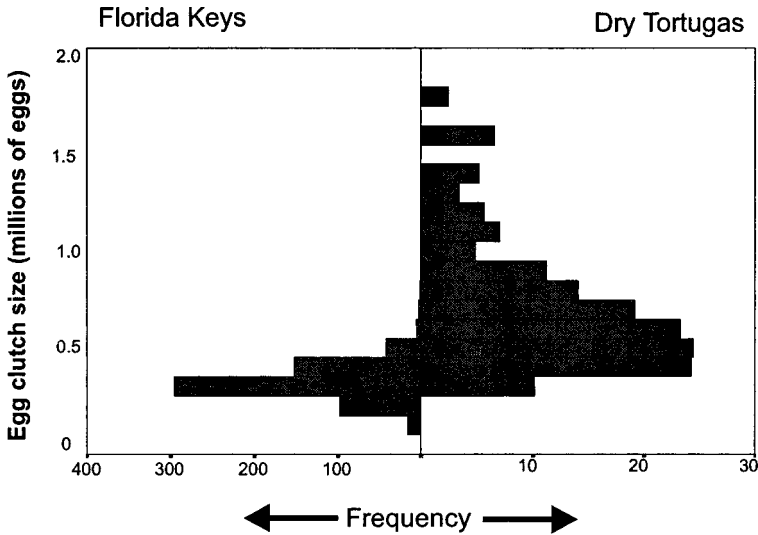


Figure 4. The distribution of egg clutch sizes in the Dry Tortugas and the Florida Keys fishery.

fishery. Thus, the smallest clutch in the Dry Tortugas contained approximately the same number of eggs as the mean Florida Keys clutch. The mean size of egg-bearers was 109 mm CL in the Dry Tortugas and 78 mm CL in the Keys fishery (Fig. 5). The smallest egg-bearer in the fishery was 57 mm CL and 70 mm CL in the Dry Tortugas.

The clutch-size to carapace-length relationship was defined in Cox and Bertelsen (1997) and will not be repeated here. Because there was very little overlap in the size of egg-bearers between the Dry Tortugas and the fishery, a least squares regression using the power equation was performed separately on the fishery and Dry Tortugas egg-bearers to examine the continuity of the clutch-size to carapace-length relationship between the two areas. When the fishery line was extended into the Dry Tortugas sizes (i.e., >100 mm CL) and the Dry Tortugas line was extended through the fishery sizes (i.e., <80 mm CL) both lines remained within the 95% prediction limits of the overall clutch-size to carapace-length relationship.

Breeding Season

The Dry Tortugas had a shorter but more intense (i.e., the percentage of female lobsters of egg-bearing size that were carrying eggs at the peak of the season was relatively high) breeding season than the Florida Keys fishery had (Fig. 6). In both the Dry Tortugas and in the Florida Keys fishery, egg-bearers appeared in March and the proportion of egg-bearers to the

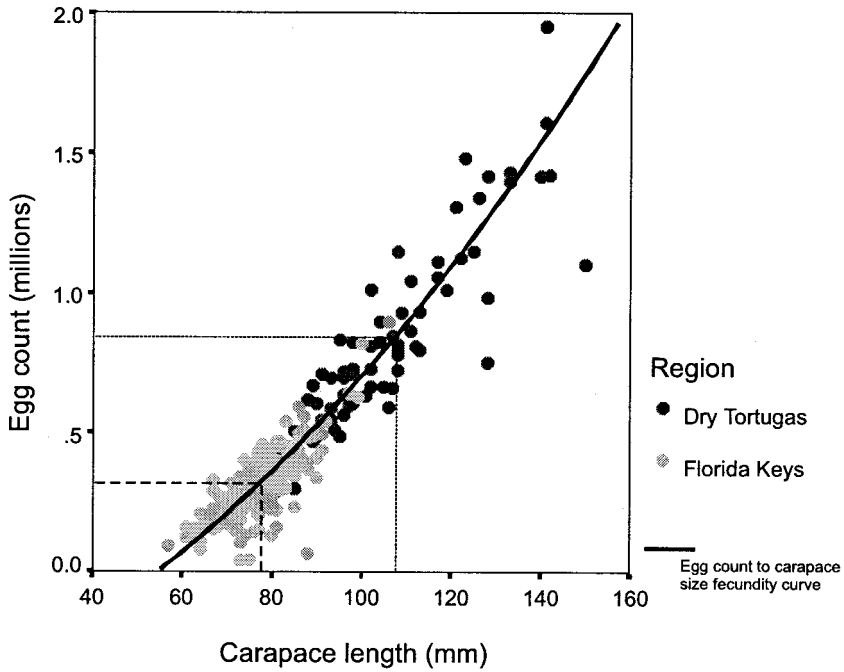


Figure 5. Scatterplot of clutch size vs carapace length of egg-bearers throughout the project. Points are coded in grayscale for Dry Tortugas and Florida Keys lobsters. The dark solid line through the points represents the power curve expressing the relationship between clutch size and carapace length. The dotted and dashed lines indicate the mean clutch size and carapace length for the Dry Tortugas and Florida Keys fishery egg-bearers, respectively.

overall egg-bearing-size population increased dramatically during April. The peak percentage of egg-bearers occurred by mid-April to early May and continued through June for both regions; however, the peak percentage was much higher in the Dry Tortugas (over 90%) than in the fishery (70%). In the Dry Tortugas, egg production fell rapidly in July and August, whereas in the Florida Keys fishery, the decline in egg production was more gradual. In the fishery, egg production continued through September (i.e., approximately 10% were egg-bearers). The largest egg-bearers (size class 95-100 mm CL and up) were found almost exclusively in the Dry Tortugas. Through inspection of rotatable 3D surface response maps (one angle is presented in Fig. 6), the peak egg-bearing percentage for this size category occurred during mid-May. The size classes 85-90 mm CL and 90-95 mm CL were found in both the Dry Tortugas and the fishery. The peak egg-bearing percentage for these size classes occurred approximately 2 weeks later (late May) in both areas. The size classes 80-85 mm CL and smaller were found almost exclusively in the fishery. The peak egg-bearing percentages for these size classes occurred in early June.

Discussion

Although the difference in the average size of male and female lobsters in both the Dry Tortugas and most areas of the Florida Keys was statistically significant, the much larger size difference in the Dry Tortugas may be more significant biologically. Before 1974, a recreational harvest of lobster was permitted in the Dry Tortugas National Park. In the early 1970s, Davis (unpubl. data) found that males were an average of 7 mm CL larger than females and that the percentage of female lobsters bearing eggs in size classes larger than 120 mm CL declined compared with smaller size classes. He hypothesized that these large females were reproductively senescent. Since Davis's (1974) study, the difference in the average size of Dry Tortugas male and female lobsters has increased to 19 mm CL and today virtually all female lobsters larger than 120 mm CL carry eggs during the breeding season (Fig. 6). Recent studies (MacDiarmid and Butler 1999, A.B. MacDiarmid and others, Florida Marine Research Institute, unpubl. data) suggested that superior male size was important for the success of breeding pairs. Female lobsters were much less likely to mate with smaller males than with larger ones, and if they did mate with a smaller male, a significantly smaller clutch size was produced. We suggest that the reason for the reduced fecundity in large females at the Dry Tortugas during the 1970s was that very large males, required for reproductive success of large females, were nearly absent then. In our study, perhaps the overall low percentage of female lobsters bearing eggs from April to July in the Florida Keys (Fig. 6) is due to the relative rarity of large males in the fishery (see Fig. 2). However, other untested factors, such as the nutritional status of animals in the two populations, might explain the differences in the percentage of egg-bearing females in the Dry Tortugas and Florida Keys.

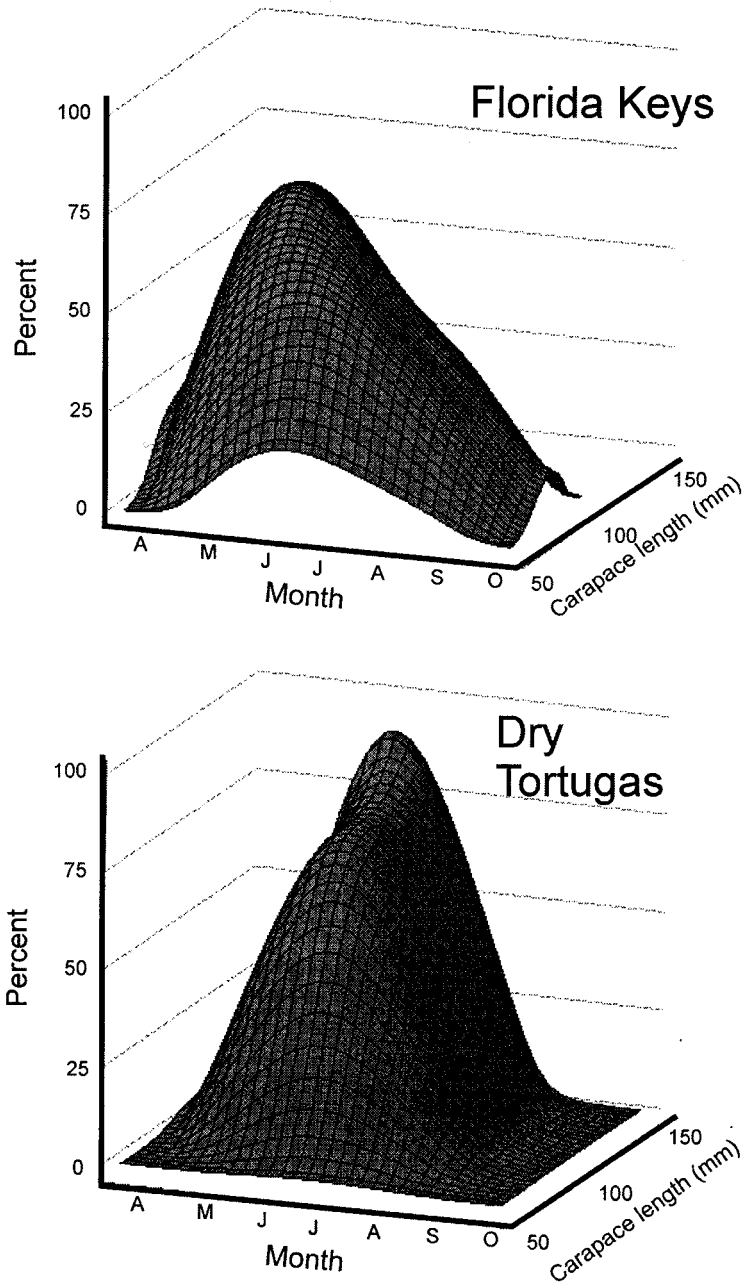


Figure 6. The percentage (by month and size) of the egg-bearing-size population carrying eggs, for the Dry Tortugas and Florida Keys fishery. The smoothed response surface was generated using a normal smoothing kernel.

The differences in male to female sizes, the temporal dynamics of the breeding season, and the size of egg-bearing females compares favorably to earlier studies (Davis 1974, 1975; Lyons et al. 1981; Gregory et al. 1982; Hunt et al. 1991) (Table 2). Overall, these trap-based studies found a larger size of smallest females with eggs and a larger first size class with >50% egg-bearing females than this diver-based study. These differences may be artifacts of trap studies. Very small lobsters (<65 mm CL) can escape from traps (see Lyons et al. 1981) and egg-bearers tend to avoid traps (Kanciruk and Herrnkind 1976). The Looe Key study (Hunt et al. 1991) was conducted in a small (0.5 km²) sanctuary within the Florida Keys fishery. At Looe Key, the difference in size between males and females (8 mm CL) was intermediate to the Dry Tortugas (19 mm CL) and the fishery (1-5 mm CL). The smallest egg-bearers (62 mm CL), however, were much closer in size to the smallest egg-bearers in the fishery than in the Dry Tortugas. In the Dry Tortugas in 1974, shortly after recreational lobster fishing was banned, males averaged 7 mm CL larger than females (G.E. Davis, unpubl. data), much like the small Looe Key sanctuary (Hunt et al. 1991). The smallest egg-bearer found by Davis (unpubl. data) was 78 mm CL, which is much larger than found in our Dry Tortugas study (70 mm CL). However, an unknown portion of his data were taken from traps and during our 3-year study, we found only 4 egg-bearers (out of 126 egg-bearers) smaller than 78 mm CL in the Dry Tortugas.

Although large females produce eggs earlier in a season than small females (Lipcius 1985), peak egg production by size class seems independent of the overall size distribution of a local population. For example, those females between 85 and 95 mm CL exhibited a peak percentage of egg-bearers in late May whether they were the smallest egg-bearers in the Dry Tortugas or the largest egg-bearers in the fishery. Hence the timing of spawning is more likely a function of size than location.

Estimates of annual mortality of legal-sized lobsters throughout the south Florida fishery range from 40% to 60% (Robert Muller, Florida Marine Research Institute, pers. comm.). Although our surveys were conducted along a narrow geographical band within the fishery (see Fig. 1), fishing mortality within the area surveyed was likely similar to that across the entire fishery. However, our data did not show a dramatic decline in density along the Florida Keys reef tract. Several factors may explain this. First, our observations were made early in the open fishing season. Major changes in density may be evident only later in the open fishing season. Second, in the first month of the fishing season, some commercial fishing effort was concentrated north of and nearshore of the Florida Keys and then moved offshore toward the reef tract in subsequent months (Tom Matthews, Florida Marine Research Institute, pers. comm.). Third, a small portion of the female population (~10%) was protected from harvest because they bear eggs. Fourth, sample sizes may have been too small to detect significant differences.

Table 2. A comparison of breeding seasons, size at maturity, and male-female size differences from earlier studies and this study.

Location	Collection years	Collection method	Breeding season (>20% females with eggs)	Peak breeding season (>60% females with eggs)	Smallest female with eggs (mmCL)	First size class with >50% females with eggs (mmCL)	Mean male size-mean female size (mmCL)
Florida Keys	Lyons et al. 1981 ^a Gregory et al. 1982 ^a	Trap Trap	Apr-Sep ^d Apr-Sep ^d	na na	65 65-70	na 70-75	1-5 ?
Florida Keys	This study	Diver	Apr-Sep	Apr-Jul	57	65 - 70	2-5
Looe Key	Hunt et al. 1991 ^b	Diver	Apr-Sep	May-Jul	62	65-69	8
Dry Tortugas	Davis 1974, 1975 ^c	Trap and diver	No fall activity ^e	Apr-?	79	?	7
	This study	Diver	Mar-Jul	Apr-Jun	70	85-90	19

^a Reef sites only.

^b Fore reef sites only.

^c The male-female size difference was not reported then but rather comes from a reanalysis of the original data for this paper.

^d Generally lower percentages of egg-bearers were found in these trap studies (see Kanciruk and Herrnkind 1976); dates given here indicate the months egg-bearing females were found in traps.

^e See Kanciruk and Herrnkind 1976.

^f na = not available.

The larger average clutch size in the Dry Tortugas was due to two factors. First, the overall size distribution of female lobsters in the Dry Tortugas was larger than that in the Florida Keys. A relatively small increase in lobster size results in a large increase in fecundity because the relationship of clutch size to carapace length is a power function (Fig. 5) (Cox and Bertelsen 1997). Second, the Florida Keys lobsters began producing eggs at a smaller size than lobsters in the Dry Tortugas. The smallest egg-bearing lobster in the Florida Keys was 57 mm CL. In the Dry Tortugas, the smallest egg-bearer was 70 mm CL. The smaller size of egg-bearers in this fished population may be due to genetic pressures, phenotypic plasticity, or to slower growth rates (Gregory et al. 1982). Genetic pressures seem unlikely to underlie the difference because *P. argus* has a long-lived dispersal larva (see Moe 1991, Lipcius and Cobb 1994) which would tend to preclude any genetic isolation in the Florida Keys. However, several common fishery practices that could differentially slow growth of some Florida Keys lobsters are not present in the Dry Tortugas. One such fishery practice is the "baiting" of traps with two to four sublegal lobsters, which attract other lobsters to the vicinity of the trap. In a fishery with approximately 600,000 traps, potentially 2 million lobsters may be confined in traps at any one time (Lyons et al. 1981; Florida Marine Research Institute, unpubl. data). The confined lobsters die of starvation or predation, escape, or are released after a period of starvation. Hunt et al. (1986a) observed a mortality rate of 26% for lobsters subjected to a 4-week confinement. Average confinement in the fishery, however, may exceed 4 weeks (Hunt et al. 1986b). Weight loss attributed to starvation was observed in lobsters after 3 weeks of confinement (Lyons and Kennedy 1981). We do not know how many of these confined lobsters die, escape, or are released, but at the very least, those that return to the population are at a physical disadvantage because of starvation and must overcome a large energy deficit to resume growth.

Another fishery practice that can cause sublethal injury and slow growth is the mishandling of lobsters by fishers as they pull their traps or by divers as they capture or attempt to capture lobsters. During these activities, the legs and antennae of lobsters are occasionally broken. These appendages are regenerated, but at a metabolic cost that reduces growth (Davis 1981).

The breeding season in the Dry Tortugas was approximately 2 months shorter than that in the Florida Keys fishery. Also, the size of nearly all Dry Tortugas egg-bearing females is greater than 80 mm CL, whereas the size of nearly all egg-bearers in the fishery area is less than 90 mm CL (Fig. 4). Therefore, developing mutually exclusive hypotheses to test why the two populations produce eggs on such different time schedules would be difficult because size and location would confound any analysis. To investigate the roles that lobster size and location play in the reproductive dynamics of Caribbean spiny lobster, more research including nutritional status, in both the field and laboratory, on lobsters is needed. Research on the metabolic costs of sublethal injury and starvation plus a method to determine

the age of Caribbean spiny lobsters is also needed. Nonetheless, these data indicate major differences in reproductive patterns between exploited and unexploited areas, and suggest the importance of protecting some areas to enhance egg production at the population level.

Acknowledgments

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Efficacy of Blue Crab Spawning Sanctuaries in Chesapeake Bay

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Abstract

Sanctuaries can potentially protect a significant fraction of the spawning stock, and thereby sustain heavily exploited populations. Despite the worldwide use of marine and estuarine spawning sanctuaries, the effectiveness of such sanctuaries remains untested. We therefore attempted to quantify the effectiveness of the spawning sanctuaries for adult female blue crabs (*Callinectes sapidus*) in Chesapeake Bay. We used baywide winter dredge survey data to estimate the potential spawning stock prior to the major exploitation period, and summer trawl survey data to estimate spawning stock abundance within the Lower Bay Spawning Sanctuary and adjacent Bayside Eastern Shore Sanctuary during the reproductive period. Hence, we were able to approximate the percentage of the potential spawning stock that was protected by both sanctuaries after exploitation. On average, approximately 16% of the potential spawning stock survived to reach the Lower Bay Spawning Sanctuary and Bayside Eastern Shore Sanctuary. Even under a best-case scenario (i.e., crab residence time of 2 weeks), the sanctuaries only protected an estimated 22% of the potential spawning stock, which is well below the percentage recommended by recent stock assessments for sustainable exploitation (28%). In the worst case, a mere 11% of the potential spawning stock survived to reach the spawning sanctuaries. Hence, we recommend a substantial expansion of the spawning sanctuaries, as well as the complementary protection of other life stages

in critical habitats, such as nursery grounds and dispersal corridors. Furthermore, traditional fisheries management measures (e.g., effort control) should be used in concert with sanctuaries to thwart impediments to effective implementation of the sanctuaries, such as redirected fishing effort.

Introduction

Use of Marine Reserves

Fishing can drastically reduce the abundance of exploited stocks by growth or recruitment overfishing (Bohnsack 1990, Roberts and Polunin 1991). Similarly, environmental disturbances such as hurricanes can disrupt even the most productive ecosystems (Knowlton 1992, Hughes 1994, Butler et al. 1995). Their effects can be catastrophic, causing either dramatic population decline (e.g., Hughes 1994) or transitions between alternative states (Knowlton 1992). Marine reserves and sanctuaries can potentially moderate these impacts, enhance stocks, and facilitate long-term, sustainable exploitation (Davis 1977, Alcala and Russ 1990, Bohnsack 1993, Carr and Reed 1993, Roberts and Polunin 1993, Tegner 1993, Rakitin and Kramer 1996, Russ and Alcala 1996) by increasing abundance, average size, reproductive output, recruitment, and genetic diversity (Dugan and Davis 1993).

There is much evidence, though primarily descriptive, that details significant increases in abundance and average size of fishery species within reserves (Gitschlag 1986, Alcala 1988, Davis and Dodrill 1989, Funicelli et al. 1989, Rutherford et al. 1989, Alcala and Russ 1990, Bohnsack 1990, Yamasaki and Kuwahara 1990, Rakitin and Kramer 1996, Russ and Alcala 1996). The two major postulated benefits of this phenomenon to fishery stocks include (1) enhancement of the spawning stock, which subsequently magnifies recruitment of larvae, postlarvae, and juveniles to reserve and non-reserve areas; and (2) export of biomass to non-reserve areas when exploitable individuals migrate from protected areas to the fishing grounds (Bohnsack 1990, Polunin and Roberts 1993, Hastings and Botsford 1999, Sladek-Nowlis and Roberts 1999).

Simple prohibition of exploitation in a refuge or sanctuary does not ensure that target species will recover (Dugan and Davis 1993). Where the abundance and size of target species do not differ between reserve and exploited areas, the similarity in estimates may be due to improper sampling design, migrations outside protected zones, or the lack of critical habitats within reserves (Polachek 1990, Dugan and Davis 1993). For example, when spawner sanctuaries were established in marginal habitats, trochus snail (*Trochus niloticus*) and hard clam (*Mercenaria mercenaria*) populations did not increase (Helsinga et al. 1984, McCay 1988). Hence, empirical estimates of the impact of marine reserves or sanctuaries upon the target species are required to validate and assess the utility of the reserves. Although marine reserves and sanctuaries have become popularized as conservation tools, their effectiveness in sustaining or enhancing

marine fisheries remains virtually untested (Allison et al. 1998). Thus, we assessed the efficacy of spawning sanctuaries for the blue crab spawning stock in lower Chesapeake Bay.

Blue Crab Life History and Ecology in Chesapeake Bay

The blue crab, *Callinectes sapidus* Rathbun (Arthropoda: Crustacea: Decapoda: Portunidae), is dispersed widely along the Atlantic and Gulf coasts of North America, and has been abundant throughout Chesapeake Bay (Williams 1984, Hines et al. 1987, Lipcius and Van Engel 1990). This species is important in energy transfer in estuaries, serving as both omnivore and prey (Baird and Ulanowicz 1989). The diet of blue crabs consists mainly of bivalve mollusks, and includes conspecifics, polychaetes, other crabs, and fish (Laughlin 1982, Alexander 1986, Hines et al. 1990, Mansour and Lipcius 1991, Ebersole and Kennedy 1995).

The life history of the blue crab (Fig. 1, illustration provided by J. van Montfrans and R. Orth, Virginia Institute of Marine Science) is complex and bears upon the efficacy of sanctuaries for this species. Mating typically occurs from May through October, whereby a male couples with a female that is approaching her terminal molt to maturity. When the female undergoes the terminal molt and is in the soft-shell stage, the pair mates and the male protects the female until her shell hardens (Van Engel 1958).

After mating, females begin a migration toward the lower bay where they will eventually spawn and release their larvae in higher salinities. Those females that reach the Lower Bay Spawning Sanctuary (LBSS) and adjacent Bayside Eastern Shore Sanctuary (BESS) (Fig. 2) are protected from fishing during 1 June-15 September, which encompasses the reproductive period when most females bear eggs (Jones et al. 1990; Lipcius, unpubl. manuscript). Males do not migrate to the bay mouth, but overwinter in the deeper waters of the rivers and bay mainstem (Van Engel 1958). Some females overwinter within the sediments throughout the bay prior to completing their migration to the lower bay the following spring (Lipcius et al. 2001). Prior to the migration, blue crabs are exploited by various fisheries (e.g., peeler and pot fisheries).

Blue Crab Fisheries and Sanctuaries

The blue crab is fished heavily in Chesapeake Bay (Miller and Houde 1998, Rugolo et al. 1998). Exploitation rates have increased substantially in this decade (Miller and Houde 1998, Rugolo et al. 1998, Lipcius and others, unpubl. manuscript), resulting in a decrease in total catch per unit of effort in both the pot and winter dredge fisheries (Rugolo et al. 1998). Furthermore, the spawning stock has concurrently decreased by over 80% (Lipcius, unpubl. manuscript; Lipcius and others, unpubl. manuscript), suggesting that the population is overexploited. Caution is therefore needed in management of this fishery to avoid a stock collapse.

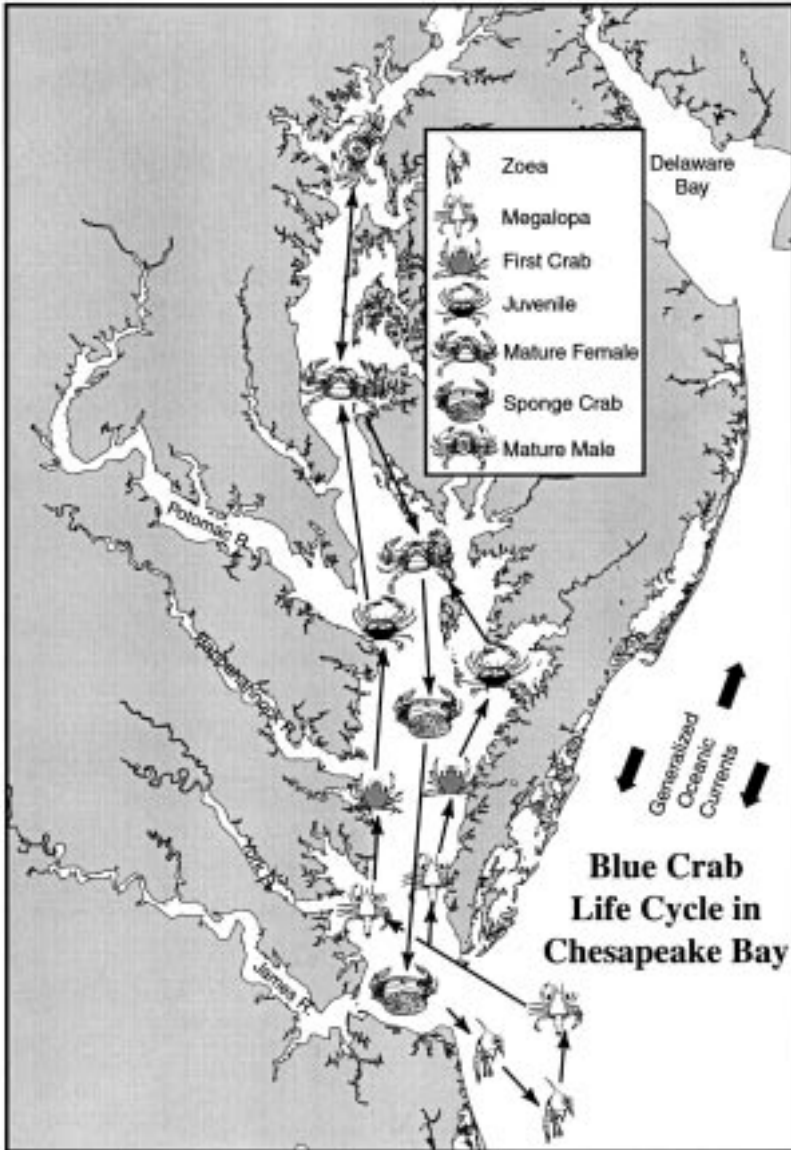


Figure 1. Life history of blue crab in Chesapeake Bay. Large heavy arrows indicate dominant summer water flow. Each stage or position in the bay is represented by a crab symbol (starting from the bay mouth): Larvae develop in coastal currents during summer and early fall; Postlarvae re-enter the estuary and settle in lower bay sea-grass beds from mid-summer through early fall; Juvenile crabs develop in seagrass and disperse up tributaries and up-bay in late summer, fall, and the following spring; Crabs mate in the bay's tributaries and shallower mainstem waters from spring through fall; Mated females migrate down-bay; Females spawn egg masses in the lower bay from late spring through summer before hatching their larvae.

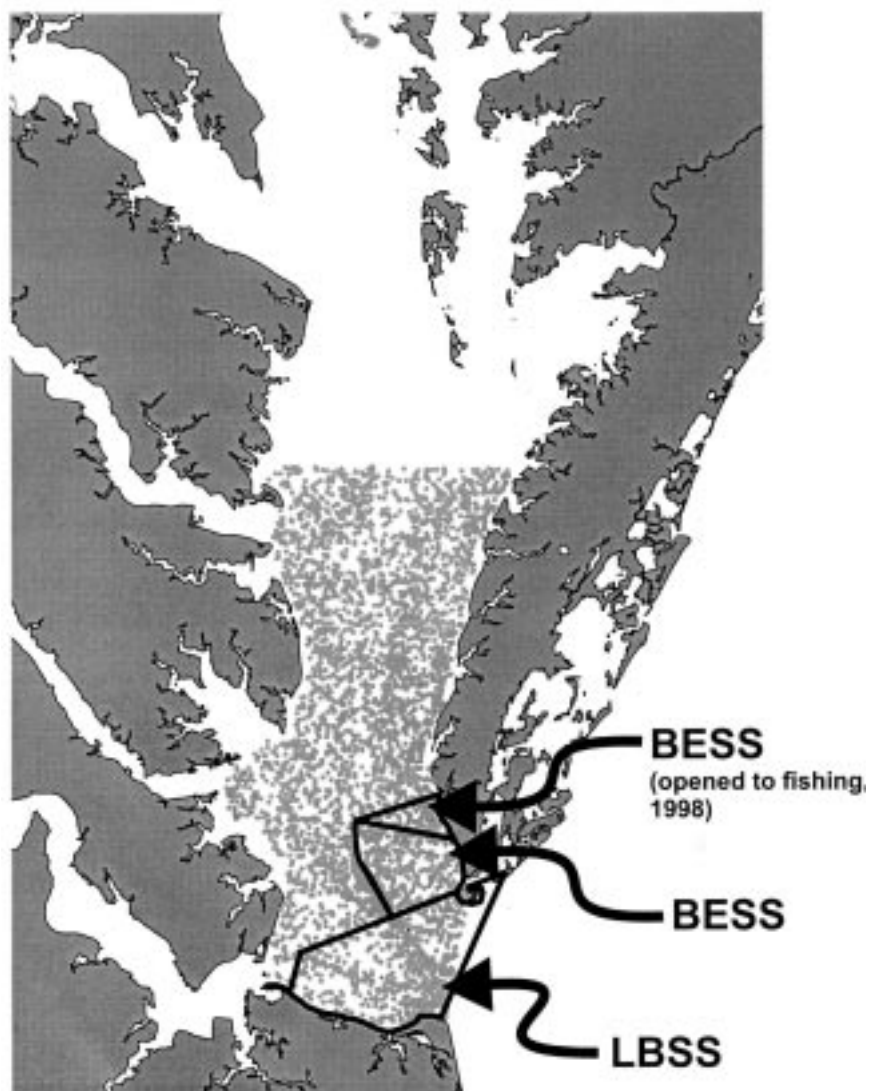


Figure 2. Lower bay blue crab sanctuary boundaries (black line) and Virginia trawl survey sampling sites 1989-1999 (gray dots). Three segments of the sanctuaries are depicted: (1) the Lower Bay Spawning Sanctuary (LBSS), which is closed to crab potting 1 June-15 September; (2) the original Bayside Eastern Shore Sanctuary (BESS), which is closed to crab potting 1 June-15 September; and (3) the current BESS which was reduced in 1998.

Because of its complex life cycle, there are several productive fisheries for the blue crab in Chesapeake Bay characterized by gear and methodology, including (1) pot, (2) winter dredge, (3) scrape, (4) peeler pound and trap, (5) trot line, and (6) recreational gear. The pot fishery (1 April-30 November) targets hard-shelled crabs, both throughout the bay and tributaries of Virginia and in the mainstem bay of Maryland. Trot lines are used exclusively in Maryland tributaries where pots are prohibited. In Virginia, about 83% of the total catch of crabs is taken by the hard crab and peeler pot fisheries (Burreson et al. 2000). The "jimmy pot" fishery is a subset which uses adult males to attract females to pots during the spring and fall when females are mating and migrating to the mouth of the bay to spawn (Van Engel 1958). In Maryland, the pot fishery takes 61-67% of the annual landings and the trot line fishery 30-36% (Burreson et al. 2000). The winter dredge fishery (1 December-31 March) primarily targets recently matured and mated female crabs that bury into the sediment in the deeper waters at the mouth of Chesapeake Bay. This fishery takes about 15% of the total crab catch in the bay (Burreson et al. 2000). The scrape fishery targets juvenile crabs in the seagrass beds mainly near Tangier Island, Virginia and Smith Island, Maryland. The peeler pound and soft crab fisheries target crabs in pre-molt status that are delivered to tanks where they are shed to the soft crab stage, and afterward sold as fresh or frozen soft crabs. Otherwise, these are sold as peelers in the bait trade. Together, the scrape and pound fisheries take only 1-2% of the total crab landings (Burreson et al. 2000). Finally, the year-round recreational fishery targets crabs mostly at the shoreline and removes an estimated additional 15% of the landings (Rob O'Reilly, Virginia Marine Resources Commission [VMRC], Newport News, VA, pers. comm., Dec. 1999).

To prevent overexploitation, Maryland, Virginia, and the District of Columbia have established various controls on the blue crab fisheries. Each fishery is regulated differently depending on whether the crabber is in Maryland, Virginia, or the Potomac River. Commercial crabbing regulations comprise license, gear, and crab size restrictions, catch limits, season, time, or area restrictions such as sanctuaries (Table 1).

One management strategy has been to establish spawning sanctuaries, where crabbing is prohibited for selected time periods. Some sanctuaries in Chesapeake Bay exist for the benefit of the blue crab (e.g., LBSS), whereas others are implied sanctuaries that are delineated for the ease of navigation or fishing. Each crab sanctuary in Chesapeake Bay affects a different segment of the crab population and its associated fishery (Table 1, Fig. 2). Both the LBSS and BESS affect the pot fishery, and are closed to ease fishing pressure upon adult females that have migrated to the lower bay to spawn and release larvae. The LBSS has been in existence for decades (Van Engel 1958); in December 1994, the BESS was established and has protected crabs from 1995 to present. The upper portion of the BESS was removed and opened to fishing in 1998 (Fig 2.) Shipping channels in Virginia are closed to potting to eliminate navigational hazards.

Table 1. Blue crab sanctuaries, both intended and implied, for Maryland and Virginia portions of Chesapeake Bay.

Name of sanctuary or implied sanctuary	Fishery affected	Dates closed	Comments
Lower Bay Spawning Sanctuary and Bayside Eastern Shore Management Area (Virginia)	Pot	1 June-15 Sept.	Closed to crab potting. Dredging begins 1 Dec.
Virginia Shipping Channels (Virginia)	Pot	Year-round	Crab pots prohibited.
Maryland Tributaries (Maryland)	Pot	Year-round	Closed to crab potting. Trot lines allowed.
Virginia Tributaries (Virginia)	Dredge	Year-round	Closed to dredging in river inlets or creeks.
Hampton Roads Sanctuary (Virginia)	Dredge	Year-round	Closed to crab dredging upriver of Hampton Roads Bridge Tunnel.

Objectives

Sound management and sustainable use of a living resource requires a strong ecological foundation (McAllister and Peterman 1992). This investigation provides the first empirical estimate of the percentage of a population protected by a sanctuary; specifically, we examined the efficacy of the LBSS and BESS. We thereby present information that will foster conservation and enhancement of the blue crab stock and its critical habitats in Chesapeake Bay. Our approach involved estimating crab abundance during two time periods. First, a winter dredge survey provided a population-wide estimate of the potential spawning stock (i.e., all adult females and immature females which would mature and spawn the following summer) prior to most exploitation. We reduced the November winter dredge survey estimates by 6 months of natural mortality (0.375 per year for 6 months). Second, a summer trawl survey within the spawning sanctuaries provided an estimate of the number of females that survived exploitation and successfully migrated to the spawning sanctuaries. The second estimate divided by the first yielded an estimate of the annual proportion of the potential spawning stock that survived natural mortality and exploitation to spawn in the spawning sanctuaries (i.e., the efficacy of the sanctuaries).

Methods

Baywide Dredge Survey

The winter dredge survey is conducted throughout Chesapeake Bay and consists of annual sampling at monthly intervals from November through March. The dredge survey sampled the blue crab population using a stratified random design, which divided Chesapeake Bay into three geographic strata: upper, middle, and lower Chesapeake Bay. Since blue crabs bury in the sediments during the winter, thereby sharply restricting their movement, sampling during the winter provides a “snapshot” of the static, sedentary population prior to extensive exploitation in the spring. Some exploitation, however, has occurred in the previous fall after the new year class of crabs has reached an exploitable size.

In the sampling, 1,500 sites deeper than 1.5 m were selected randomly, and apportioned by the area of each stratum. The upper bay stratum included the tributaries, creeks, and upper mainstem of Chesapeake Bay. The middle and lower bay strata encompassed the middle and lower portions of the bay mainstem.

Survey vessels used identical sampling gears: standard “Virginia crab dredges” (width 1.83 m) lined with hexagonal mesh (12.7 mm). At each sampling site, the vessel sampled for 1 minute at a constant speed of ~3 nautical miles per hour. LORAN or GPS coordinates were recorded at tow start and end points and were later used to calculate mean distance covered. Each crab was measured (carapace width [cw] in millimeters), and the sex, maturity, and overall condition recorded.

The stratified random survey was implemented following standard methods (Lipcius and Montane 1997). Efficiency experiments were conducted annually to provide catchability coefficients used in calculations of absolute abundance (Lipcius and Montane 1997).

From the dredge survey November data, we summed the 1+ immature females (females > 60 mm cw, but without the circular abdomen characterizing adult females) and adult females (all females with a circular abdomen, regardless of size) to represent the potential spawning stock. This spawning stock estimate was not the full potential spawning stock, as a small segment of it had been fished prior to the dredge survey. Consequently, our estimates of the proportion of the potential spawning stock reaching the sanctuaries were liberal. We then multiplied the November spawning stock by the natural mortality rate of 0.375 per year \times 6/12 months to get the spawning stock after 6 months of natural mortality.

Virginia Trawl Survey

Field Sites and Sampling

Blue crab adult females release larvae in the lower reaches of Chesapeake Bay each year from June through mid-September (Van Engel 1958, Jones et al. 1990, van Montfrans et al. 1995). Hence, an accurate measure of the spawning stock necessarily involves sampling of adult females in the spawn-

ing grounds of lower Chesapeake Bay from June through September. Our trawl samples were taken monthly in the lower bay spawning grounds (Fig. 2) from June through September and provide an estimate of the spawning stock.

Density

Adult female blue crabs were sampled with a stratified random trawl survey in the lower bay. Details of sampling are given by Lipcius and Van Engel (1990), Hata (1997), and Lipcius (unpubl. manuscript). Each density value from a single 5-minute tow served as an independent datum (i.e., number of adult females per tow); annual sample sizes usually averaged about 50 tows. Density was analyzed as the arithmetic mean number of adult females per tow.

There were no trawls taken in the LBSS in August 1998, or in the BESS in August 1995 or 1998. For years where samples were taken in all 4 months, there were significant correlations between the total abundance over all months in which the sanctuary was in effect (sum from June, July, August, and September) and the total abundance in all months excluding August. Therefore, regression equations (LBSS: $\text{Total} = 1180442 + 1.07 \times [\text{Total} - \text{August}]$, $r^2 = 0.69$, $P = 0.003$; and BESS: $\text{Total} = 355903 + 0.629 \times [\text{Total} - \text{August}]$, $r^2 = 53.3$, $P = 0.04$) were used to replace the missing August abundances. In analyses with these data, the degrees of freedom were reduced by the number of these samples.

We calculated adult female abundance within LBSS and BESS from trawl survey data. Densities were converted to abundances using each sanctuary's area and an overall trawl efficiency of 22%, which was measured for equivalent gear in Chesapeake Bay habitats (Homer et al. 1980). The 22% trawl efficiency estimate is sound, since Homer et al. (1980) used the DeLury cumulative catch method; repetitive 500 m trawls were made in a small discharge canal of the Chalk Point Power Plant in the Patuxent River, Maryland until the rate of decrease between consecutive hauls approached zero (~10 trawls). Furthermore, movements of fish and crabs into and out of the canal were minimal during daytime when efficiency studies were conducted (Homer et al. 1979). Trawl efficiencies for blue crabs averaged 25% in July and 19% in September, yielding a mean efficiency of 22% during the summer and fall (Homer et al. 1980).

Calculations

Crab densities from trawl survey data were converted to abundances as follows: (1) The arithmetic mean monthly density of adult female crabs per trawl was estimated from 1989-1999. (2) The average distance covered during each 5-minute trawl was estimated from 1990-1994 to be 385 meters per trawl (Paul Gerdes, Virginia Institute of Marine Science, Gloucester Point, VA, pers. comm., May 1997). (3) The estimated width of the trawl (5.182 m) was multiplied by the mean distance covered by the trawl to obtain mean

area covered by each trawl ($5.182 \text{ m} \times 385 \text{ m}$ per trawl = $1,995 \text{ m}^2$ per trawl). (4) The mean monthly number of crabs per trawl was multiplied by the area covered by each trawl to obtain density per hectare. For example, in June 1989 in the LBSS, 1.57 crabs per trawl divided by $1,995 \text{ m}^2$ per trawl = 7.88×10^{-4} crabs per m^2 or 7.88 crabs per hectare. (5) The area covered by the LBSS sanctuary is 39,600 hectares, and the area of the BESS was 19,400 hectares for 1995-1997, which was changed to 16,000 hectares for 1998-1999 (Tina Hutcheson, VMRC, Newport News, VA, pers comm., Dec. 1999). This value was then multiplied by each monthly trawl estimate of density to obtain the total number of crabs residing within each sanctuary's bounds in each month. (6) Since trawling is only 22% effective (Homer et al. 1980), each value was multiplied by 4.55 to estimate the absolute number of crabs residing in the sanctuary. (7) Monthly estimates of crab abundance were summed for each year to get an estimate of total annual abundance of crabs in each sanctuary (using only 1995-1999 for the BESS). (8) To account for crab residence time, abundance estimates were multiplied by 1, 1.5, and 2.

Efficacy of the Lower Bay Spawning and Bayside Eastern Shore Sanctuaries

We estimated the efficacy of the blue crab sanctuaries, the LBSS and BESS, by calculating the percentage of all adult females in the Bay that resided within each sanctuary using the following equation:

$$\Sigma AF_{\text{sanctuary}} / SS_{\text{Bay-May}} = \text{Sanctuary Efficacy}$$

where $\Sigma AF_{\text{sanctuary}}$ was the sum over 4 months (June-September) of adult female crabs in both sanctuaries (determined from summer trawl surveys) and $SS_{\text{Bay-May}}$ was the potential spawning stock of female crabs, determined from the baywide dredge survey in November and reduced by natural mortality over 6 months (= spawning stock in May).

Our estimates of the spawning stock reflect the number of spawning events, whether by individual females or females spawning multiple times, and are therefore consistent with recent stock assessments (Miller and Houde 1998, Rugolo et al. 1998). These estimates give equal weight to crabs spending a small or large amount of time in the sanctuary, since each crab that enters was assumed to spawn once. After a female spawns within a sanctuary, she leaves, possibly to return and spawn again. Therefore, estimated number of crabs protected by the sanctuary depends upon each crab's residence time in the sanctuary. For example, when sampling is monthly and a crab's residence time is 2 weeks, our sampling underestimates by $1/2$ the number of crabs in the sanctuary. Hence, we examined the sensitivity of our estimates to residence time. Our estimates can be recalculated to incorporate new empirical estimates of residence time as these data become available.

Crab residence time within the sanctuary is unknown, but is likely near 2-4 weeks (McConaugha 1992, Prager 1996). To examine the sensitivity of our abundance estimates to residence time, we selected residence times of 2, 3, and 4 weeks. We therefore generated three sets of estimates for crab abundance in the sanctuaries: one for a minimum residence time (2 weeks, multiplication factor of 2), yielding a maximum abundance estimate; one for an average residence time (3 weeks, multiplication factor of 1.5), giving an average crab abundance; and one for a maximum residence time (4 weeks, multiplication factor of 1), yielding a minimum abundance estimate. If, in the future, crab residence time is precisely determined, the most accurate of our three estimates can be used, since our assumptions and calculations for three different residence times are discussed herein. For simplicity, most of the results are portrayed for a mean residence time of 3 weeks.

Finally, using the baywide abundance of all 1+ females available 1 June (which represent the potential spawning stock) and abundance of crabs within each sanctuary, we estimated the percentage of the total spawning stock that reached each of the two sanctuaries (LBSS and BESS) and was therefore protected by them. The fraction of the spawning stock protected by the sanctuaries was calculated as follows: the sum of females in each sanctuary over 4 months ($\sum AF_{\text{sanctuary}}$) was divided by the estimated total number of females in the bay in May ($SS_{\text{Bay-May}}$) to calculate the percentage of the spawning stock that was protected (i.e., sanctuary efficacy).

Densities by Geographic Zone

We also examined crab densities in the two lower bay sanctuaries in relation to the area that was removed from the BESS and opened to fishing in 1998 (Fig. 2) and the rest of the lower bay (not contained within a sanctuary). Samples were not taken in all areas in all months; data from months where sampling in a given area was not conducted were replaced with annual averages from months where sampling was completed. A two-way analysis of variance was performed using area and year as factors; degrees of freedom were reduced by the number of estimated values.

Results

Baywide Female Abundance

The baywide dredge survey abundance of 1+ females at the end of May (from November dredge survey abundance reduced by six months of natural mortality) ranged from a high of 190 million crabs in the 1990/1991 season to a low of 42 million in the 1998-1999 season, with an average of 111.4 ± 15.5 (S.E.) million crabs (Fig. 3). Most of the high annual abundances occurred in or before 1994; those from 1995 to the present were substantially lower.

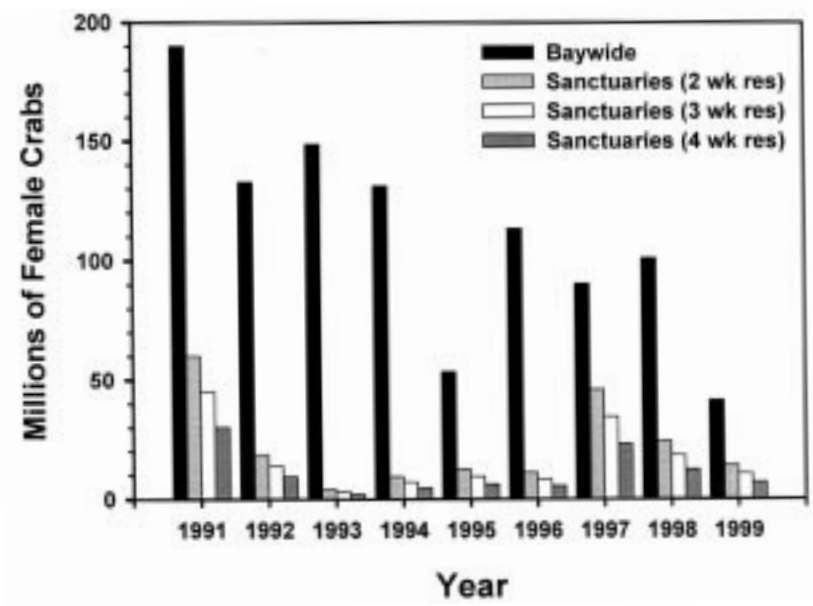


Figure 3. Female crab abundance baywide and within sanctuaries. Annual baywide abundance of 1+ females (mature and immature) is from November winter dredge survey data, 1991-1999 seasons (dark shading). The season of a given year includes November of the previous year (e.g., 1991 season includes November of 1990). Lighter-shaded bars are the abundance of adult females in the Lower Bay Spawning Sanctuary and the Bayside Eastern Shore Sanctuary combined under the assumption of different residence times—multiplication factors of 2 for 2 weeks, 1.5 for 3 weeks, and 1 for 4 weeks.

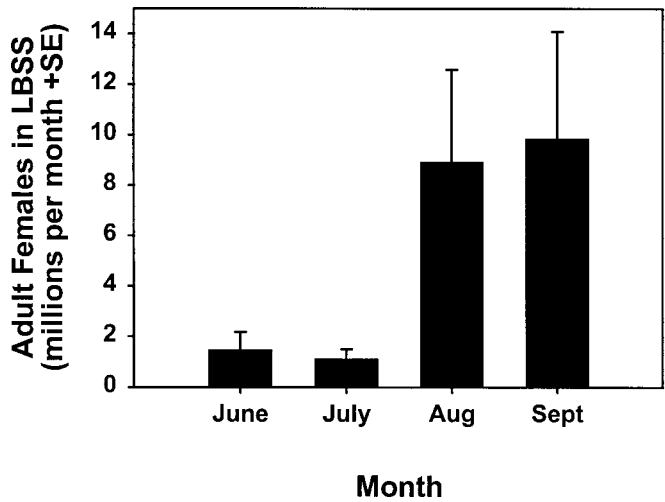


Figure 4. Mean monthly abundance of crabs within the LBSS (millions of females + S.E.) from 11 years (1989-1999) from VIMS trawl survey data and an assumed 3-week residence time.

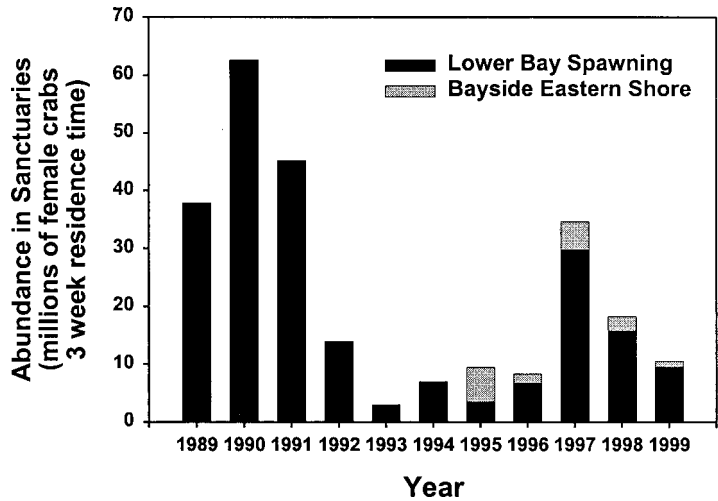


Figure 5. Abundance of adult female crabs within the LBSS (dark shading) during 1989-1999 and the BESS (light shading) during 1995-1999 (the years since establishment of this sanctuary) under the assumption of a 3-week residence time, resulting in the total annual number of crabs protected from fishing pressure in the lower bay 1 June-15 September. Note that the area of the BESS was reduced in 1998.

Female Abundance within Sanctuaries

Adult females enter the lower bay sanctuaries in June and continue to arrive through September (Lipcius et al. 2001). Across the 11 years investigated for the LBSS, crabs were significantly more abundant in August and September than in June and July (Fig. 4; ANOVA, d.f. = 3,39, $F = 2.85$, $P = 0.049$; SNK test). Assuming a residence time of 3 weeks, 3-62 million female crabs were protected by the LBSS (Fig. 5). The BESS protected an additional 1-6 million crabs, which was reduced to 1.0-2.5 million after the BESS was diminished in 1998 (Fig. 5).

Percentage Surviving within Sanctuaries

On average $16 \pm 4\%$ (mean \pm S.E.) of the potential spawning stock was protected by the sanctuaries, assuming a 3-week residence time (Fig. 6). With 2-week and 4-week residence times, the average percentages of the spawning stock protected by the sanctuaries were $22 \pm 5\%$ and $11 \pm 3\%$, respectively (Fig. 6). On average, the percentage of crabs protected was lower during 1991-1994 (mean = 10.4%), when crab abundance was high, than during 1995-1999 (mean = 21.0%), when abundance was low (Fig. 6).

Densities by Geographic Zone

Although the LBSS had highest densities (Fig. 7), there were no significant differences in density by sanctuary or non-sanctuary area (ANOVA, $P > 0.05$). Sample sizes were low, however, particularly in the area removed from the BESS.

Discussion

On average, approximately 16% (range of means = 11-22%) of the Chesapeake Bay's potential spawning stock of the blue crab was protected by a combination of the Lower Bay Spawning Sanctuary (LBSS) and Bayside Eastern Shore Sanctuary (BESS). This estimate is unique in being a first attempt to assess the efficacy of a sanctuary quantitatively. Although the existing blue crab sanctuaries apparently protect a fraction of the potential blue crab spawning stock, is it enough to promote sustainable exploitation?

Miller and Houde (1998) proposed that approximately 28% of the "virgin" spawning stock of the blue crab should be protected for long-term sustainable exploitation. This percentage was derived from a total mortality rate (Z) of 1.275, which was the sum of a 0.9 fishing mortality rate (Miller and Houde 1998) and 0.375 natural mortality rate (Rugolo et al. 1998). On average (i.e., crab residence time of 3 weeks), the spawning sanctuaries only protected an estimated 16% of the potential spawning stock. Furthermore, some small portion of the potential spawning stock was exploited prior to our winter survey, such that our estimates were liberal (i.e., higher than the expected true fraction). Accordingly, we conclude that the spawning sanctuaries at best protect about $\frac{3}{4}$ (~22%), and at worst about $\frac{1}{3}$ (~11%)

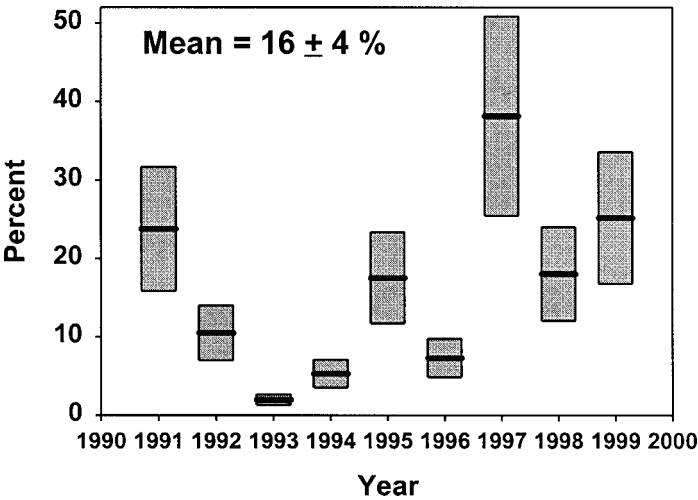


Figure 6. Mean (3-week residence time) annual percentage of adult female crabs in both sanctuaries out of the total number of female crabs baywide on 1 June. Positive and negative extent of error boxes represent the estimates for 2-week and 4-week residence times, respectively.

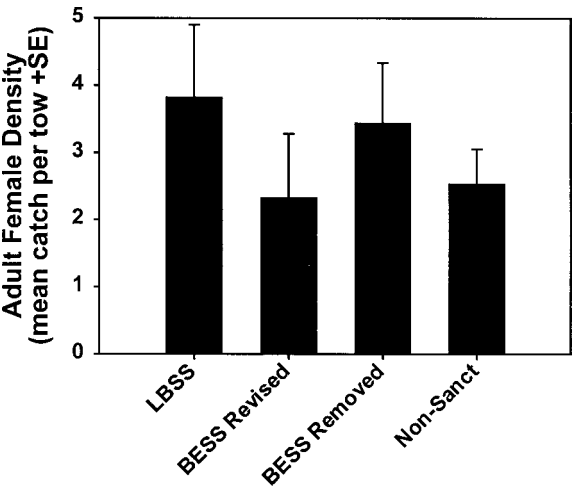


Figure 7. Mean adult female crab densities in the different sanctuary and non-sanctuary areas. LBSS = Lower Bay Spawning Sanctuary, BESS Revised = Bay-side Eastern Shore Sanctuary with the current area, BESS Removed = the small pie-shaped area that was removed from the BESS in 1998, and Non-Sanct is the rest of the lower bay that is not included in either sanctuary. Estimates were made from 1989-1999 trawl survey data.

of the estimated sustainable blue crab spawning stock. We therefore recommend a substantial expansion of the lower bay blue crab sanctuaries to arrive at a minimum of 28% protection. Furthermore, we suggest that the sanctuary area added be within the “deepwater corridor” (i.e., channels greater than 13 m) where there are significantly higher densities of adult female crabs than in the shallows (Lipcius et al. 2001). There should also be attention to complementary effort controls that limit displaced effort, which could abrogate any value of expanded sanctuaries. Finally, we recommend modeling of the effect of the expanded sanctuaries upon exploitation rates and spawning stock abundance (e.g., Miller and Houde 1998).

Although the added protection of the BESS was not exceptional, in years when crab abundances were low (e.g., 1995 and 1996) this sanctuary almost doubled the number of crabs protected from exploitation, and was therefore a worthwhile addition to the spawning sanctuary. Furthermore, crab densities within the removed portion of the BESS were among the highest in the lower bay, and the reduction in area of the BESS in 1995 significantly diminished the abundance of protected blue crabs. Hence, we also recommend reinstatement of this portion of the BESS to the spawning sanctuaries.

Given that the lower bay spawning sanctuaries are necessary but not sufficient in preserving a sustainable portion of the spawning stock, the addition of a proposed deepwater migration corridor for adult females could enhance the percentage of protected females in the spawning grounds (Lipcius et al. 2001). This, in addition to an expansion of the existing spawning sanctuary, may protect a sufficient proportion of the blue crab spawning stock, though various problems associated with sanctuaries and reserves, such as redirected effort, need to be addressed (Lipcius, unpubl. manuscript). Temporal expansion of the spawning sanctuaries might also appear to be a desirable management strategy since mating and egg production begin in May and the sanctuaries are not in effect until 1 June.

In sum, we have presented an empirical estimate for the efficacy of spawning sanctuaries for the blue crab in Chesapeake Bay which indicates that the existing sanctuaries do not protect a sufficient fraction of the spawning stock for sustainable exploitation. We suggest the addition of a deepwater corridor coupled to the spawning sanctuaries in the lower bay to selectively conserve female crabs migrating to or residing in the lower bay spawning grounds (Lipcius et al. 2001). If fishing effort is not substantially redirected, an expanded sanctuary would promote a more stable and abundant spawning stock interannually (Lipcius and others, unpubl. manuscript). Based on our analyses, an expansion of the existing spawning sanctuary seems necessary to conserve the blue crab spawning stock in Chesapeake Bay.

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Simulation of the Effects of Marine Protected Areas on Yield and Diversity Using a Multispecies, Spatially Explicit, Individual-Based Model

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Abstract

The OSMOSE (Object-oriented Simulator of Marine biOdiverSity Exploitation) multispecies model is used to simulate the effects of Marine Protected Areas (MPAs) in the framework of nontargeted multispecies fisheries. The modeled theoretical populations are structured according to age and size. The predatory behavior rules by which they interact are implemented at the fish school level. Each species is attributed a mean distribution area within which, at each simulated year, the larval production is randomly distributed. The results of the simulations show that at high fishing rates, the setting of an MPA can enable the maintenance of the mean overall catches at a high level. In particular, for exploitation rates resulting in mortality rates greater than F_{MSY} , implementing different sizes of MPA highlights the existence of an optimal size for the MPA. Furthermore, the comparison of the effects induced by the direct reduction of the fishing effort, and by the closing of some fishing areas, suggests that this latter management measure is more efficient in terms of catch maximization and biodiversity conservation. This theoretical advantage is supposed to result from a particularity inherent to implementation of MPAs, which would indeed enable the preservation of not only a global fraction of the populations but also a set of trophic interactions that are localized in space and time. However, these results must be cautiously considered, as other po-

tentially important parameters have not been taken into account in the present work such as diffusive and migratory characteristics of the resource.

Introduction

With fishing effort intensifying on an increasing number of marine species, marine biodiversity conservation is becoming a critical issue for management (Hammer et al. 1993, Carlton and Butman 1995, Boehlert 1996, Eichbaum et al. 1996, Richards and Maguire 1998). One approach which is advocated for protecting marine biodiversity and promoting the sustainable use of marine resources is the implementation of Marine Protected Areas (Plan Development Team 1990, Ticco 1995, Bohnsack and Ault 1996, Eichbaum et al. 1996, Botsford et al. 1997, Hall 1998, Lauck et al. 1998, Castilla 1999). MPAs would allow the re-creation of natural refuges, which in the past have been too deep, isolated, and inaccessible to the exploitation (Dugan and Davis 1993). Along with this aim of conserving natural ecosystems, MPAs also provide an insurance against stock collapse (Attwood et al. 1997). Empirical and theoretical studies suggest that MPAs would allow increased yields, particularly when fishing mortality rates are important (e.g., Russ and Alcala 1990, Dugan and Davis 1993, Man et al. 1995, Lauck et al. 1998, Guénette and Pitcher 1999). Testifying to the increasing interest given to marine refuges for the maintenance of coastal ecosystems, the World Conservation Union has set before itself the objective to ban fishing from 20% of coastal waters by the year 2000 (IUCN 1992). However, there is still currently a lack of criteria to determine the optimal spatial limits of protected areas, as well as a lack of in situ observations to judge their long term consequences. Modeling work on marine reserves, then, takes its whole importance by allowing simulation of the effects of refuges in different configurations of the exploitation and the resource. On the other hand, the necessity of considering interactions between species in the study of MPAs is highlighted but scarcely taken into account in practice (Hall 1998). In this context, the individual-based model OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation) is used to investigate the potential effects induced by the implementation of an MPA on the exploitation of multispecies assemblages. The study is limited to the influence of refuge size and initial fishing level on both catches and diversity of the exploited ecosystem.

Methods

The Multispecies Model OSMOSE

An Individual-Based Model

The individual-based approach consists in following the fate of all individuals in a population, by assigning them some behavior rules that take

into account local interactions between individuals and with their environment (Huston et al. 1988, DeAngelis and Gross 1992, Van Winkle et al. 1993). It indeed postulates that minor events between individuals can have significant effects on the dynamic and the global state of the populations (Judson 1994).

One of the main hypotheses of the OSMOSE model is predation opportunism. This opportunism can readily be managed at the individual level by applying the "localization principle" which establishes that an individual is affected exclusively by the organisms that are located in its spatio-temporal vicinity (DeAngelis and Gross 1992). The choice of an individual-based approach is also justified by the second modeling hypothesis, namely that the criterion for the selection of prey is based on body size, and this can be characterized at the individual level.

OSMOSE is developed in the object-oriented language Java (JDK 1.1.3, Sun Microsystems). One important step in the development of OSMOSE was the choice of the biological entity corresponding to a computer individual. To allow significant gain in calculation time, the model is not brought down to the individual fish level but to an aggregated level corresponding to a group of fish having similar biological attributes and behavior rules regarding the modeled processes. The "super-individual" of the model, i.e., the unit of action and interaction, is a group of fish having the same size, the same spatial coordinates, requiring similar food, and belonging to the same species (therefore having similar physiological and morphological characteristics). Such aggregative behavior can be related to schooling behavior which occurs during at least one stage in the life cycle of about 80% of fish species (Burgess and Shaw 1979). Fish schools, however, appear to be more heterogeneous than those ideally implemented in the model. Pitcher (1983) suggests a general definition for schooling as being a group of fish in polarized and synchronized swimming. The size of schools can vary with time (Misund 1993) as well as its species composition (Bakun and Cury 1999, Fréon and Misund 1999). Despite these observations, strong homogeneity characterizes fish schools regarding fish size and body form (Fréon 1984, Pitcher et al. 1985). Thus, for convenience, the "super-individual" of the model will be called a fish school in the following sections.

OSMOSE architecture is based on a hierarchy since a fish school belongs to an age class, which in turn, belongs to a species. Four computer classes are then implemented: the class "system," the class "species," the class "cohort," and the class "fish school." This structure allows the study of some key variables at different levels of aggregation, in particular the abundance or the biomass of fish by age and by species.

The Biological Processes at Stake

The hypotheses of the model OSMOSE, as well as their implementation, are presented in detail by Shin and Cury 2001. This multispecies model allows the study of the spatial dynamics, structured in age and size, of a great number of species that interact. The time step of the model is one

reproductive period t , which in general, is one year in high-latitude ecosystems (Russel 1976, Froese and Pauly 1997). This step value is adopted by default for the set of simulations that will be subsequently described. Fish schools displace in a two-dimensional grid with closed boundaries. At model initialization, a certain number of object "species" are created, with the assignment of some attributes such as von Bertalanffy growth parameters, reproduction parameters (age at maturity, relative fecundity), longevity, and mean distribution areas by species and age. The object age classes and schools, which inherit their species biological parameters, are then successively created. The abundance of each age class and fish school can be determined by two different methods depending on the available information and the simulation objective: either from species abundances that are provided as input to the model, or from the ecosystem size spectrum (Shin and Cury 2001). Finally, each school is randomly distributed in the area attributed to its species and age class. Within each simulated year t , the fish life cycle can then be modeled, following the stages that are now described in an order which reflects the one implemented in the model.

Carrying Capacity Constraint. In OSMOSE, the carrying capacity corresponds to the upper limit of the viable biomass of all nonpiscivorous fish of the system. The piscivorous state of fish, that can be specified in the input, depends on their taxonomic identity and their age. For the set of simulations on MPAs, we chose to have age 1+ fish considered as piscivorous, and age 0 nonpiscivorous. The carrying capacity dynamic can be modeled in different ways depending on the investigated ecosystem (stationary, periodic, random, or with the occurrence of an anomaly).

At the beginning of each iteration t , the total biomass of nonpiscivorous fish is compared to the system carrying capacity. If it exceeds the carrying capacity, then the abundance of nonpiscivorous fish schools is reduced down to the implemented level of carrying capacity. The reduction in biomass operates uniformly among the nonpiscivorous schools: the same fraction of biomass is removed.

Foraging and Predation. This stage only concerns the piscivorous fish of the system. The order in which fish schools act is randomly set at each new time step t . School displacement is directed by the search of the adjacent cell with the highest biomass in potential preys. Once it has moved (or stayed in its cell), each fish school proceeds to the feeding phase, thereby causing an explicit predation mortality for each school preyed upon. It is remembered that two criteria form the basis of the predation process: an individual can potentially feed on any species provided that (1) there is a spatio-temporal co-occurrence (at time t , fish schools have to be located in the same cell to be considered accessible); and (2) the predator/prey size ratio does not exceed a certain threshold (estimated at about 3.5 in FishBase 97, Froese and Pauly 1997). An initial consequence of these rules is that a species can occupy different trophic levels in the system depending on the

age class considered (Bond 1979, Rice 1995). Therefore, two species can simultaneously be predator and prey of each other and predation opportunism takes into account the possibility of cannibalism. These trophic patterns are consistent with the observations of very diversified and time-varying diets of fish in different ecosystems in the world (e.g. Gislason and Helgason 1985, Crawford 1987, Alheit 1987, Mittelbach and Persson 1998).

Finally, when all fish schools have achieved feeding activity, a predation efficiency ξ is calculated for each fish school. This coefficient is determined by the ratio between the food biomass ingested by a school and the food biomass required to fulfill its vital functions. From values available for several species, it is estimated that a fish should annually consume 3.5 grams of food per body gram (Laevastu and Larkins 1981, Gislason and Helgason 1985, Longhurst and Pauly 1987).

Growth. Mean annual growth rates in length are calculated from the von Bertalanffy model (1938). This mean rate is readjusted to take into account the amount of food consumed by a fish school during a time step. A critical threshold ξ_{crit} can be determined for predation efficiency beyond which it is considered that the food ration is dedicated to fish growth. A simple approximation is to consider that if a school predation efficiency $\xi \geq \xi_{crit}$, then growth rate in length varies linearly with ξ such that (1) for $\xi = \xi_{crit}$, the rate is null, (2) for $\xi = (\xi_{max} + \xi_{crit})/2$, with $\xi_{max} = 1$, growth rate equals the mean growth rate calculated by the von Bertalanffy model.

Starvation Mortality. Starvation mortality is supposed to affect fish schools when the food ration is too low for fish maintenance requirements. Beverton and Holt (1957) advocate the possible existence of a starvation mortality for adult stages of fish in a linear model linking natural mortality rates to fish density. By considering that, for each species, nutritional resources are limited, this linear model is applied with the hypothesis that the greater the density of fish, the less the fish food ration will be. Hence, starvation mortality rates of fish schools are linearly expressed in relation to predation efficiency when $\xi \leq \xi_{crit}$.

Reproduction. Let Φ_s be the relative fecundity of species s , SB_s its spawning biomass, $B_{s,a}$ the biomass of age class a , a_{ms} its age at maturity, and A_s its longevity. Assuming that the sex ratio equals 1:1 for all species, and noting $N_{s,0,t+1}$ the number of eggs spawned by species s at the end of the time step t , the following equation is applied:

$$N_{s,0,t+1} = \Phi_s SB_{s,t} \quad \text{with} \quad SB_{s,t} = \frac{1}{2} \sum_{a=a_{ms}}^{A_s} B_{s,a,t}$$

Hence, the number of eggs spawned each year depends explicitly on fish growth. And as growth variability is implemented in relation to the

food intake, the reproduction process also depends implicitly on the food conditions that are encountered, locally in time and space, by each fish school. On the other hand, from this linear relationship, recruitment levels emerge as a consequence of the annual survival of eggs and juveniles, in relation with the predation process and with the annual level of the system carrying capacity.

Marine Refuge Implementation

Assumptions

For the set of realized simulations, marine reserves are considered to be permanent and consist of areas that are protected from all types of biomass extraction, regardless of the species considered (Bohnsack and Ault 1996). Marine reserves are explicitly represented in space and are characterized by a relative size RS , expressed in percentage of the total distribution area of the exploited species. In the circumstances, all species of the system are considered to be exploited: MPA size is then expressed in percentage of the whole grid of simulation. As for the fishery, it is considered as being nontargeting and as exerting a global annual fishing mortality F for all species and ages (recruitment age is fixed at 1 for all species). Hence, the underlying assumptions are an identical catchability for all species and a homogeneous distribution of fishing effort. This exploitation configuration is generally the one for artisanal fisheries which are strongly opportunistic and for which a single trawl or purse-seine haul can contain a great number of commercial species. The fishing scenario that is implemented is certainly simplifying, but the principle is to represent a fishery that is flexible enough for natural transfers of fishing effort to occur from one species to another, when setting up a marine refuge.

When establishing an MPA, fishing effort, which generates a fishing mortality rate F , is considered to be redistributed on the reduced area which is accessible to fishing. This redistribution is global; it is applied independently of stock identity. Thus, fish that are located out of the marine reserve are submitted to an effective annual fishing mortality rate F_e increasing with reserve size (Guénette and Pitcher 1999):

$$F_e = F(1 - RS)^{-1} \quad (1)$$

Based on Pope's (1972) analysis, it is assumed that fishing mortality rate is instantaneously applied in the middle of the simulated year. Hilborn and Walters (1992) consider the error induced by this approximation as negligible if the total annual mortality rate is less than 1. The spatial distribution of the fishing effort is not taken into account, as it is uniformly applied to all fish schools in age of recruitment (ages 1+). Other sources of mortality (by predation and starvation) occur during the whole time step, when local successive actions are accomplished by each fish school of the system.

Biomass transfer out of MPAs is supposed to occur since age 1+ fish execute local displacements in a time step. By contrast, no large-scale migration has been implemented: all age groups of the same species are assumed to have the same distribution area. Concerning age 0 fish schools, they are uniformly distributed over their species distribution area, consecutively to the annual reproduction stage. This assumption, which is supposed to account for large-scale processes of larval dispersion and diffusion (in particular by physical currents), is often used in models of marine reserves (Quinn et al. 1993, Attwood and Bennett 1995, Hastings and Botsford 1999).

Simulation Parameters

A set of $S = 50$ species is implemented, species biological parameters and distribution areas being randomly attributed. The simulated species are all assumed to be piscivorous from their second year of life (ages 1+). For the sake of simplicity, the distribution areas which are represented by a set of 150 adjacent cells are only defined at the species level without differentiation regarding fish age. Fish schools, of which the number is fixed at 50 per age class, move and interact in a grid of 15×15 cells. Carrying capacity is fixed at 10^6 tons and its dynamic is assumed to be stationary. To initialize species abundances, the size spectrum of the North Sea ecosystem during the period 1977-1993 is used (Rice and Gislason 1996). Preliminary simulations have allowed for the selection of a species sample. The species kept for the study are those which are viable without exploitation for 100 simulations, each simulation being 200 years in length. A set of 21 species among the 50 initial ones were then selected, for which different fishing scenarios have been simulated. For each set of fishing mortality and reserve size parameters, 100 simulations of 200 years have been carried out, from which have been calculated the mean results that are expounded in the next section. RS is allowed to vary between 0 and 0.8, assuming that equation (1) is valid in this range of reserve size, i.e., fisheries maintain their activity up to a limit of 20% of accessible zone. Each RS value corresponds to a single set of contiguous cells, i.e., to a single refuge area, of which the localization is randomly chosen for each simulation.

Results

Effects of Reserve Size on Fishing Yields

To investigate the potential effects of marine refuges on multispecies assemblages, we first focused on the overall catch of the system, all species combined. The results, which are expressed in terms of the total catch averaged on 100 series of 200 years of simulation, are represented in Fig. 1. It is assumed that the time series produced by the simulations correspond to catch oscillations around the equilibrium. Then, mean catches provide an estimation of equilibrium values.

The MSY (maximum sustainable yield) of the multispecies assemblage without MPA is obtained for $F = 0.3$. For F values lower than F_{MSY} , refuges have a negative effect on fishing yields regardless of their size. For F values greater than F_{MSY} , it appears that the larger the MPA, the more the MSY is obtained for higher values of fishing mortality. On the other hand, from a certain size of the refuge, namely beyond a relative size RS of 50%, the shape of the relationship changes: up to a maximal value of $F = 0.8$, mean yields do not decrease. Rather, they level off.

Two management measures can then be compared, the first consisting of directly reducing fishing mortality, the second consisting of reducing the area accessible to fishing. Consider, for example, the extreme case where all species are exploited at a rate of $F = 0.8$. At constant catchability, the measure which would consist of reducing the fishing effort by half ($F = 0.4$) would result in a negligible increase in yield. By contrast, the implementation of an MPA of $RS = 50\%$ would result, on average, in an appreciable increase in yield. The catch level which would be reached is indeed less by only 7% than the total MSY obtained without refuge, i.e., the theoretical maximal level of yield in the long term. At this exploitation level, the reduction of 50% of the fishing zone would correspond to an optimum in the refuge size as mean overall catches are concerned.

In general, for exploitation rates greater than F_{MSY} , the observed relationship between mean total catch and MPA size is nonlinear. Indeed, an optimal size of the MPA exists for each exploitation level. For $F = 0.5$ for example, the optimal relative size would equal 40% (Fig. 2).

Effects of MPA Size on Species Diversity

Along with the analysis on mean yields, the Shannon index of diversity H' has been calculated for the same set of simulations. This index, which corresponds to a cardinal measure of biodiversity (Cousins 1991), can account for species richness as well as for species evenness, i.e., the distribution of species relative abundances. It is a common measure of ecosystem biodiversity (Begon et al. 1996):

$$H' = - \sum_{s=1}^{S=21} \frac{N_s}{N} \log_2 \left(\frac{N_s}{N} \right) \quad \text{with} \quad N = \sum_{s=1}^S N_s$$

Here, N_s represents an average on 100 simulations, of the mean abundance of species s , calculated over the duration of each simulation, namely 200 years.

In the case of a scenario without marine reserve, Fig. 3 shows that the Shannon index remains remarkably constant over a large range of fishing mortalities, even beyond $F_{MSY} = 0.3$. Species diversity begins to change dramatically for a fishing mortality value greater than 0.45. Implementing an MPA thus allows for an appreciable increase in the assemblage diversity. For an initial situation where fishing causes a mortality rate of 0.6, for

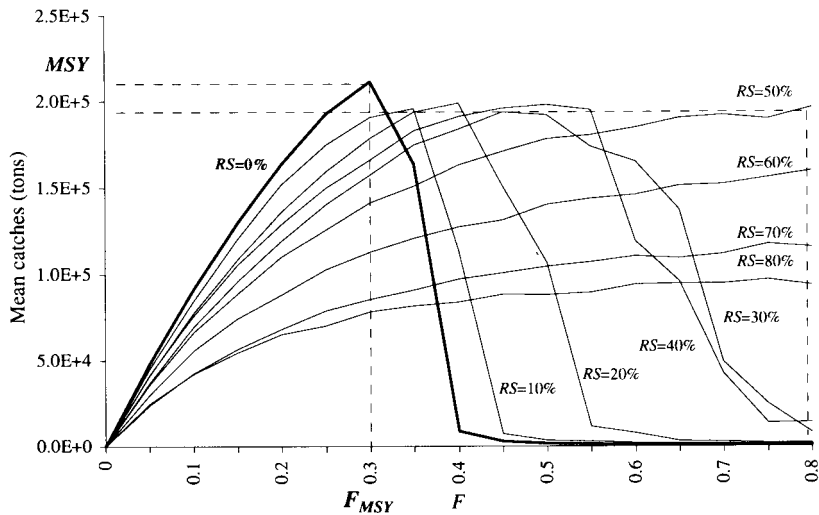


Figure 1. Mean catch, all species together, against fishing mortality rate F . Different MPA relative sizes are implemented (RS in % of the total distribution area of the species). The thick curve represents the mean catch obtained without MPA implementation.

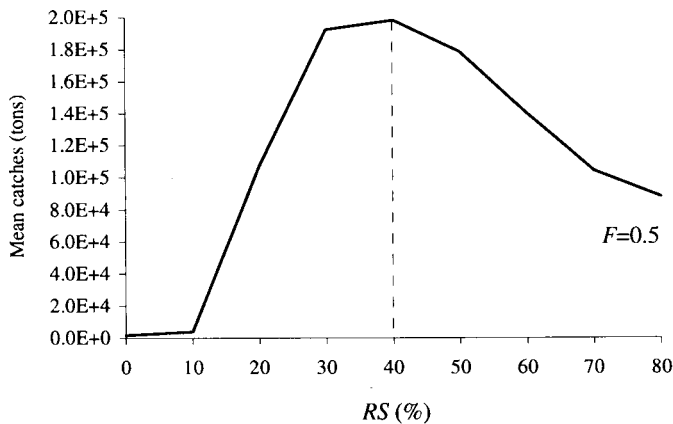


Figure 2. Mean catch, all species together, against MPA relative size for a fishing mortality rate F equal to 0.5.

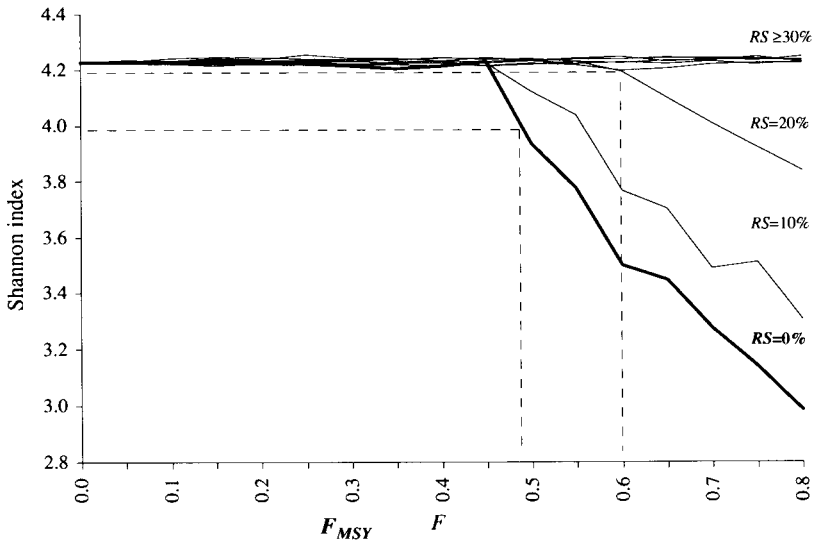


Figure 3. Shannon diversity index H' against fishing mortality rate F . Different MPA relative sizes are simulated (RS ranges from 0% to 80%). The thick curve represents the diversity index obtained without MPA implementation.

example, the diversity index obtained in the long term by closing 20% of the fishing area ($H' = 4.19$) would be superior to the one obtained by reducing the fishing effort by 20% ($H' = 3.98$). In parallel, for the same exploitation configuration, these two management measures appear to be equivalent in terms of yield increase. The theoretical gain obtained is negligible in this case (Fig. 2). For a given exploitation rate, the general shapes of the curves of the Shannon diversity index and of the yield against MPA size are different. Indeed, there is no optimal size of the refuges concerning Shannon diversity since globally, the larger the MPA, the higher the species diversity with a plateau obtained for relative sizes superior to 30%, whatever the implemented fishing mortality rate might be (Fig. 3).

Discussion

The present work affords new considerations on how to integrate multispecies assemblages for MPAs considered as a tool for fisheries management. The variables that are studied are indeed global (overall catch and diversity index). They concern the dynamics of multispecies assemblages, hence allowing particular aspects of ecosystem management to be addressed. The implemented fishing scenarios are simplified and first allow for the corroboration of results already obtained at the species level. A

result that is frequently obtained when modeling MPAs is that at high exploitation rates, refuges indeed prevent the long-term decrease of the catches (e.g., Polacheck 1990, Man et al. 1995, Gu  nette and Pitcher 1999, Hastings and Botsford 1999). In the framework of generalist multispecies fisheries and for exploitation rates greater than F_{MSY} , the simulations that were undertaken with OSMOSE show that the implementation of MPAs would further permit overall catches to increase at a level often greater than the one obtained by a directly equivalent reduction of fishing effort. At each exploitation level (greater than F_{MSY}), there is an optimal size of the MPA in terms of fishing yield in the long term. The relationship between fishing yield and reserve size is indeed nonlinear (Fig. 2) for high fishing mortality rates: on the left part of the curve, yields increase with the reserve size. This phenomenon is probably linked to a better survival of fish within the MPA, resulting in an age structure of the populations that include more mature and aged individuals. Growth and recruitment overexploitation can thus be avoided, while allowing fishing yields to increase by the diffusion of adults out of the protected areas as well as by the dispersion of larval production (Dugan and Davis 1993, Rowley 1994, Gu  nette and Pitcher 1999, Maury and Gascuel 1999). On the right part of the curve, yields decrease with marine reserve size. In this configuration, it is assumed that the system has reached its carrying capacity level, this latter indirectly determining the maximum recruitment level, all species confounded (Shin and Cury 2001).

The variation of species diversity with MPA size has been simulated as well. For this management criterion and in the case where $F > 0.45$, the larger the MPA size, the higher the Shannon diversity index. For high exploitation rates, the implementation of a refuge area cannot necessarily significantly increase the long-term yields but, in contrast, can induce an appreciable increase in the Shannon diversity index. This result assumes a long-term reversibility of the phenomenon of population biomass decrease; i.e., the minimal condition is that no species goes extinct. Indeed, the Shannon index quantifies both species richness (species number) and species evenness. In the case where no MPA is implemented, simulation results show that species richness does not decrease for $F < 0.7$. Thus, for fishing mortality rates ranging between 0.45 and 0.7, these values being theoretical, one can consider that implementing an MPA results in an increase of the exploited multispecies assemblage in the long term.

The simulations thus suggest that by implementing MPAs, there can theoretically be a compromise between both objectives of yield maximization and marine biodiversity protection. For both criteria, the results show that in the case of a global management of fishing resource, the reduction of fishing area can have a greater impact than an equivalent direct reduction of fishing effort. First, by preserving an area where fishing is banished, a fraction of each species biomass is preserved, as is already the case for diverse measures of fishing effort reduction (e.g., quotas, fishing gear number, mesh sizes). Second, by implementing MPAs, a trophic web is

preserved; i.e., a set of species and interactions that are localized in space and time. By contrast, the global reduction of fishing effort does not result in avoidance of local overexploitation phenomena, which in turn, can lead to the disappearance of links between species which are important in the global dynamic of the system.

Refuge implementation, however, remains a complex problem with the necessity to determine their localization as well as their size, even sometimes their duration and their restriction to a few species and activities of biomass extraction. Our simulations are restricted to the investigation of the effects of the MPA size. The results show that this parameter is really to be taken into account if the management goal is the maximization of catches in the long term. In 1992, the World Conservation Union (IUCN 1992) had an aim to close 20% of the world coastal waters to fishing by the year 2000. This general measure, which was essentially intended to avoid resource collapse, can be considered to be an application of the precautionary approach in a context where 60-70% of world marine resources appear to be fully exploited to overexploited (Garcia et al. 1999). The simulations indeed show that for overexploited stocks (in the condition that $0.45 < F < 0.7$), the implementation of arbitrarily sized MPAs could permit the diversity of ecosystems to increase. The investigation of some particular ecosystems should hereafter enable the search for optimal sizes of MPAs in an attempt to increase yields, in particular, by taking into account the resource initial level of exploitation. In addition, numerous studies show that the more or less diffusive and migratory characteristics of the resource condition the effects of MPAs (Beverton and Holt 1957, Polacheck 1990, Attwood and Bennett 1995, Gu  nette and Pitcher 1999, Maury and Gascuel 1999). This is not considered in the present study.

The results are hence to be related to the simulation context where fish school displacements are linked to the search of the highest densities in potential prey (Shin and Cury 2001). Maury et al. (2001) show that such local movement can be observed for Atlantic yellowfin tuna. In the model, the extent to which fish schools can displace each year is theoretical and linked to cell size. Implementing different sizes of the simulation grid (in cell number) can make the cell size and hence the foraging range of fish vary. Shin and Cury (2001) show that when grid size varies from 10 to 35 cells, there is little effect on the level of system biomass.

On the other hand, the larvae dispersion hypothesis, which reproduces the fact that larval retention areas and adult distribution areas are not necessarily the same for many species, is likely to influence MPA efficiency since it regularly provides the fishing zones with new recruits (Gu  nette et al. 1998). Thus, the refuge plays the part of the source and fishing the one of sink (Roberts 1998).

In this particular frame of simulation, the OSMOSE model has produced some simple results by confronting two criteria of management of multispecies communities exploitation, with the purpose of better understanding the phenomena that occur with MPA implementation. When the

investigation of real cases is foreseen in the future, species migration and diffusion schemes will then have to be taken into account.

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A Deepwater Dispersal Corridor for Adult Female Blue Crabs in Chesapeake Bay

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Abstract

In marine ecosystems, there is no empirical evidence for the utility of dispersal corridors in conservation, despite widespread migrations by mammals, fish, and invertebrates. We investigated the potential for a deepwater dispersal corridor (> 13 m depths) in protecting adult females of the blue crab, *Callinectes sapidus*, en route from shallow-water nursery and mating areas to the spawning sanctuary in lower Chesapeake Bay. We used existing survey data for the population, both baywide before spawning occurs (winter dredge survey), and in the spawning grounds during reproduction (spring-fall trawl survey) over several years. Survey catches (CPUE, catch per unit of effort) were standardized and stratified by depths shallower and deeper than 13 m, and areas within and outside the spawning sanctuary. The key findings were: (1) the CPUE of adult females was significantly higher in the corridor than in adjacent shallow-water habi-

tats, both prior to the reproductive period and during the migratory and reproductive period; (2) the corridor was selective for adult females; and (3) a sanctuary-corridor complex, composed of the spawning sanctuary and protected corridor, had higher abundances and lower variation in abundance of the spawning stock between years than either the sanctuary or the corridor alone. Hence, a sanctuary-corridor complex should promote a less variable and more abundant spawning stock interannually, if displaced fishing effort is controlled. In contrast, adult males, juvenile males, and juvenile females were most dense in habitats shallower than 13 m. A protected, deepwater dispersal corridor coupled to the spawning sanctuary in the lower bay would therefore selectively conserve adult females either en route to or resident in the spawning grounds, whereas the remainder of the stock would remain susceptible to exploitation.

Introduction

Marine reserves and sanctuaries (= protected areas) may conserve and enhance exploited populations, thereby resulting in their establishment worldwide under the assumption that they facilitate long-term, sustainable exploitation (Bohnsack 1993, Roberts 1997, Allison et al. 1998, Guenette et al. 1998). Dispersal corridors may complement reserves in the conservation of species and diversity (Rosenberg et al. 1997, Beier and Noss 1998), though their utility remains uncertain due to the paucity of supporting empirical evidence (Hobbs 1992, Inglis and Underwood 1992, Simberloff et al. 1992). Experimental and logistical difficulties have precluded the necessary experimental evidence to validate the utility of corridors in conservation (Hobbs 1992, Inglis and Underwood 1992, Simberloff et al. 1992). The application of corridors will most likely be suited to particular landscapes, habitats, and species (Rosenberg et al. 1997), with the most promising species being those for which dispersal (e.g., spawning migration) is a key feature of the life cycle, such as the blue crab.

In the marine environment, there is widespread use of migration pathways by marine mammals, fish, and invertebrates (Herrnkind 1980, Rose 1993, Morreale et al. 1996, Colbourne et al. 1997, Estrella and Morrissey 1997, Acosta 1999, Micheli and Peterson 1999), though no conclusive evidence exists for the utility of marine dispersal corridors in conservation. Hence, we assessed the efficacy of a deepwater dispersal corridor for females of the blue crab, *Callinectes sapidus*, as they migrate from shallow-water nursery and mating areas to the spawning grounds in Chesapeake Bay.

Blue Crab in Chesapeake Bay: Life History, Exploitation, and Sanctuaries

The blue crab, *Callinectes sapidus* Rathbun (Arthropoda: Crustacea: Portunidae), is dispersed widely along the Atlantic and Gulf coasts of North

America (Williams 1984), is abundant throughout Chesapeake Bay (Hines et al. 1990, Lipcius and Van Engel 1990), and supports the world's second largest crab fishery in tonnage (Lipcius and Eggleston 2000). A detailed description of the life history and fisheries for the blue crab in Chesapeake Bay is provided in Seitz et al. (2001). The relevant portions of the life history deal mostly with the reproductive segment of the population. After a terminal maturity molt and mating in the oligohaline and mesohaline portions of Chesapeake Bay, adult females migrate to lower Chesapeake Bay to spawn in the summer, or overwinter and then spawn the following spring and summer (Van Engel 1958, Tagatz 1968). In Chesapeake Bay, maximal egg extrusion and larval release occur in summer, principally from July through mid-September either as a single midsummer peak or as bimodal early summer and late summer peaks (Jones et al. 1990, Prager 1996).

For decades, the blue crab spawning stock in Chesapeake Bay has been partially protected from exploitation from 1 June to 15 September by a sanctuary in the lower bay spawning grounds (Seitz et al. 2001). However, the sanctuary and various catch or effort controls have not protected a sufficiently large fraction of the spawning stock (Seitz et al. 2001) to avert an approximate 70% reduction in the baywide population (Lipcius and others, unpubl. manuscript), nor a 84% decrease in spawning stock biomass from 1994-1999 (Lipcius, unpubl. manuscript). Despite the need to protect a minimal proportion of the spawning stock for future recruitment (Tang 1985, Rothschild 1986, Lipcius and Van Engel 1990, Miller and Houde 1998, Rugolo et al. 1998), the spawning sanctuary apparently has not maintained the spawning stock at sustainable levels due to the intense exploitation of the population (Miller and Houde 1998, Lipcius and others, unpubl. manuscript) prior to its arrival in the spawning sanctuary (Seitz et al. 2001). Similarly, marine reserves are ineffective when they do not protect all exploitable stages in the life history prior to their maturation into the spawning stock (Allison et al. 1998). The blue crab spawning stock therefore requires supplementary protection of all stages in the life history and throughout critical habitats in Chesapeake Bay for effective conservation. Thus, we have examined a potential extension of the existing spawning sanctuary into a sanctuary-corridor network, with this investigation emphasizing a deepwater dispersal corridor (>13 m depths) from nursery and mating areas to the spawning sanctuary in the lower bay (Fig. 1). Depth of the corridor was chosen due to anecdotal fishery observations of concentrations of adult females at depth.

Specifically, we first characterized the size structure and interannual CPUE of female blue crabs in lower Chesapeake Bay, and then examined hypotheses that:

1. The CPUE of adult females is significantly higher in the deepwater dispersal corridor than in adjacent shallow-water habitats during the migratory and reproductive period;

Chesapeake Bay

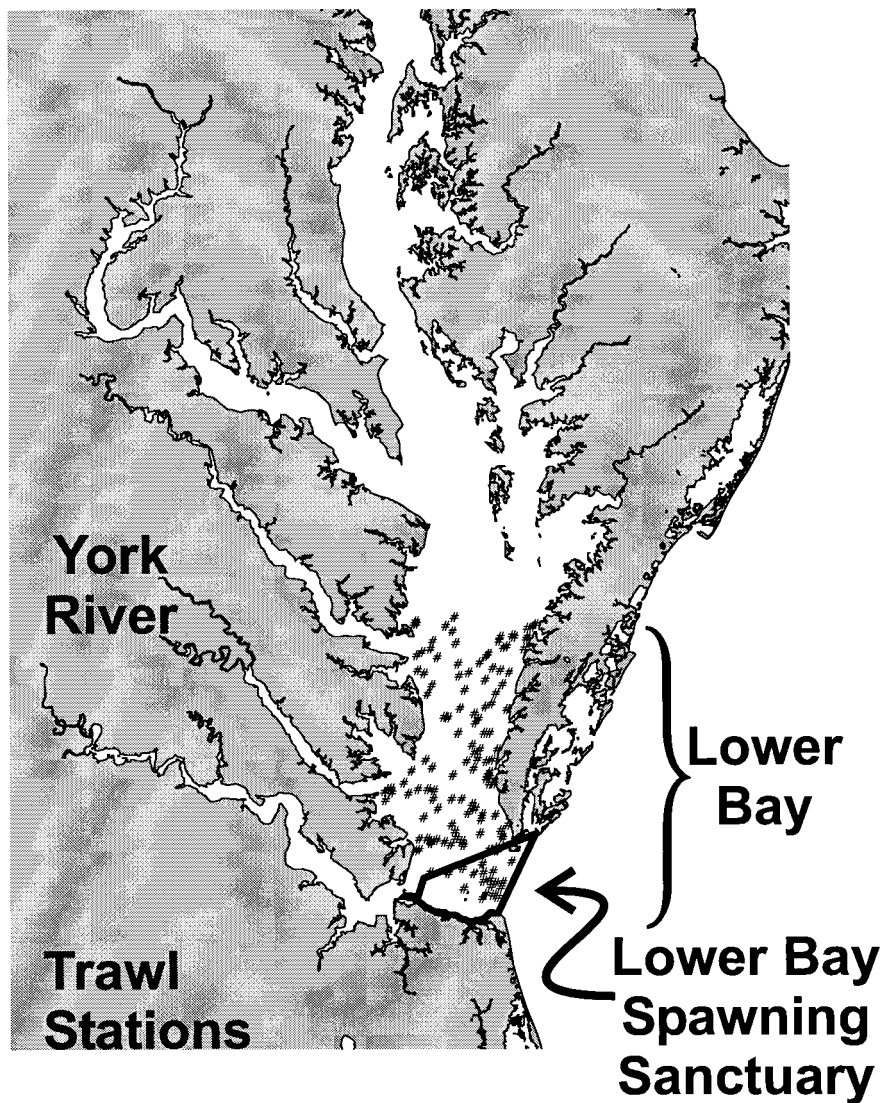


Figure 1. Chesapeake Bay spawning sanctuary. The spawning sanctuary is displayed as the outlined area near the bay mouth. Representative sampling stations are displayed for the trawl survey in the lower Chesapeake Bay spawning grounds during 1997. Approximately 50 stations were sampled monthly from July through September each year.

2. The deepwater dispersal corridor is selective for adult females (i.e., no other life-history stages, such as juveniles and adult males, are dense in the deepwater corridor); and
3. The CPUE of adult females is also significantly higher in the deepwater dispersal corridor than in shallow-water habitats during winter prior to the reproductive period.

Furthermore, we compared CPUE and variation in CPUE in the existing spawning sanctuary, the proposed deepwater corridor, and a sanctuary-corridor complex integrating the spawning sanctuary and deepwater corridor, to assess the hypothesis that:

4. A sanctuary-corridor complex produces lower variation and higher abundance interannually in the protected spawning stock than either the spawning sanctuary or the deepwater corridor alone.

Methods

CPUE of Adult Females in the Corridor and Shallow-Water Habitats during Reproduction

Adult female blue crabs were sampled monthly in the lower bay spawning grounds (Fig. 1) from spring through fall. Details of sampling are given by Lipcius and Van Engel (1990) and Lipcius (unpubl. manuscript). Each CPUE and size value came from single tows, which were collected with similar methods throughout the study period, and which served as independent data points (i.e., number or mean size of adult females per tow); annual sample sizes usually averaged about 50 tows.

CPUE was analyzed as the log-transformed, standardized number of adult females per tow. Log ($10x + 1$) transformation was used to normalize the data and reduce heterogeneity of variance (Underwood 1997). In all cases, variances were either homogeneous (Cochran's *C* statistic) or, if heterogeneous, the *F* test in analyses of variance was rejected at an alpha level lower than that used in the test for homogeneity of variance (Underwood 1997). Abundance was calculated as the product of mean CPUE, corrected for efficiency (Seitz et al. 2001), and area of each region.

In addition, we examined the size structure of females in the region of the sanctuary and corridor. Mean size per tow was used in size analyses, rather than all individual sizes, because the mean size per tow provided an independent data value which could be used in parametric analyses (e.g., analysis of variance), whereas each individual size was not independent of tow and invalid as an independent value in the parametric analyses. Further details of size analyses are provided by Lipcius (unpubl. manuscript). Size data did not require standardization nor transformation to meet assumptions of normality and homogeneity of variance. Size structure of

females in the spawning grounds was characterized by monthly size frequencies.

Selectivity of the Corridor

Juveniles, immature males, immature females, and adult males were sampled monthly in the lower bay (Fig. 1) from spring through fall, as for adult females. Juveniles are < 60 mm cw (= carapace width), immature males < 120 mm cw, and mature males > 120 mm cw. Immature females are those females > 60 mm cw, but without the circular abdomen characterizing adult females. All females with the circular abdomen are adults, regardless of size.

CPUE of Adult Females in the Corridor and Shallow-Water Habitats before Reproduction

We sampled the blue crab population in winter (late November-March) by a baywide winter dredge survey using a stratified random design, which divided Chesapeake Bay into three geographic strata (Fig. 2). The advantages of sampling in winter over summer are: (1) blue crabs are not exploited in most areas of Chesapeake Bay during the winter, except in the lower Chesapeake Bay by the winter dredge fishery, and (2) blue crabs bury in the sediments during the winter, thereby sharply restricting their movement, which justifies the assumption of negligible immigration and emigration in the estimation of abundance.

Each year, 1,500 sites were selected randomly, and apportioned by the area of each stratum. The upper bay stratum included the tributaries, creeks, and upper mainstem of Chesapeake Bay, which are characterized by lower salinities, except near the mouths of tributaries in the lower bay. The middle bay stratum encompassed the middle mainstem of the bay, whereas the lower bay stratum circumscribed the spawning grounds (Fig. 2). Further details of sampling are provided by Lipcius and others (unpubl. manuscript). Each crab was measured (mm cw), and the sex, maturity, and overall condition recorded. At each sampling site, depth, salinity, water temperature, and dissolved oxygen were recorded and a sediment sample was collected.

Variation and Abundance in the Sanctuary, Corridor, and Sanctuary-Corridor Complex

The CPUE and abundance data for the spawning sanctuary and deepwater corridor were used in the comparison of (1) the existing spawning sanctuary, (2) the proposed deepwater corridor, and (3) a sanctuary-corridor complex integrating the sanctuary and deepwater corridor. Coefficients of variation were derived from the annual mean CPUEs in each zone for 1990-1997.

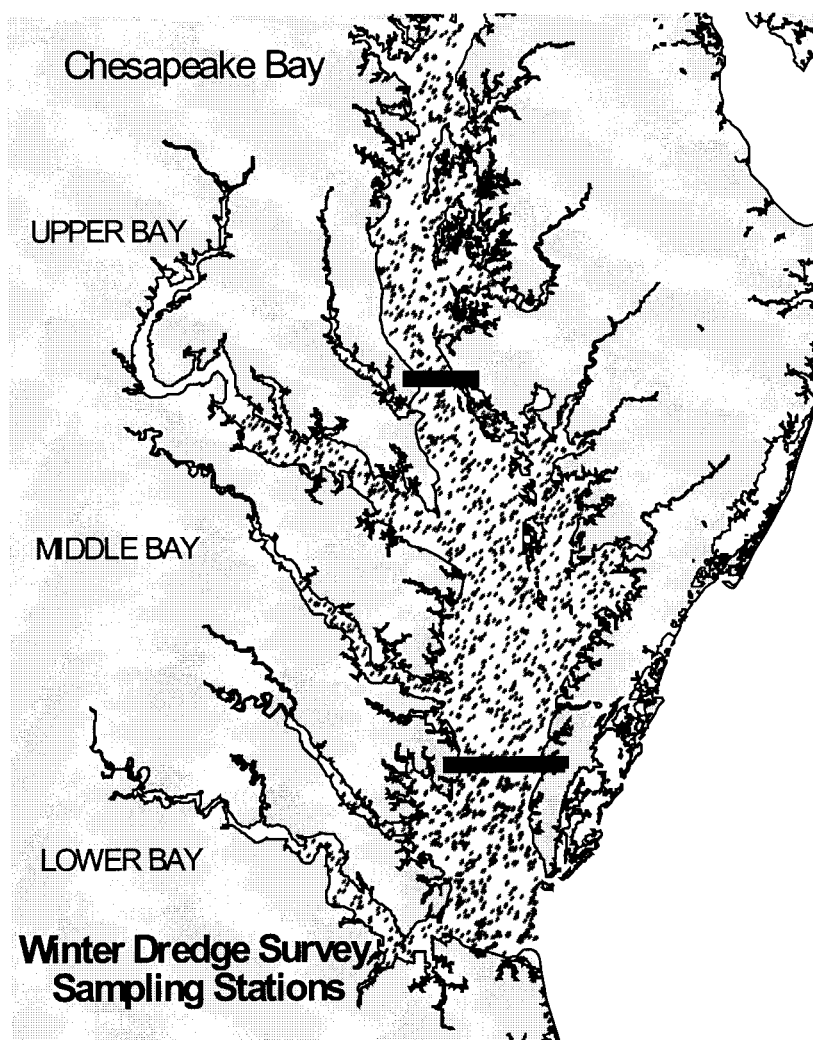


Figure 2. Representative sampling stations for the dredge survey during the 1990-1991 winter season. Sampling strata, divided by solid horizontal lines, included: upper bay mainstem and all tributaries, middle bay mainstem, and lower bay mainstem. Usually 1,500 stations were sampled annually.

Results

Size Structure and Interannual CPUE in Lower Chesapeake Bay

In April, females comprised at least two year classes ($t-1 = 0+$ and $t-2 = 1+$ and greater; t is the current year). The $0+$ year class had a mean size near 30 mm cw, and the $1+$ approximately 140 mm cw (Fig. 3). The $0+$ year class would have recruited in year $t-1$, and the $1+$ year class in year $t-2$, or before. Most growth occurred after June, when the $0+$ year class began to merge with the $1+$ year class (Fig. 3). Adult females in the $1+$ year class generally do not molt and grow after their pubertal molt to maturity (Van Engel 1958), thereby maintaining a relatively constant size distribution (Fig. 3). In September the new $0+$ year class was evident, resulting in a population composed of at least three year classes which recruited in years t , $t-1$ and $t-2$ (Fig. 3). Much of the $0+$ year class had entered the $1+$ year class by November so that the adult female segment of the population was composed of at least two year classes (from years $t-1$ and $t-2$). Migration by adult females to the lower bay spawning grounds occurs between May and November (Fig. 3), with peaks subsequent to the spring and fall “peeler runs” whereby pubertal or recently matured and mated females migrate down the tributaries and bay toward the spawning grounds (Van Engel 1958).

Adult female CPUE (Fig. 4a) and size (Fig. 4b) declined significantly during 1994–1997, both within the nominal deepwater corridor, in the lower bay outside the sanctuary, and in the spawning sanctuary (ANOVA, $P < 0.05$). Without regard to depth, there was no consistent trend toward greater CPUE or mean size of adult females in the sanctuary or outside the sanctuary (Fig. 4a,b), although mean size was larger outside the sanctuary in some years (Fig. 4b), probably due to size-selective exploitation of adult females before reaching the spawning grounds (Lipcius and others, unpubl. manuscript).

CPUE of Adult Females in the Corridor and Shallow-Water Habitats during Reproduction

In summer, adult females had a higher CPUE in deep water, both significantly so in the deepwater corridor zone outside the sanctuary (Fig. 5a, ANOVA, $P < 0.05$), and as a trend within the spawning sanctuary (Fig. 5b, ANOVA, $P > 0.05$). Within the spawning sanctuary, adult females represented the only segment of the population captured at moderate to high levels (Fig. 5b).

Selectivity of the Corridor

Outside the sanctuary, only adult females were characterized by high CPUE values in the deepwater corridor (Fig. 5a). Juveniles and immature males and females had significantly higher CPUE values in shallow-water habitats

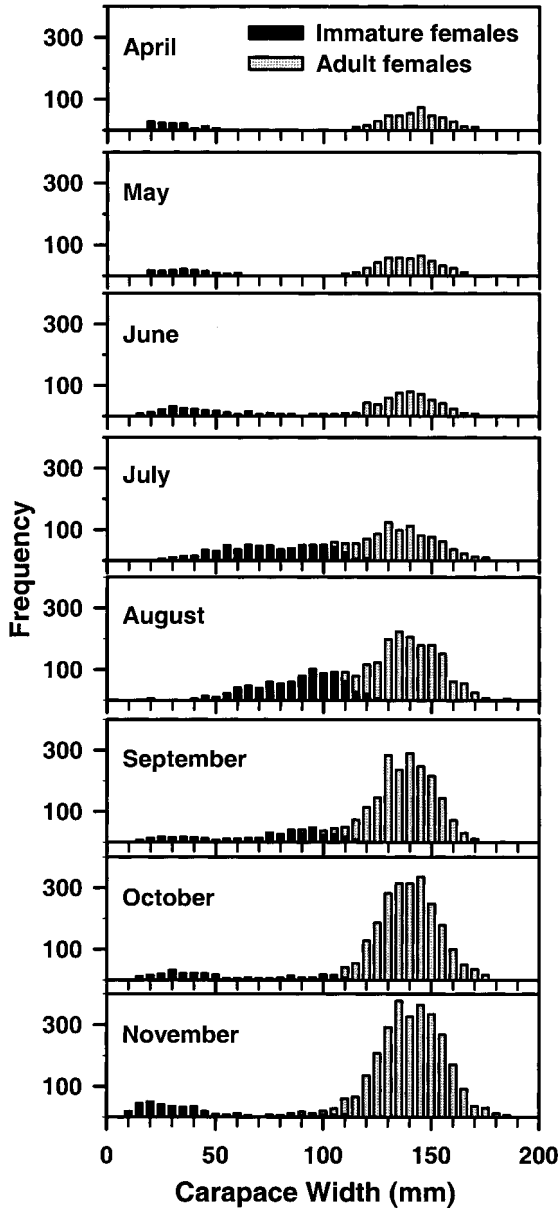


Figure 3. Composite of size frequencies of females captured by the trawl survey in the mainstem spawning grounds from 1990 to 1997, July-September; approximately 50 trawl tows were taken monthly. Mature females (= adults) are differentiated by their rounded abdomens. Note that adult females generally cease to grow after their pubertal molt, resulting in a static size distribution for adult females through time.

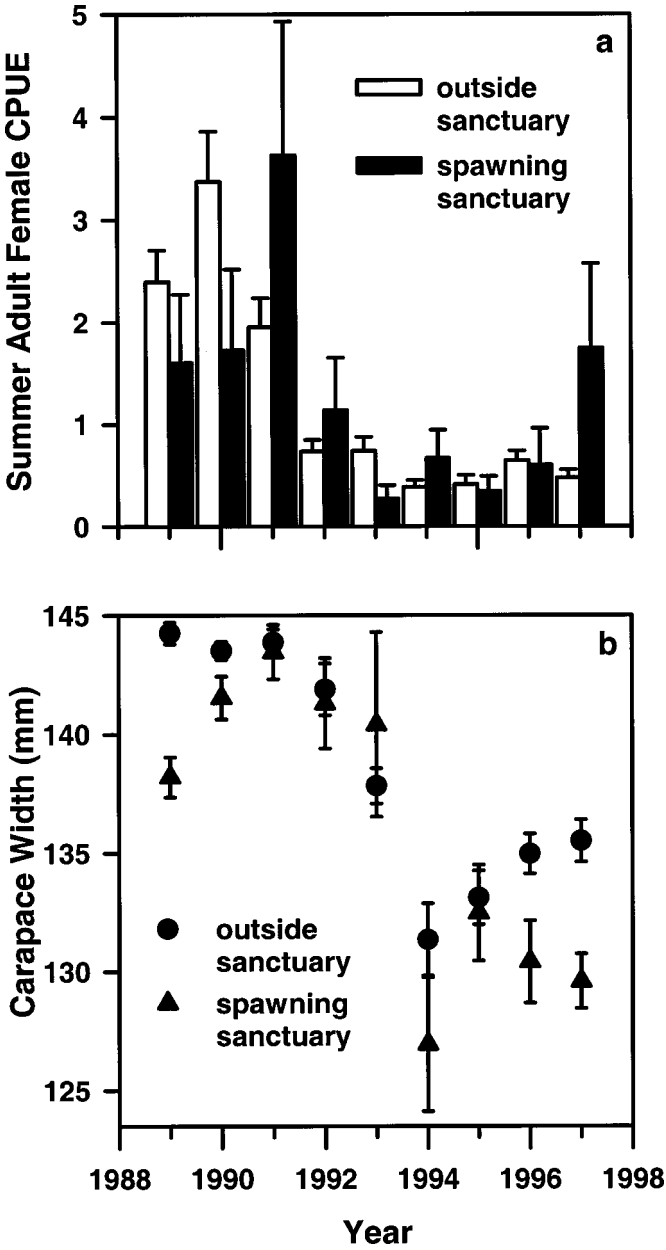


Figure 4. Interannual mean CPUE (a) and size (b) of adult females during summer in lower Chesapeake Bay, as sampled by the trawl survey, both inside and outside the spawning sanctuary. Vertical bars depict 1 S.E.

than in the deepwater corridor, where they were sparsely distributed (Fig. 5a, ANOVA, $P < 0.05$). Adult males were sparse and equally distributed in shallow and deep waters (Fig. 5a, ANOVA, $P > 0.05$).

CPUE of Adult Females in the Corridor and Shallow-Water Habitats before Reproduction

In winter, adult females had significantly higher CPUE values in deep than shallow habitats (Fig. 6, ANOVA, $P < 0.05$) in all years (Fig. 7), whereas total abundance was greater in the shallower habitats due to their much greater area (Fig. 8). A considerable and consistent fraction (approximately 20–25%) of all adult females resided within the boundaries of the deepwater corridor (Fig. 8). In contrast, CPUE and abundance levels of adult males, juvenile males, and juvenile females were significantly higher in habitats shallower than 13 m (Fig. 6, ANOVA, $P < 0.05$).

Variation and Abundance in the Sanctuary, Corridor, and Sanctuary-Corridor Complex

Highest abundances alternated between the spawning sanctuary and deepwater corridor with no apparent pattern (Fig. 9), other than the general increase in abundance in late summer as females migrated to the spawning grounds (Figs. 3 and 9). Highest abundances could be in the spawning sanctuary (Fig. 9: 1994, 1996–1997), in the deepwater corridor (Fig. 9: 1993, 1995), or in both areas (Fig. 9: 1990–1992).

The average fraction of adult females in the spawning sanctuary was 20.4%, in the deepwater corridor it was 26.7%, and in the shallow habitats outside the sanctuary 52.9%. The fractions in the deepwater corridor and spawning sanctuary did not differ significantly (ANOVA, $P > 0.05$), whereas these were significantly lower than that in the shallow-water area outside the sanctuary (ANOVA, $P < 0.05$). Hence, the abundances and fractions of adult females in the spawning sanctuary and deepwater corridor were generally complementary.

We also characterized and contrasted the variation in abundance in the spawning sanctuary, in the deepwater corridor, and in the collective zone encompassing the spawning sanctuary and deepwater corridor (= sanctuary-corridor complex) (Fig. 10) during years of low abundance (1992–1997). Abundance varied least in the sanctuary-corridor complex, with a coefficient of variation of 38% (Fig. 10a). In contrast, the coefficients of variation in the sanctuary and corridor were substantially higher at 90% and 64%, respectively (Fig. 10b,c), mostly due to interannual alternation of abundance between the sanctuary and corridor. For instance, abundances were high in the sanctuary and low in the corridor during 1996 and 1997, and conversely, low in the sanctuary and high in the corridor during 1993 and 1995 (Fig. 10b,c). Consequently, annual abundance in the sanctuary-corridor complex (Fig. 10a) was much more constant from year to year than in either the sanctuary (Fig. 10b) or the corridor (Fig. 10c).

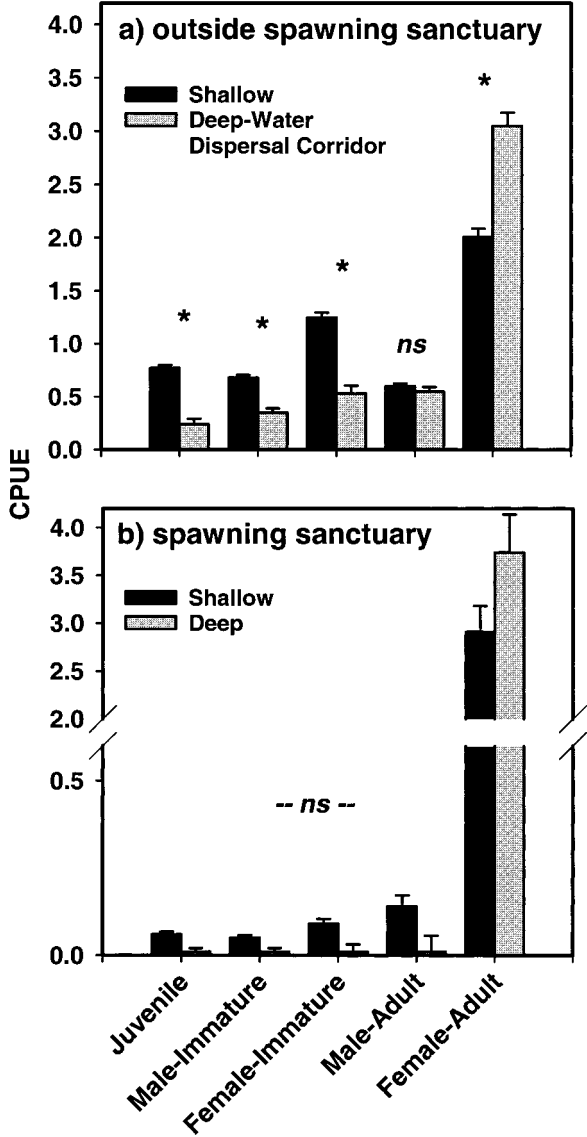


Figure 5. Mean CPUE of blue crab life-history stages during summer, as sampled by the trawl survey, both outside (a) and within (b) the spawning sanctuary in lower Chesapeake Bay. Shallow depths are < 13 m; deep habitats and the deepwater dispersal corridor are > 13 m. Juveniles are those crabs < 60 mm cw, immature males are < 120 mm cw, and mature males are > 120 mm cw. Immature females are those females > 60 mm cw, but without the circular abdomen characterizing adult females. Vertical bars depict 1 S.E. * $P < 0.05$; ns $P > 0.05$ for comparisons of depth zones.

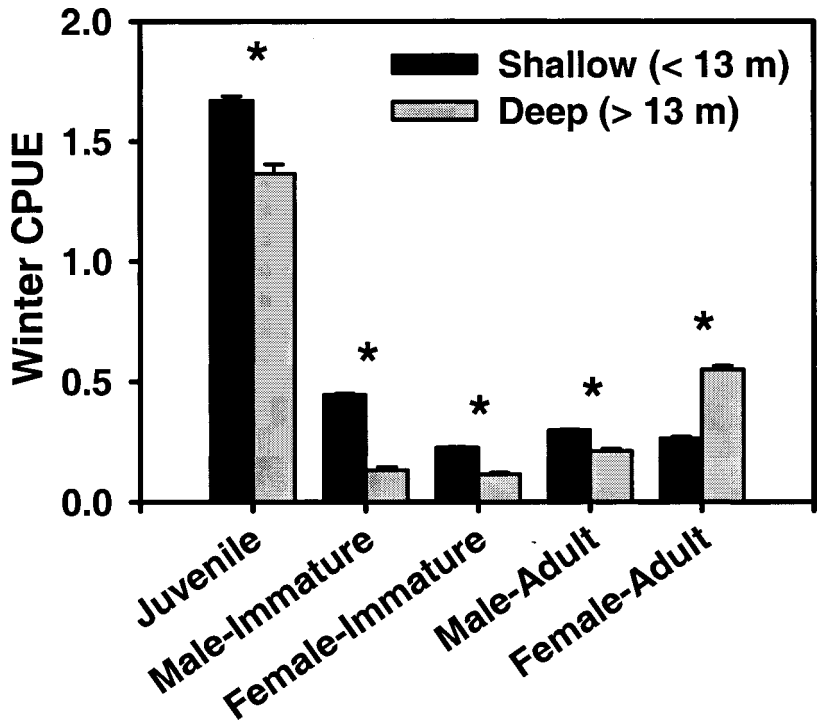


Figure 6. Mean CPUE of blue crab life-history stages in Chesapeake Bay during winter, as sampled by the baywide dredge survey. Juveniles are those crabs < 60 mm cw, immature males are < 120 mm cw, and mature males are > 120 mm cw. Immature females are those females > 60 mm cw, but without the circular abdomen characterizing adult females. Vertical bars depict 1 S.E. * $P < 0.05$; ns $P > 0.05$ for comparisons between depth zones.

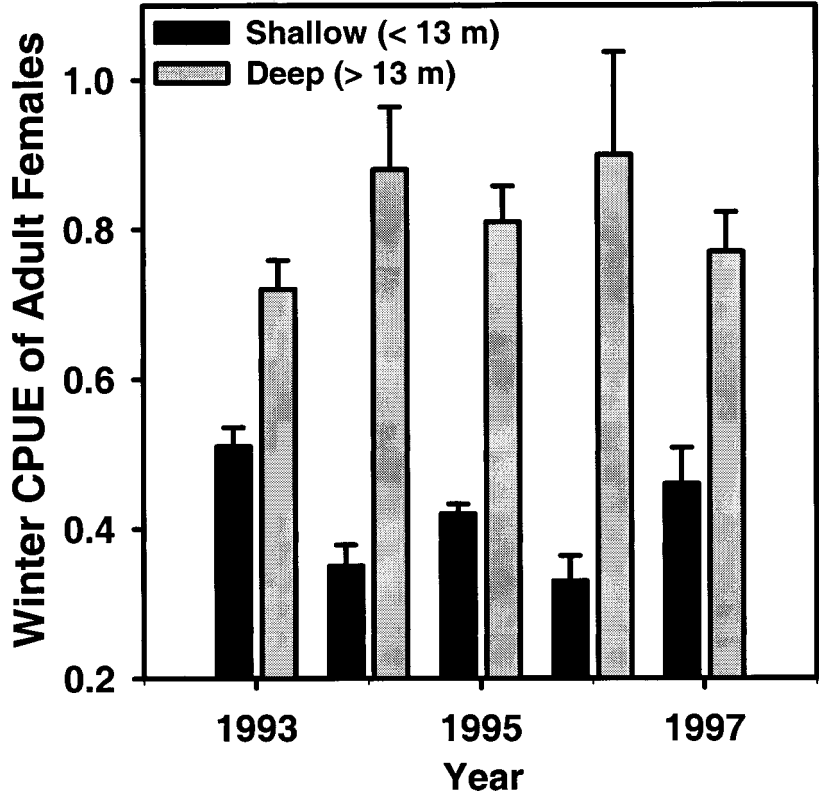


Figure 7. Mean CPUE of adult females baywide during winter, both in shallow (< 13 m depths) and deep (> 13 m depths) habitats. Vertical bars depict 1 S.E. CPUE in the deep habitats was significantly higher than that in shallow habitats (ANOVA, $P < 0.05$).

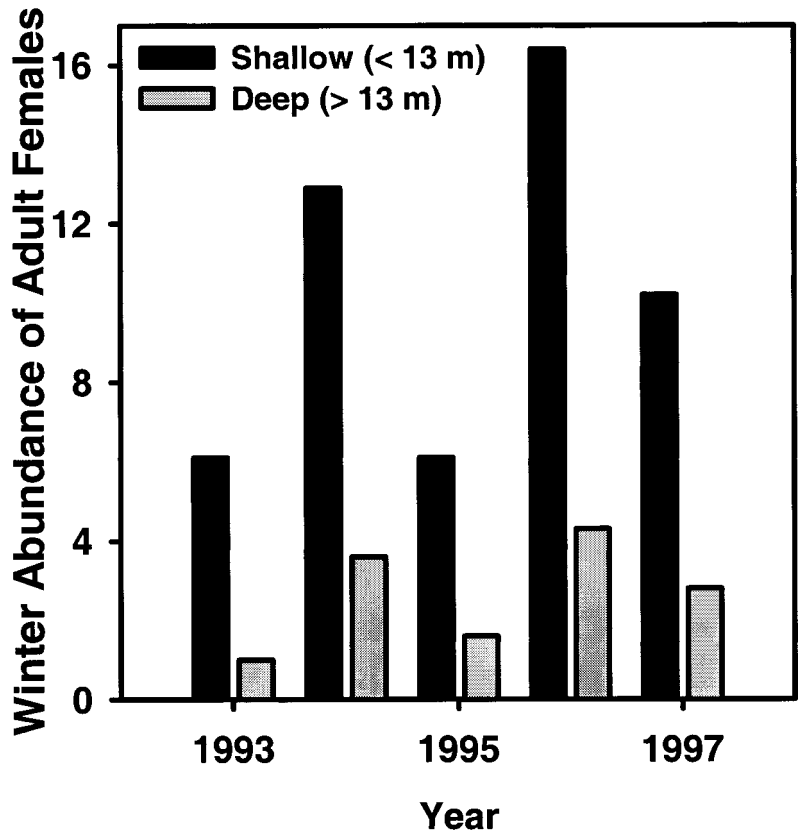


Figure 8. Abundance of adult females baywide during winter, both in shallow (< 13 m depths) and deep (> 13 m depths) habitats. Abundance was calculated as the product of the mean annual CPUE and the areal extent of each zone.

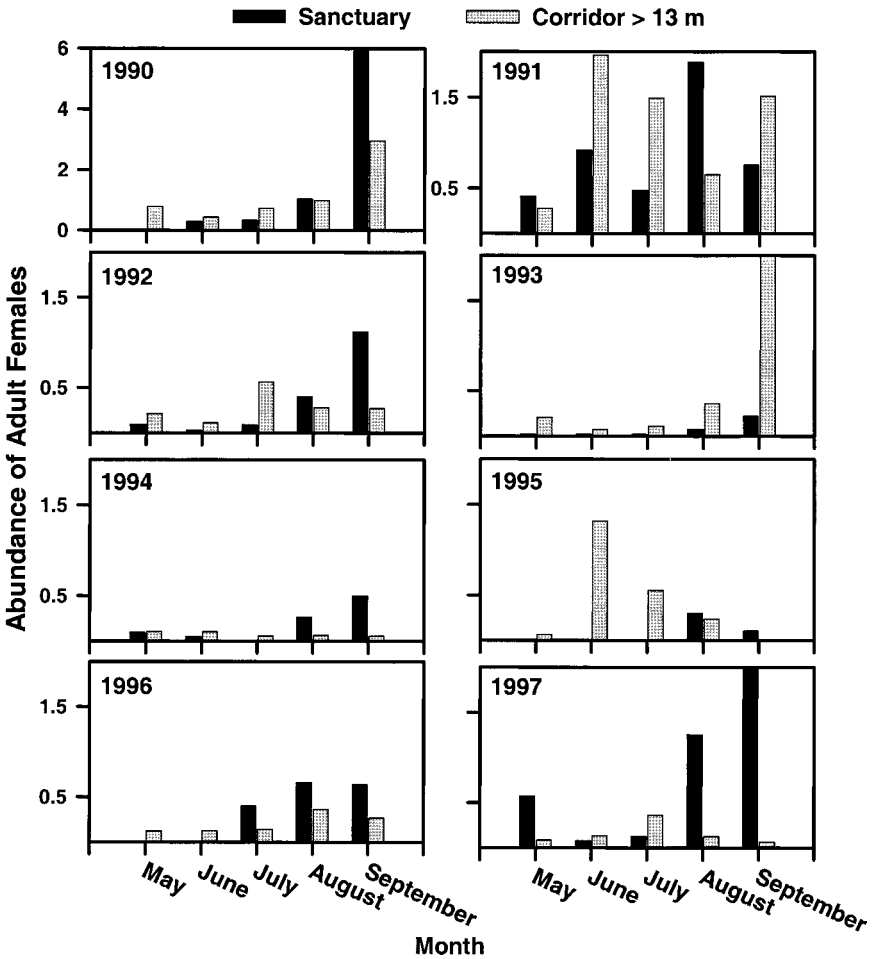


Figure 9. Monthly abundance of adult females during summer in lower Chesapeake Bay, residing either in the spawning sanctuary or within the deepwater (> 13 m depth) corridor outside the spawning sanctuary. Abundance was calculated as the product of the mean annual CPUE and the areal extent of each zone.

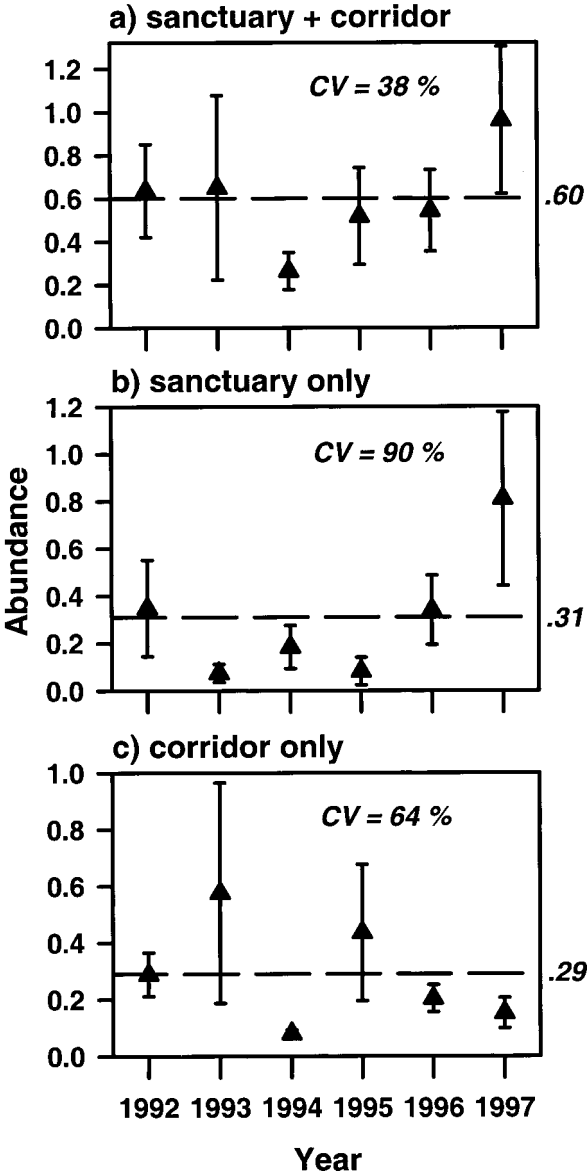


Figure 10. Annual CPUE of adult females during summer in lower Chesapeake Bay, residing in the (a) collective zone encompassing the spawning sanctuary and deepwater (> 13 m depth) corridor, (b) spawning sanctuary only, and (c) deepwater corridor only. Abundance was calculated as the product of the mean annual CPUE and the areal extent of each zone. Coefficients of variation ($C.V. = S.D./mean \times 100\%$) are indicated, as well as the mean (dashed line) for each zone.

Discussion

Dispersal corridors may be useful in conserving species or diversity, although the effectiveness of corridors remains uncertain due to the paucity of empirical evidence. In the marine environment, there is no conclusive evidence that corridors facilitate faunal conservation, despite the widespread existence of migration pathways between divergent habitats utilized by marine mammals, fish, and invertebrates (Herrnkind 1980, Rose 1993, Morreale et al. 1996, Colbourne et al. 1997, Estrella and Morrissey 1997, Acosta 1999, Micheli and Peterson 1999). Herein we investigated the potential for a deepwater dispersal corridor (> 13 m depths) in protecting a key fraction (i.e., adult females) of the blue crab population en route from shallow-water nursery and mating areas to the spawning sanctuary in lower Chesapeake Bay. Adult female CPUE and size declined significantly after 1993, both within the corridor and in the spawning sanctuary, similarly to that observed previously (Lipcius and others, unpubl. manuscript; Lipcius, unpubl. manuscript). In addition, the existing spawning sanctuary has not protected a sufficient fraction of the spawning stock for long-term, sustainable exploitation (Seitz et al. 2001). Hence, further protection of the spawning stock, such as that potentially provided by a sanctuary-corridor network, is needed to conserve a sustainable exploited population in Chesapeake Bay.

Our key findings were: (1) the CPUE of adult females was significantly higher in the corridor than in adjacent shallow-water habitats, both prior to the reproductive period and during the migratory and reproductive period; (2) the corridor was selective for adult females; and (3) a sanctuary-corridor complex, composed of the spawning sanctuary and protected corridor, had higher abundances and lower variation in abundance of the spawning stock between years than either the sanctuary or the corridor alone. Hence, a sanctuary-corridor complex would protect a less variable and more abundant spawning stock interannually, provided that fishing effort is not redirected markedly.

Adult females were the only segment of the population at moderate to high CPUE within the spawning sanctuary and in the deepwater corridor outside the sanctuary. Outside the sanctuary, adult females had higher CPUE values in the deepwater corridor than in shallow habitats, as they migrated to the lower bay spawning grounds. Furthermore, CPUE in the corridor might be higher than that measured, if exploitation were eliminated and fishing effort were not displaced to intercept those females migrating to the corridor and sanctuary. Juveniles and immature males and females had significantly higher CPUE values in shallow-water habitats outside the sanctuary; adult males were approximately equally distributed in shallow and deep waters. None of these constituents of the population had high CPUE within the deepwater corridor. A protected, deepwater dispersal corridor in the lower bay coupled to the spawning sanctuary would therefore selectively conserve adult or maturing females either en route to

or resident in the spawning grounds, whereas the remainder of the stock (adult males, juvenile males, juvenile females) would remain susceptible to exploitation.

In different years, highest abundances vacillated between the spawning sanctuary and deepwater corridor. In addition, the average fraction of all adult females in the lower bay that resided in the spawning sanctuary was 20.4% and in the deepwater corridor it was 26.7%, which did not differ significantly. Hence, the abundances and fractions of adult females in the sanctuary and deepwater corridor were complementary. Moreover, the interannual variation in abundance was lowest in the sanctuary-corridor complex, with a coefficient of variation of 38%, whereas the respective coefficients of variation in the sanctuary and corridor were substantially higher at 90% and 64%, mostly due to the interannual alternation of abundance between the sanctuary and corridor. Consequently, annual abundance in the sanctuary-corridor complex was not only higher, but also much more constant from year to year than in either the sanctuary or the corridor.

The utility of a deepwater corridor in the middle and upper bay is questionable. Summertime hypoxia (Diaz and Rosenberg 1995) likely precludes utilization of the deepwater corridor in the middle and upper bay during the migratory and reproductive period. However, if females utilize the deepwater corridor during spring and early summer prior to the onset of summertime hypoxia, or during the fall after hypoxia dissipates, then protection of the deepwater corridor throughout the bay during the spring and fall migrations may be warranted. Further sampling of the deepwater corridor during spring, summer, and fall in the middle and upper bay is necessary to test these assertions.

Conclusions and Recommendations

Adult females are consistently found in substantial numbers within the confines of the deepwater migration corridor, whether during the overwintering period or during the spawning season. A protected deepwater migration corridor (Fig. 11) would nearly selectively protect adult females en route to the spawning grounds, whereas the remainder of the exploitable segment of the stock (i.e., adult males, juvenile males, juvenile females) would be minimally impacted and remain susceptible to the crab fisheries. Consequently, we propose that a protected deepwater dispersal corridor is an effective means of protecting adult females as they migrate to the spawning grounds, particularly in those middle bay and lower bay regions that are impacted negligibly by summertime hypoxia.

We therefore suggest that to conserve and enhance the blue crab spawning stock, the existing spawning sanctuary should be expanded into a sanctuary-corridor network. The first step in the development of a sanctuary-corridor network involves protection of the proposed deepwater corridor (Fig. 11) in summer. Concurrently, there should be (1) consider-



Figure 11. Proposed initial extension of the spawning sanctuary into the deepwater corridor in lower Chesapeake Bay and 13-m depth contour (based on NOAA depth charts). The sizes of the arrows reflect the densities of adult females in the different areas. Note that we assume that there are relatively few females during the reproductive period in deep waters of the middle and upper portions of Chesapeake Bay due to summertime hypoxia and anoxia, though this assumption remains untested. The spawning sanctuary is displayed as the shaded area near the mouth of the bay. The proposed sanctuary-corridor complex was adopted by the Virginia Marine Resources Commission on 27 June 2000.

ation of complementary effort controls to preclude displaced effort, which might nullify any benefits of a protected corridor, as well as (2) simulations of the impact of the network upon exploitation rates and population growth rates (e.g., Miller and Houde 1998). Second, there should be an examination of other critical habitats deserving protection, such as shallow-water corridors and habitats utilized by other benthic phases in the life cycle; these include settlement habitats, nursery grounds for young juveniles (e.g., seagrass beds and marshes), feeding sites of juveniles and adults (e.g., marshes and mud flats), and mating areas, all of which might be linked into the network by protected dispersal pathways. The network could also incorporate pelagic habitats used by the planktonic stages (i.e., larvae, postlarvae, and young juveniles). Some of the habitats are presently protected (e.g., spawning sanctuary in the lower bay, de facto sanctuaries such as shipping channels), and should be integrated into the network. Ultimately, the baywide sanctuary-corridor network could be used as a permanent management tool to protect that fraction of the stock which will maintain the blue crab population in Chesapeake Bay at long-term sustainable levels, as well as to protect critical shallow-water habitats such as seagrass beds and fringing marshes.

Advantages of a sanctuary-corridor network include efficient enforcement, reduction of fishing mortality, and preservation of critical Chesapeake Bay habitats (e.g., seagrass beds). The use of a sanctuary-corridor network does not preclude other effective management measures, but it may allow for the abolition of ineffective regulations that hinder exploitation and conservation alike. Finally, we posit that the blue crab in Chesapeake Bay serves as a model marine system for the study of the efficacy of sanctuaries and dispersal corridors for sustainable resource use in the marine environment.

Addendum

The sanctuary-corridor complex was adopted, with some modifications, by the Virginia Marine Resources Commission on 27 June 2000.

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Managing with Reserves: Modeling Uncertainty in Larval Dispersal for a Sea Urchin Fishery

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Abstract

The commercial fishery for the northern California red sea urchin, *Strongylocentrotus franciscanus*, began in 1985, peaked in 1989, and has declined steadily since that time. An alternative to traditional management is spatial management using no-take reserves that may improve the management of this and other fisheries. We formulated a size-structured metapopulation model with 24 patches and a dispersal matrix to address the key issue of larval linkages between reserve and fished patches. We explored four conceptual models of metapopulation connectivity including source-sink, limited distance, larval pool, and headlands dispersal models. These models indicated that the mode of dispersal led to potentially large differences in reserve performance. Larval pool models require little knowledge of spatial patterns in order to design an effective reserve network, while source-sink dynamics require a detailed understanding of larval dispersal if reserves are to be an effective means of fisheries management. Reserve networks can be optimized with knowledge of larval dispersal patterns; however, they are rarely known with certainty. A decision analysis used to evaluate alternative dispersal modes suggested a reserve system comprising approximately 25% of the total area can maintain catch in the red sea urchin fishery, buffering uncertainty in the pattern of larval replenishment and fishing mortality rate.

Introduction

Marine reserves have been proposed as an alternative management strategy to arrest the decline in catch of the northern California red sea urchin fishery. Kalvass and Hendrix (1997) detail the fishery and its management, and point out the large reduction in biomass since the beginning of the fishery. While this decline is likely due to the "fishing up" effect, there is concern that the fishery may be recruitment overfished and will continue to decline. Here we attempt to address the question of spatially variable dispersal patterns in reserve design. The specific details of reserve placement are investigated in reference to knowledge of larval dispersal patterns and sources. Many factors contribute to the productivity of a particular location including growth, mortality, recruitment, and habitat features; however, we focus on a subset of simple, conceptual dispersal models to gain insight, and focus future attention on how reserves can be used in a fishery management context. We address reserve performance in terms of total catch versus percent area in reserves. We do not analyze other potential benefits of marine reserves, nor do we discuss other possible fishery management. These pose significant questions for future studies that can make use of the results obtained here.

Recent reviews of no-take marine reserves have pointed out the potential benefits to fisheries (Bohnsack 1990, Rowley 1994, Guénette et al. 1998, Murray et al. 1999). These benefits include reducing the likelihood of stock collapse (Quinn et al. 1993, Guénette and Pitcher 1999, Sladek-Nowlis and Roberts 1999), accelerating the rate of stock recovery and decreasing variability in annual catches (Sladek-Nowlis and Roberts 1999), serving as reference sites for collecting fishery-independent data (Allison et al. 1998), and preventing degradation of habitat caused by fishing (Allison et al. 1998, Dayton 1998).

One management goal of no-take reserves is to maintain sufficient reproductive capacity to provide recruits to adjacent fished areas. Consideration of the temporal and spatial nature of larval production, dispersal distance (Quinn et al. 1993, Botsford et al. 1994), and local oceanographic features (Carr and Reed 1993, Morgan and Botsford 1998) will influence the reserve siting decision. Previous authors have recommended a metapopulation approach to reserve networks with strategically placed reserves connecting metapopulations (Man et al. 1995, Stoner and Ray 1996, Roberts 1998). Reserve networks have also been proposed as a better way to protect source populations that produce larvae which recolonize fished, thus sink, locations (Pulliam 1988, Tuck and Possingham 2000). Here we define a metapopulation for a meroplanktonic species as a series of local, sedentary adult populations distributed along a coastline linked by larval dispersal (Botsford et al. 1994).

In the absence of fishing mortality, increases in the size and abundance of individuals in reserves has occurred (Roberts and Polunin 1991, Rowley 1994, Stoner and Ray 1996). Because larger individuals have a greater

per capita reproductive output than smaller individuals (e.g., Kalvass and Hendrix 1997 for the red sea urchin) reserves can increase the reproductive capacity of the population. Despite this evidence, there is still little documentation of reserves supplying benefits to adjacent fished areas (McClanahan and Kaunda-Arara 1996, Russ and Alcala 1996, Crowder et al. 2000), although theoretical studies predict fishery enhancement (Sladek-Nowlis and Roberts 1999).

Hastings and Botsford (1999) pointed out that an equivalence in yield to traditional management could be achieved with spatial management, but most modeling studies predict increased fishery yields under limited situations, most commonly when fishing pressure is unusually high. Greater enhancement occurs when larvae replenish nearby fished populations (Quinn et al. 1993, Holland and Brazee 1996, Guénette and Pitcher 1999, Sladek Nowlis and Roberts 1999). Although these models evaluated catch with regard to a variety of factors, none examined the specific spatial pattern of larval replenishment except Quinn et al. (1993). In this study, larvae were allowed to move to one or more adjacent patches. It was concluded that the distance between reserves should be less than the dispersal distance of the larvae.

The question of larval dispersal from a reserve location to a fished site is fundamental to the design and performance of a reserve network. Roberts (1997) estimated "transport envelopes" for larvae passively transported in prevailing currents of the Caribbean Sea, in an attempt to map linkages between populations. These maps allowed reefs to be identified as sources or sinks depending on the number of "upstream" or "downstream" populations. This study pointed to the need to address larval dispersal pathways in the design of reserve networks.

Although the duration of the larval stage is known for a variety of species, there is little else available to model larval dispersal pathways from adult spawning site to larval settlement site. Direct observations have been possible for a few species with relatively large larvae that disperse over relatively short distances (Davis and Butler 1989, Carlon and Olson 1993). Other studies have identified the physical mechanism underlying larval dispersal by sampling larval distributions in the plankton and recruitment over space and time concurrently with hydrographic measurements (Wing et al. 1995b, Hare and Cowen 1996, Miller and Emlet 1997). Studies have compared settlement variability over space on a variety of scales from meters to many kilometers (Sewell and Watson 1993, Wing et al. 1995a), although the relationship between settlement and recruitment to the fishery is often uncertain. Circulation models and satellite information on flow can also contribute to an understanding of the movement of planktonic larvae with specific physical and behavioral characteristics (Botsford et al. 1994, Keough and Black 1996, Polovina et al. 1999).

Because little is known of dispersal pathways, we are relegated to using models or likely transport paths to assess the effects of reserves on the metapopulation dynamics of meroplanktonic species. Carr and Reed (1993)

outlined conceptual larval replenishment models and qualitatively described their appropriateness to species with different life history characteristics. Adult populations can be linked in different ways based on the planktonic duration of larvae and regional circulation characteristics. The focus here is slightly different from that of Carr and Reed (1993) in that several dispersal models are evaluated in the context of the uncertainty of the dispersal pathway for one particular species, the red sea urchin. The models outlined by Carr and Reed (1993) form the basis of the current modeling, by serving as alternative states of nature covering a range of possible dispersal linkages. We include one additional model of dispersal based on ongoing research of sea urchin settlement and recruitment in northern California (Wing et al. 1995b, Morgan et al. 2000b). One important goal of this work is to make managers aware of the explicit assumptions regarding the pattern of larval dispersal and the effect this has on reserve performance and fishery yield. We attempt to generalize elements associated with understanding the pattern of larval dispersal to marine reserve design.

Methods

Metapopulation Model

Using a metapopulation model we evaluate the role of larval dispersal in maintaining meroplanktonic metapopulations in the face of fishing and reserves. The model consists of 24 independent size structured subpopulations linked in the larval stage by a dispersal matrix representing combinations of larval origins and destinations. Each subpopulation is modeled using von Bertalanffy growth with individual variability in asymptotic length. We use the red sea urchin as an example based on our familiarity with this species and a reasonable understanding of its life history. Parameter values representing typical growth and mortality of red sea urchin in northern California are used (Morgan et al. 2000a). We assume no adult movement between patches, constant annual fishing mortality, and no interannual recruitment variability due to environmental stochasticity. Because our interest is in the influence dispersal models have on spatial patterns of productivity, all growth and mortality parameters are the same for each subpopulation. A length-fecundity relationship, and size at sexual maturity for red sea urchins from Kalvass and Hendrix (1997) are used to model the production of larvae from each subpopulation.

Recruitment in the model incorporates Beverton-Holt density dependence between the larval and settlement stage of development. Post-settlement density dependence is likely influenced by the availability of protective spine-canopy habitat (Tegner and Dayton 1977). Thus density dependence is set such that successful settlement is dependent on the number of larvae attempting to settle and the amount of juvenile habitat available. The upper limit on carrying capacity is assumed to be the same for all sub-

populations and only the dispersal between subpopulations varies. Previous evaluation of the model by Botsford et al. (1999) derived values for the Beverton-Holt relationship, and we use those here. These values lead to model behavior in which the implementation of no-fishing reserves has an influence on catch (i.e., fishing at realistic rates reduces the number of settlers arriving at each site), but does not lead to local extinction.

We use equilibrium catch as the metric with which to compare the efficacy of no-fishing reserves. Catch after 100 years of constant fishing is calculated for each of four conceptually different larval dispersal models (Fig. 1). With no reserves catch is first calculated for each of the dispersal models to establish a baseline with which to evaluate reserves as a management tool. For fishing rates of $F = 0.5$, $F = 1$ and the rate which led to the highest maximum sustainable yield (MSY), we evaluated different reserve designs, including percent area and reserve position.

The first model, limited distance dispersal, is represented by a Gaussian curve centered on the exporting site with different standard deviations corresponding to different dispersal widths, narrow contrasted with wide. Two different dispersal widths are evaluated (i.e., different standard deviations in the Gaussian function, S.D. = 0.1, 1.0). We make the assumption that all 24 sites are arrayed along a linear coastline, such that larvae are lost from subpopulations located on the edges. The second dispersal model considered is a source-sink scenario where one source population supplies larvae to itself and either three or five other populations equally, while sinks supply no larvae (i.e., "black hole sinks"). For the source-sink model we calculated catch based on knowledge of the location of larval sources, and also predicted catch based on the probability that one or more reserves placed randomly included a source location using the hyper-geometric distribution.

The third model, larval pool dispersal, is characterized by each subpopulation contributing larvae to a common pool based on the abundance of adult, and receiving $1/24$ of the larvae in the pool. In the case presented here, where carrying capacity, growth, and mortality are the same for all sites, the larval contributions from each subpopulation are identical, unless fishing occurs.

The final dispersal model, the headlands model, is based on field studies of larval settlement and recruitment in northern California (Wing et al. 1995a,b; Morgan et al. 2000b). This latter model makes no assumptions regarding the source location of larvae (all sites contribute), but the delivery pattern is unequal between locations, (i.e., each site receives different numbers of larvae from a common larval pool). It is based on results that suggest that during active upwelling larvae are transported southward and offshore, and retained in frontal zones and coastal eddies. Then, during relaxation of upwelling winds, current reversals transport invertebrate larvae northward to settle at predictable sites (Wing et al. 1995a,b; Morgan et al. 2000b). From these studies in northern California, areas immediately to the north of headlands are those that first come into contact with the

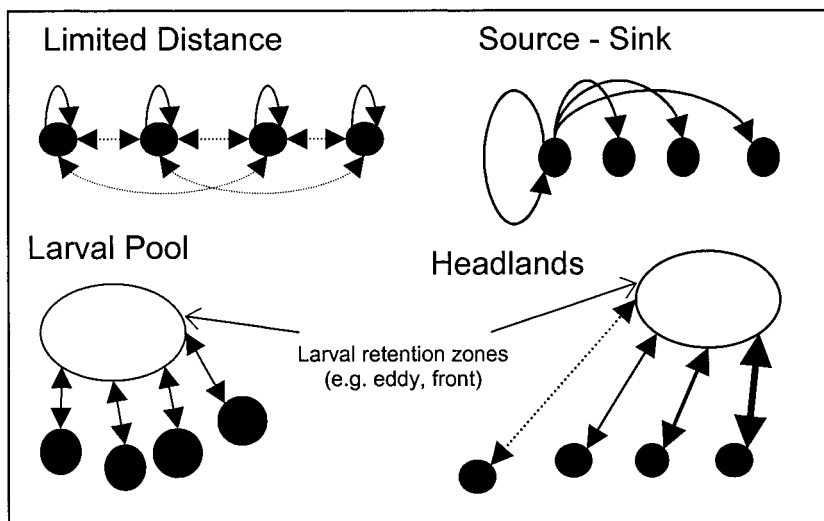


Figure 1. Conceptual models depicting possible larval linkages for a meroplanktonic metapopulation. Line weights represent different levels of transfer between patches. Dark circles represent individual patches.

poleward and onshore relaxation flow. As a result there is a gradient from south to north above headlands in the number of relaxation fronts that reach a site. We set up dispersal as a system with two separate headland cells, each with independent 12 patch metapopulations. For each 12-site set of cells, all sites contribute to the larval pool relative to the local abundance of adult sea urchins, but each site receives different numbers of larvae. Larval delivery for each site declines as a linear function from south to north within each set of 12 sites (Fig. 1).

Decision analysis was used to determine the optimal reserve configuration. The four dispersal models were considered as alternate states of nature with a probability of occurrence. We assigned the same probability of occurrence to each of the dispersal models assuming each was equally likely ($P = 0.25$). The weighted average catches for each fishing rate, reserve configuration and dispersal model were calculated to provide a basis for assessing the efficacy of marine reserves.

Results

Under equilibrium conditions, reserves enhanced catch when local populations were recruitment overfished. The fishing rate leading to MSY for our red sea urchin metapopulation varied depending on the dispersal matrix (Fig. 2). A fishing rate of $F = 0.2$ lead to MSY under larval pool models, but

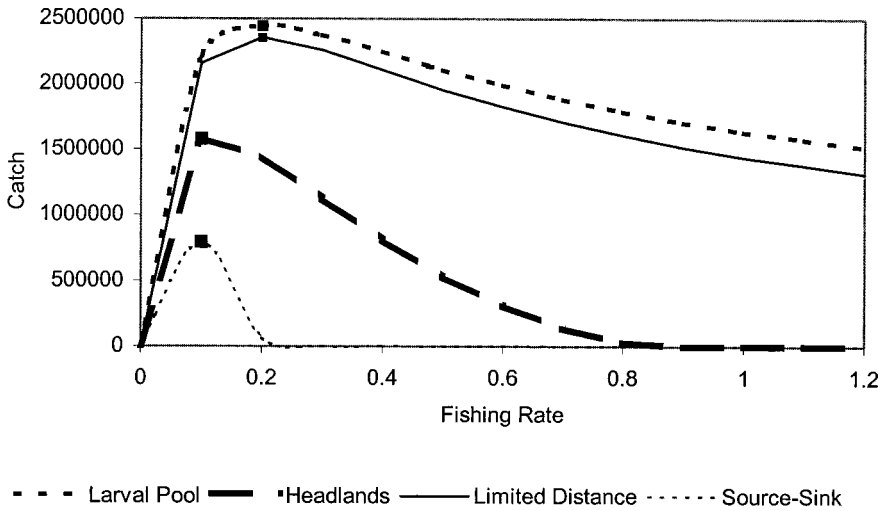


Figure 2. Maximum yield curves for different larval dispersal models with no reserves.

resulted in overfishing and a population collapse under the source-sink scenario. Furthermore there existed an equilibrium fishing value for larval pool and limited distance dispersal models over the range of values from $F = 0.1$ to 1.2 , but under models with more restricted larval dispersal, catch led to extinction at lower fishing rates ($F = 0.2$ for source-sink, $F = 0.8$ for headlands). When specific larval dispersal patterns were included into the metapopulation model such that production across space was variable, different aspects of reserve design became important.

Limited Distance Dispersal

Maximum sustainable yield for two limited distance models with different dispersal widths occurred at a fishing rate of $F = 0.2$ (Fig. 2, Fig. 3). At F equal to MSY, reserves did not enhance catch for either of the dispersal widths. Dispersal width led to varying performance of the reserve systems at higher fishing rates. At a fishing rate, $F = 1$, with equally spaced reserves, the greatest yield occurred with four reserves (17%) for the wide dispersal width, and with six reserves (25%) for the narrow dispersal width (Fig. 3). Reserve spacing needed to be closer than the maximum dispersal distance of larvae. At $F = 0.5$ and $F = 1$, catch increased with the area in reserve up to an optimal value and then declined for both dispersal distances. Spacing was the critical parameter since each site was able to supply larvae when protected. When reserves were spaced optimally, narrow dispersal width led to slightly greater catch than wide dispersal width due

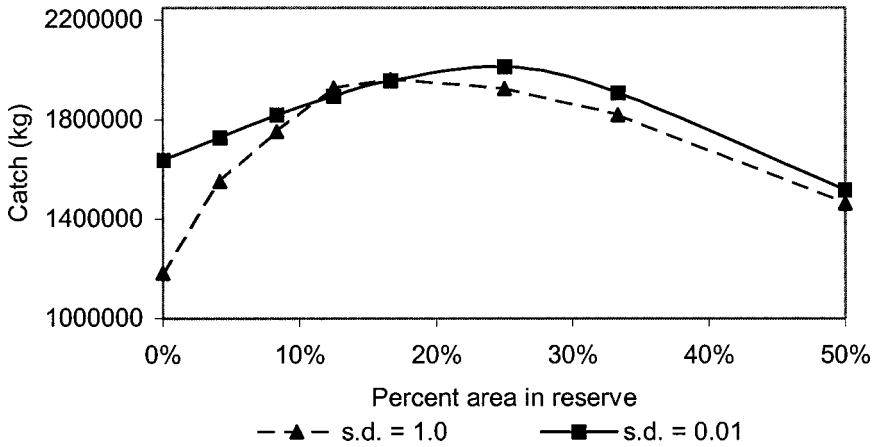


Figure 3. Catch with reserves for two different limited-distance dispersal width models for $F=1$ (S.D. refers to the standard deviation of the dispersal width).

to larvae from patches at the edges of the model boundary exiting the metapopulation system. The wider dispersal width had a greater loss of larvae. This result is partly an artifact of the way in which we modeled dispersal; i.e., without a reflecting boundary. However, the greater the dispersal width the greater the opportunity to rescue more distant fished populations. With only one or two reserves in place, reserves placed in the center of the range such that all larvae remained in the metapopulation were more effective than reserves positioned on the edge where larvae exited the system.

Source-Sink Dispersal

Maximum sustainable yield under source-sink conditions was much lower than for the other dispersal models (Fig. 2). Sinks in our model were “black-hole sinks” with no flow of larvae to the source population. This dispersal configuration resulted in a reduction in the number of successfully reproducing individuals by 75% in the case where one in four sites was a source. Catch under the source-sink model improved at MSY and when overfishing occurred, if source populations were protected (Fig. 4). Again, at $F = \text{MSY}$ if reserves were not optimally placed (i.e., randomly), catch declined as reserve area was added, although the decline was slight. If high rates of fishing were allowed in source areas, the entire population rapidly collapsed. This placed a premium on locating reserves at source locations. The highest yields were obtained when all sources were protected, and sinks were heavily exploited (Fig. 4). This was true for F equal to MSY and at $F = 1$ (Fig. 4).

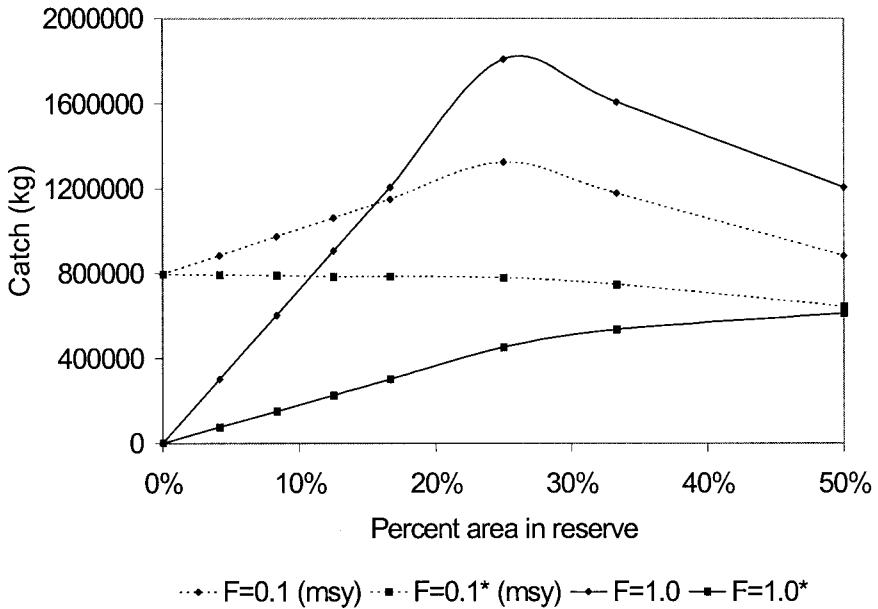


Figure 4. Catch with reserves for source-sink dispersal, at two fishing rates. * Random placement without knowledge of source locations.

In the more likely case where the source of larvae was unknown, we calculated the predicted catch based on the probability that one or more reserves placed randomly included a source location. At $F = 1$, catch increases with the number of reserves as the probability of locating a reserve by chance on a source location increases. Predicted catch increased with the number of reserves, up to 50% of the area in reserve for $F = 1$, but not for $F = 0.1$. Protecting sink populations never positively impacted yield.

Larval Pool Dispersal

Maximum sustainable yield occurred at a fishing rate of $F = 0.2$ with no reserves (Fig. 2). The amount of area to set aside in a reserve system was a function of the targeted fishing rate only. At $F = 0.5$, an increase in catch over the no reserve case was observed for percent reserve coverages of 4% (1 in 24) to 16.7% (4 in 24) with an optimum catch at 8.3% (2 in 24) (Fig. 5). With over 17% of the area in reserve catch declined with greater area in reserve. A similar pattern was observed for $F = 1$, except that notably, the increase in percentage catch was greater with reserves, although the optimum number of reserves was the same (16.7%). In contrast with the other dispersal models, the position of reserves had no influence, as all sites contribute and receive larvae equally.

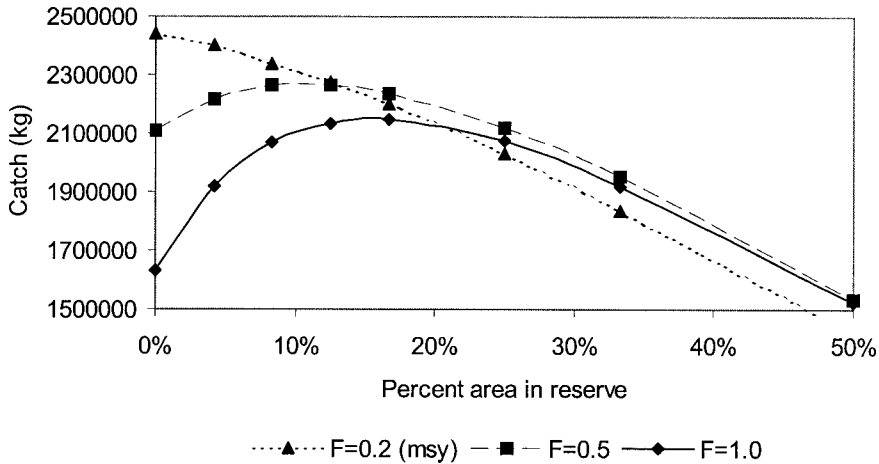


Figure 5. Catch with reserves for larval pool dispersal for three fishing rates.

Headlands Dispersal

Maximum sustainable yield without reserves occurred at a fishing rate of $F = 0.1$ (Fig. 2). At $F = 0.9$, the metapopulation was extinct at 100 years. When fishing rates exceeded MSY, reserves enhanced catch (Fig. 6). At $F = 0.5$, the optimal position and 25% of the area in reserve resulted in a nearly 60% increase over $F = 0.5$ and no reserves. For $F = 1$, the case was even more dramatic, as catch was not sustainable at $F = 1$ without at least one reserve.

With this dispersal model, the location of the reserves was important since no two patches were alike. When larvae were redistributed unequally from a common pool, spatial variability in recruitment lead to patches with different levels of biomass (Fig. 7). These results demonstrated not only that an increase in reserve area was needed with increased fishing mortality rates, but also that the position of the reserve could influence reserve performance. Although we did not detail all of the possible scenarios, these results suggested that as fishing rate increases the position of the reserve becomes more important. As an example, at $F = 1$ with one reserve, position alone accounted for a 15% difference in yield. While it was important to identify and protect the most productive sites at a fishing rate of $F = 1$, at a lower fishing mortality rate, $F = 0.5$, protecting the most productive patch resulted in a loss of yield, which was not made up for by transfer of larvae from this site. These more abundant populations with greater larval production, produced a higher standing biomass and thus had a greater contribution to the catch. Results (not shown) also indicated that, for $F = 0.5$, catch from three optimally placed reserves can exceed catch from four non-optimal reserves.

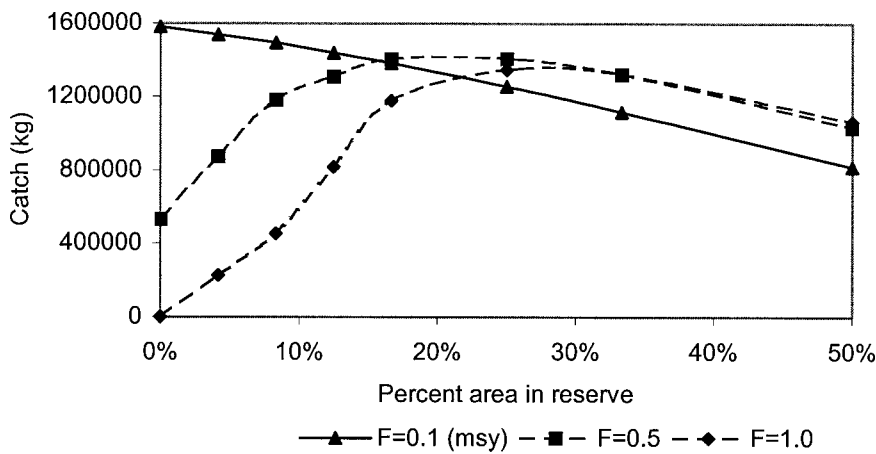


Figure 6. Catch with reserves for headlands dispersal at three fishing rates. Reserves placed to optimize catch.

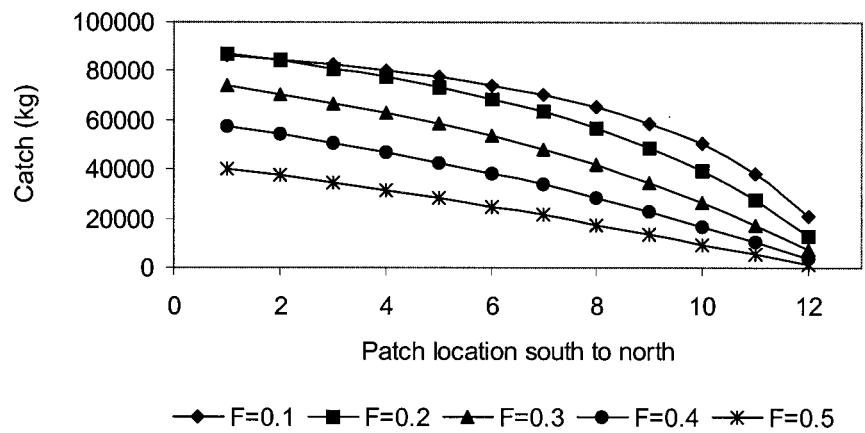


Figure 7. Catch for individual patches under headlands dispersal at various fishing rates without reserves. Areas with highest settlement sustain the greatest catch (e.g., site 1 vs. site 12).

Decision Analysis

Despite the widespread use of generic larval pool dispersal models, the present results suggest that they represent a best-case situation, and there is substantial evidence from field studies to suggest that they do not adequately describe larval dispersal patterns. Still, we are unable to adequately characterize the larval dispersal phase of the vast majority of species with any certainty. Therefore we assigned probabilities to the different dispersal models assuming each of the four was equally likely. The results of this averaging, when analyzed in the context of a fishing rate goal of MSY, indicated that the highest catch was obtained at $F = 0.1$, although $F = 0.2$ produced a very similar catch (Fig. 8). However, there was a drastic reduction in catch for higher fishing rates without a reserve ($F = 0.3$ and larger). At these higher fishing rates catch increased with greater area in reserve, and the loss of catch due to overfishing was much greater than the loss in catch due to removing areas from fishing. As the area in no-take reserve was increased, the variability in catch due to uncertain fishing rate was much narrower over the range of fishing rates, and this variability continued to decline up to approximately 25% of the area in reserve.

Discussion

Marine reserves are a robust management option for dealing with uncertainty in the mode of larval dispersal when fishing rate cannot be precisely determined or controlled (Fig. 8). With one reserve in our metapopulation (4% area) catch variability declined considerably, and landings increased substantially above the no reserve case for fishing rates above $F = 0.3$. Given the well-documented problems in assessing stocks and setting fishing rates (Walters and Maguire 1996), this result supports the use of marine reserves as a management tool. However, it should be noted that this result is based on a weighted average of four different dispersal models, which may have considerable error should one particular dispersal model be correct.

The role of larval dispersal is critical to the performance of a reserve system when knowledge of the underlying spatial patterns in dispersal patterns exist. Most modeling studies do not explicitly account for spatial variation in larval dispersal, assuming a generic, "larval pool" model of dispersal. Recently, evidence of substantial genetic heterogeneity in open marine populations has contradicted this larval pool assumption (Hedgecock 1994, Edmands et al. 1996, Moberg and Burton 2000). The present analysis shows that "larval pool" dispersal is the most optimistic scenario for catch enhancement through the use of marine reserves, and that other dispersal patterns can lead to very limited benefits or may even exacerbate conditions in poorly designed and implemented reserve systems. Calculations of maximum sustainable yield highlight this fact; MSY for one model can result in extinction if another dispersal model is in fact more appropriate (Fig. 2).

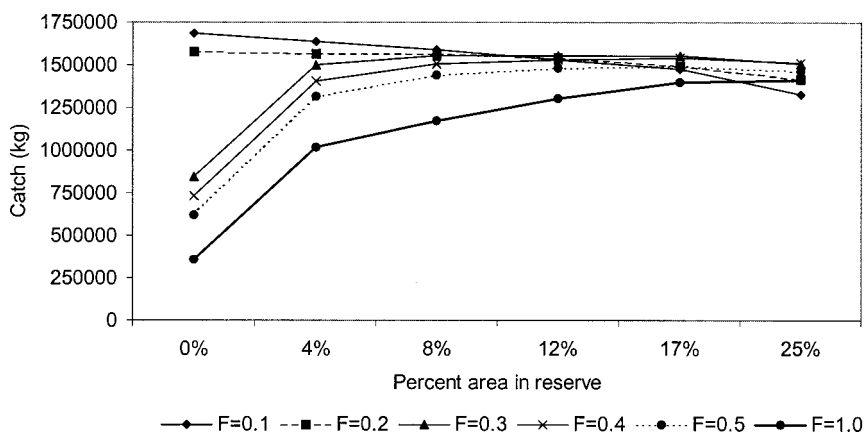


Figure 8. Decision analysis using average catch for each of the four dispersal models (equally weighted).

The appropriateness of the fishing rates used in this study in part relies on the present fishing rate in the northern California red sea urchin fishery. Morgan et al. (2000a) calculated fishing rates at 11 sites in 2 consecutive years and found a wide range of fishing mortality rates (0.12–1.87). Spatial and temporal variation in recruitment could bias these estimates in a positive direction (Morgan et al. 2000a); however, given this wide range of estimates, the values of F used in this study are likely conservative. The estimates of fishing mortality also indicate that in most cases fishing is well above the MSY calculated for all of the dispersal models. In light of this, a 25% total area reserve would benefit management of this population, although caveats to this recommendation must be noted. For example, in our modeled metapopulation all other sources of productivity are purposefully eliminated despite knowledge of spatial variation in growth and mortality rates (Morgan et al. 2000a).

The secondary question of where to place the reserves is unfortunately more difficult to ascertain. Although the headlands model appears to predominate in the years studied, evidence from red sea urchin size distributions in northern California indicates that occasionally recruitment events occurred over larger spatial scales (Morgan et al. 2000b). However, in light of the high estimated F (Morgan et al. 2000a), the pattern of recruitment (Wing et al. 1995a,b; Morgan et al. 2000b) and the modeling results presented here, locating reserves in productive areas to the north of headlands would be a good first step in implementing a reserve network.

Although it is generally perceived that no-fishing reserves require less management effort than traditional regulations, appropriate controls on fishing are still required with a reserve system in place. One of the signifi-

cant points of this and previous modeling studies (Beverton and Holt 1957, Holland and Brazee 1996, Guénette and Pitcher 1999) is that the size of a reserve system needs to be a function of the targeted fishing mortality rate. Other models have suggested reserves greater than 70% of the fishable area are needed to deal with uncertainties in management, and errors and bias in fishery management (Lauck et al. 1998).

This study also demonstrates that it is important to incorporate larval dispersal in management analysis of reserve design. These conceptual models point out different factors that will influence reserve design if a particular model is representative. Limited dispersal models suggest reserves on the edges of population ranges can be ineffective if larvae are lost to unfavorable patches, and that reserves spaced too widely cannot "rescue" distant patches. This result is consistent with ecologically realistic conditions in which short-lived planktonic larvae disperse relatively short distances compared to more long-lived larvae. Species with short-lived larvae would be better protected by smaller, closely spaced reserves, while species with longer-lived larvae need larger areas, but can withstand greater distances between reserves. This study agrees with earlier results that found spacing of reserves was a function of fishing rate and dispersal ability (Quinn et al. 1993). Limited distance dispersal requires appropriate spacing between reserves to ensure replenishment of fished areas between distant reserves.

We also note that a fishing rate set to $F = 0.2$, which is the MSY for the larval pool and limited distance dispersal models, results in extinction in the source-sink model, with the very same demographic parameters. Variation in spatial productivity due to differences in larval replenishment as well as the optimal size of the system can result in drastic differences in the performance of reserve systems. For example, if, as a tradeoff for closing areas to fishing, increases in fishing rate are allowed in remaining areas, precautions should be taken to protect source populations. A reserve design error that mistakes a source for a sink may exacerbate fishing conditions, leading to a more rapid stock collapse.

Further confounding the area required to offset fishing mortality is the shape and curvature of the stock-recruitment curve (Botsford et al. 1999, Parrish 1999) and density-dependent reproductive success. Yield in populations with strong density dependence may be disadvantaged by increased density inside reserves that leads to a reduction in per capita reproductive potential (Parrish 1999). Conversely, yield in species with broadcast spawning subject to Allee effects may be enhanced by reserves (Quinn et al. 1993, Botsford et al. 1999). Using a Beverton-Holt relationship Botsford et al. (1999) showed that changing the slope of this relationship at the origin could either increase or decrease yield as reserves were added to a fishery.

Previous authors have proposed using regional circulation patterns as criteria for designing reserve networks to maintain linkages between adult populations (Carr and Reed 1993, Morgan and Botsford 1998, Starr 1998). Here we present an analysis of the importance of larval dispersal patterns

on fishery yield. While maximizing larval export from reserves is an important goal for fishery management, few studies have evaluated the assumptions regarding this important life history period. Further studies of oceanographic features, such as frontal regions and coastal eddies, which accumulate larvae will likely improve our ability to successfully site reserves.

The analyses presented here for conceptual dispersal models appropriate to mesoscale metapopulation structure suggest that considerable research is necessary to adequately determine spatial patterns of productivity and correctly site reserves. The simple nature of these analyses, however, points to areas of concern with spatial management. First, mistakes in identifying either source or sink locations can have detrimental effects. Second, controls on fishing mortality still need to be in place, albeit with a greater buffer for uncertainty, if reserves are implemented. As with other management options, no-take reserves should be considered an additional tool in the effort to manage fisheries. Finally, if marine reserves are to be effective management solutions, then they must apply broadly to a range of species. The results of these analyses are appropriate to other meroplanktonic species, such as rockfish, but species that migrate as adults or shift distributions from one year to the next are not amenable to analyses herein.

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Reflections on the Symposium “Spatial Processes and Management of Marine Populations”

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First, I want to thank the organizing committee for proposing that I prepare a wrap-up of the symposium. This symposium was of particular interest to me because I have been working on spatial issues in fisheries science for several years. There were many presentations which provide a rather representative sample of the research presently conducted on the subject. I found the program of the symposium very interesting, and I believe the other participants did as well.

Rather than providing a detailed description and analysis of the presentations, I give a general impression of them, and then offer some perspectives in terms of future research topics and methodological approaches. These reflect only my opinion, and I would be happy to generate some discussions around them.

Overview of the Contributions

By definition *space* provides support for all processes; this is where they take place and interact with one another. For this fundamental reason, considering processes within a spatial context enables us to improve our understanding of the dynamics of fish populations and fisheries, and to explore their dependence on environmental factors and other factors.

Processes driving fisheries dynamics take place at different spatial scales. A specific time scale is associated with each spatial scale. The finer the spatial scale, the finer the time scale of a process. Processes can roughly be grouped into small-scale processes and meso- and large-scale processes. In this symposium, about 80 papers and posters were presented. I compiled some basic statistics about the processes they dealt with (Table 1).

Table 1. The number of presentations that addressed particular spatial processes.

Spatial processes	Number of presentations
Small spatiotemporal scales (individual fish, school)	
Vertical positioning and vertical movements	1
Aggregative behavior	2
Movements tied to local foraging behavior of fish	6
Local dispersion of fish	7
Behavior with respect to fishing gear or observation device	2
Local search of fishers for resources	7
Larger spatiotemporal scales (population, community, ecosystem)	
Migrations	11
Spatial distributions	44
Large range dispersion, e.g., larval dispersion	14
Allocation of fishing effort	14
Spatial management	14
Changes in the area of distribution (expansions, contractions)	4
Market constraints, access rights	2
Total number of presentations	80

Several remarks can be made about the topics covered in this symposium.

1. Several topics were hardly touched. Regarding small-scale processes, these include vertical movements and positioning, aggregative behavior, and behavior of fish with respect to gear or to observation device. A few presentations dealt with local foraging behavior, local dispersion, and local search of fishermen for resources. As for larger scales, questions related to the areas of distribution (expansions, contractions, shifts) and issues of economics and access rights were rarely discussed.
2. There were many more presentations on meso- and large-scale processes than on small-scale processes. This might be due to the scale at which most data have been collected. It is also the main scale at which we perceive populations and exploitation to interact, and the scale at which management intervenes.
3. In general, presentations focused more on spatial distributions than on movements (e.g., migration and dispersion). Horizontal spatial distributions within the area of distribution of populations were the subject of 44 presentations. An explanation for this is that there is a lack of available information on movement. In addition, it is difficult to

analyze data that are both spatial and temporal, like trajectories, and studies of movement typically rely on such data. This is pertinent for animal movement, but also for the allocation of fishing effort.

4. More than 40 presentations dealt with the relationship between spatial distributions of abundance and/or biological parameters and environmental factors. Among these, many presentations concentrated on early life stages. These relationships were mainly investigated through correlation analyses of habitat or environmental variables, and abundance or biological parameters. They provide empirical characterizations of habitat and habitat preferences which may be incorporated into models to evaluate the influence of the abiotic environment upon the dynamics of the population and the fishery. Such area characterizations may also help to design marine protected areas (MPAs). Aside from these habitat studies that concerned mostly demersal and benthic species, a number of presentations focused on dispersion of eggs and larvae and recruitment processes. In particular, for pelagic species in upwelling zones, recruitment is the complex end result of several combined processes linked to different hydrological components (e.g., Penven and Roy and Lluch-Cota et al. 2001). A limited number of presentations were based on mechanistic models based on deterministic mathematical equations. These mostly concerned recruitment processes in environments that are strongly driven by hydrodynamic processes (e.g., Penven and Roy, and Morgan and Botsford 2001). Beyond their heuristic value, mechanistic models that explicitly incorporate such components may improve predictions of recruitment once they become more operational.
5. A majority of presentations were based on the analysis of scientific catch data (Table 2). Commercial catch and logbook data were the second most used information. Surprisingly few presentations were interested in acoustic and tagging data, which are nevertheless particularly well-suited for spatial analyses. The prevalence of analyses based on scientific catch data might be due to several reasons. First, most of the scientists here were trained as biologists or ecologists, and it is indeed quite natural for us to rely on the data we collected. Second, survey data sets are frequently available in disaggregated form compared to commercial data. Third, it seems more intuitive to study populations using fishery-independent data. Also, it is apparently easier because we do not have to cope with the confounding features of exploitation. However, scientific survey data have some disadvantages. First, they rarely provide seasonal coverages, as surveys are most often conducted once a year. Hence, analyses based on survey data show instantaneous snapshots of distributions at the spatiotemporal scale of the survey. Most studies focus on interannual variations of spatial distributions, and ignore seasonal effects. The second drawback of scientific catch data is a relatively small sample size. In contrast, commercial

Table 2. Types of data used in the presentations of the symposium. Not all the presentations used data.

Biological and fishery data	Number of presentations
Visual/video	5
Scientific catches	34
Commercial catches	11
Logbooks	10
Tagging data	3
Acoustic data	7
Total number of presentations	80

data generally provide a good temporal coverage and large sample sizes (see, for instance, the data used by Sampson 2001).

- 6. There were few presentations on species interactions (five presentations).
- 7. Few presentations focused on fishers' behavior, fishing effort dynamics, and the resulting consequences for assessment and management. The session on Patterns in Fishery Behavior comprised only 9 presentations.
- 8. The session on Marine Protected Areas and Experimental Management was quite extensive, with 12 presentations. Approximately half of the presentations reported management experiences with MPAs, whereas the other half presented modeling approaches to evaluate effects of MPA management on population dynamics and/or biodiversity.

Perspectives

For the purpose of improving diagnostics and predictions for management issues, there are a few topics that, in my opinion, deserve further investigation. Most were mentioned during the symposium, but they were rarely the focus of presentations. I briefly discuss some of these objectives for future research, in terms of theme, methodology, and data collection.

Analysis of Available Data

The presentations made during the symposium show that the available scientific and commercial data contain a substantial amount of information about spatial processes. Most presentations provided analyses of data that were collected for other purposes. In the past, most of these data

already have been analyzed in aggregated form, such as average abundance indices computed from survey data. Spatial analyses obviously require space- and time-disaggregated information, and this may yield totally different insights. During the symposium, extensive analyses of long time-series of survey data were presented. Next, it is probably necessary to modify existing survey designs for the purpose of spatial analyses. In addition, the collection of commercial catch data, which do not always have the appropriate spatial resolution, could also be modified. None of the presentations given during the symposium really dealt with the issue of sampling designs for studying spatial processes.

Given the cost of surveys or field experiments, we ought to analyze all the data we have before collecting further information. Going a bit further, data analysis and modeling approaches must provide us with arguments to direct future data collection and help to improve sampling designs. A model is not an end result but rather a tool that should be used in conjunction with data analysis and data collection, in an iterative approach.

Small-Scale Processes and Scale Transfer

It is now acknowledged that large-scale processes impact fisheries dynamics and should be accounted for in studies related to management. However, this is also likely to be true to a certain extent for small-scale processes. The key question is, then, what are the large-scale consequences of such small-scale processes? Small-scale processes that pertain to fish behavior, like aggregation, species interactions, or behavior with respect to gear, may severely impact catchability and thus abundance indices and stock assessment. In the future, underwater video devices, whether conducted from remote-operated vehicles (ROV), towed from a vessel, or manually handled by divers, will likely provide novel information in this respect. In addition, it is a direct and nondestructive observation technique that may prove particularly relevant in marine reserves. However, the pertinence of such observation means for fisheries science remains to be demonstrated, because of the associated logistical constraints. In addition, methods for analyzing this type of observation are not yet fully developed.

Regarding tools for analysis, methods integrating data collected at several observation scales should be developed. Regarding modeling tools, individual-based models (IBMs) are specifically aimed at identifying the macroscopic consequences of processes occurring at the scale of the individual. Thus, they may be appropriate to assess scale transfers. With sound techniques for validation with respect to prior knowledge and data, these models could become more quantitative tools for evaluation purposes.

Spatiotemporal Dynamics of Processes

Another issue relates to the importance of the temporal dynamics of spatial processes. Both fish and fishers have their own dynamics of spatial distribution, with associated migrations, dispersion, and other movements.

Knowledge about animal movements, whether it be migration patterns or dispersion, is in general fuzzy; i.e., general patterns and mechanisms were identified, but no real quantification of movement and dispersion rates is available. In particular, metapopulation structures are poorly known. For example, Morgan and Botsford presented alternative hypotheses regarding the dispersion scheme of larvae within urchin metapopulations. As stressed by Botsford and Hastings, such knowledge gaps prevent us from correctly evaluating the impact of MPAs on population dynamics. On the exploitation side, the dynamics of allocation of fishing effort among fishing grounds and among possible fishing activities is poorly known in general. This is probably related to the lack of studies on fishermen dynamics, a long-lasting situation that had already been emphasized in the past by Hilborn (1985). Fishing effort allocation is the result of between-trip (see Pelletier et al. 2001) and within-trip strategies (see Sampson 2001), local search for resources, interactions between fishing vessels, and reaction to management measures (e.g., spatial closures) and to changing conditions for exploitation (see Evaluating Spatial Management, below). The question of effort allocation might thus be considered at the scale of the fishing operation, at the scale of the fishing trip, or at the scale of the year. The factors determining fishing effort allocation may refer to environmental and socio-economic constraints, to the fisherman's individual behavior and previous experiences with the fishery. As with catchability, the allocation of fishing effort over time and space may dramatically affect the relationship between fishing effort and fishing mortality. Therefore, it is of primary importance for stock assessment and for evaluating the consequences of management measures upon population and fisheries dynamics.

Understanding the dynamics of fish movements and fishing effort allocation basically relies on the analysis and modeling of temporal trajectories in a two- or three-dimensional space from time series of maps or spatially distributed data. While studies of population movements may still benefit from continuing improvements in tagging and remote-tracking techniques, a substantial amount of information about exploitation features will most likely emerge from the development of vessel monitoring systems. Additional fisher interviews may be carried out to provide complementary information. Such data will undoubtedly improve our understanding of fishing effort allocation. However, analyses of trajectories or time series of maps are no trivial matter and may require sophisticated techniques; for instance, multivariate analyses of time series that allow for characterization and classification. Similarly, modeling spatiotemporal dynamics may not be straightforward. Once again, IBMs may be useful for modeling individual trajectories. A trajectory may also be seen as a succession of states that may be modeled through probabilistic models, e.g., Markovian approaches. When it comes to modeling, the question of how to model movements is inevitably raised. Apart from IBMs, two classes of models are currently used: diffusion-advection-reaction models based on discretized differential equations, and island (or compartmental) models.

Because the algebra of movement is totally different in the two models, their results may be fundamentally different. Selecting a model for movement should depend not only on the characteristics of the dynamics to be modeled, but also on the objectives and the scale of interest.

Integration of Several Sources of Information and Knowledge

As mentioned in the Overview, space is the support of the interaction of several dynamics. In fisheries, resources and exploitation are the most evident ones, but other dynamics also interact, like the abiotic environment, ecosystem, management, economy, and potentially other human activities co-occurring with the exploitation. At some stage, a proper evaluation of fisheries dynamics requires the interfacing of these dynamics which may operate at different scales. Such approaches logically lead to multidisciplinary projects (see, e.g., Ault et al., Holland), and to the integration of several types of knowledge and information. A first step in this direction arises from the exponential development of geographic information systems (GIS) in fisheries (14 presentations talked about GIS in the symposium), and more generally of fisheries information systems (FIS) (Fairweather et al.). GIS allows simultaneous visualization of different types of information. However, they remain a descriptive, although powerful, tool. Evidencing and testing for spatial patterns or relationships between variables need inferential methods that may possibly be coupled with GIS. Some statistical frameworks may be particularly suited for integrating information. Several types of information including both numerical and qualitative data may be integrated and synthesized through multivariate descriptive analyses. Bayesian techniques are appropriate to combine prior knowledge and data, or several data sets. In the same line of thought, different pieces of information collected at different times may be combined using, for instance, likelihood approaches (Maunder 2001) or state-space modeling.

In fisheries science, models that integrate multiple dynamics are developed with the objective of evaluating the management of the fishery or ecosystem (see Evaluating Spatial Management, below).

Recruitment Processes and Areas of Distribution

Another area of research pertains to recruitment processes, particularly in relation to physical processes. As mentioned earlier, models that couple hydrodynamics and larval concentration and dispersion should lead in the end to better predictions of recruitment strength. Breaking down observed relationships into actual underlying processes is really needed to make progress in predictive models of recruitment.

In many cases, areas of distribution are not precisely delineated. This might be a consequence of the spatial design of catch surveys that are included within the area of distribution of the species of interest, and sometimes focus on main abundance areas. Acoustic data may help in determining

the extent of the area of distribution, but only for some species. Expansions, contractions, and shifts in areas of distribution might lead to misleading assessments. As exemplified by Die et al. in the case of the Australian prawn fishery, declines in CPUEs might correspond to a stable abundance if the area of distribution has been increasing. It can also go the other way around and lead to over-optimistic stock assessments.

Evaluating Spatial Management

Spatial management includes MPAs and more generally any management measure that is specific to a certain area. First, it would be necessary to systematically conduct extensive studies of the dynamics of populations and exploitation before implementing any MPA, so that the impact of this measure can be correctly assessed with respect to prior conditions. The presentations by Shirley et al. and Taggart et al. provide an example of such baseline studies.

Second, an important point pertains to changes in fishing effort allocation in reaction to spatial closures. The reaction of fishers to management measures should be addressed in the evaluation of those measures, since the subsequent redistribution of fishing effort toward other zones bears consequences on population dynamics.

Last, models aimed at assessing the impact of MPAs are still under development and deserve further investigations, although several examples were presented during the symposium (Holland, Morgan and Botsford 2001, Pelletier et al. 2001, Shin and Cury 2001). In this regard, the identification of spatial features of population dynamics is crucial since very different results may be obtained depending on model assumptions, as illustrated by Morgan and Botsford 2001. in the case of larval dispersal schemes for urchin. MPAs may also be seen as a particular kind of fishing experiment. For instance, because no-take reserves are fully protected from fishing, they may be very informative in terms of fishery-independent population processes, and for evaluating the effect of fishing on biological parameters, and more generally to distinguish fishing effects from environmental effects.

Conclusion

The study of spatial processes, and the subsequent implications for management, generally requires extended, massive and multivariate information. It may also need sophisticated quantitative methods (although not always: several presentations of the symposium were very informative, although they relied on basic techniques). This may require particular skills and training. Spatial studies may be challenging, but at the same time, they are closer to the real dynamics, because space provides the support for actual processes. This might be what makes spatial studies attractive and fashionable. It is obvious that people like to see maps, and things that

move on maps. Also, maps are more concrete and more attractive than tables of numbers. Therefore, spatial tools may be an appropriate way to convey scientific messages to the industry and to fishery managers. But like any method of representing scientific results, maps might also be misleading. The tools we are developing should thus be considered from the heuristic standpoint, but also from the standpoint of both education and communication. This is my suggestion to answer a concern expressed in the first session of this conference regarding our role in producing and disseminating knowledge for management.

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