Biology, Assessment, and Management of

North Pacific Rockfishes

23RD LOWELL WAKEFIELD FISHERIES SYMPOSIUM

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About the Proceedings Book and the Symposium

Fisheries researchers and managers will find invaluable the twenty-eight peer reviewed manuscripts in this book. The book is important because it exemplifies the recent advancements that have been made in understanding topics such as rockfish life history, population dynamics, age and growth, genetic population structure, and stock assessment. In spite of enormous challenges that face rockfish researchers and managers, improved knowledge on these topics should result in enhanced management and conservation of rockfish populations. The contributions in this volume are not only important to those studying Pacific rockfishes but also to a wider audience involved with fisheries oceanography, genetics, stock assessment, and fisheries management.

The rockfish symposium is the 23rd Wakefield Fisheries Symposium, organized by Alaska Sea Grant. It was held as part of the 2005 annual meeting of the American Fisheries Society, Creating a Fisheries Mosaic. One of the tenets of the Wakefield Symposium Series is that fishery managers and policy makers must have credible, research-based information on which to base management decisions. This principle is ever more important for the assemblage of rockfish species in the genus *Sebastes*. Rockfish species are diverse, are difficult to distinguish, and have a large and enthusiastic following in the commercial and recreational fishery. It is not surprising, given the array of color polymorphisms in some species, that *Sebastes* translates to "magnificent" (M.S. Love, M. Yoklavich, and L. Thorsteinson. 2002. *The Rockfishes of the Northeast Pacific*. University of California Press).

Some of the 100+ rockfish species of the northwestern and northeastern Pacific are currently experiencing declines in abundance, especially off the coast of California, Oregon, and Washington. Some rockfish are more vulnerable to exploitation based on species-specific life history traits such as long life, variable recruitment success, habitat fidelity, and changing oceanographic conditions. In the long tradition of Lowell Wakefield Fisheries symposia, this rockfish symposium extended the knowledge base and helped bridge the gap between contemporary rockfish science and management challenges since the Wakefield rockfish symposium held in 1986 in Anchorage.

The symposium convened scientists, fishery managers, and industry to discuss rockfish biology, taxonomy, assessment techniques, and management strategies to promote sustainability and conservation on both sides of the North Pacific.

The symposium was coordinated by Sherri Pristash, University of Alaska Fairbanks, Alaska Sea Grant College Program. Organizing committee members are Jane DiCosimo, North Pacific Fishery Management Council; Tony Gharrett, University of Alaska Fairbanks, School of

Fisheries and Ocean Sciences, Juneau Center; Jon Heifetz, NOAA Fisheries, Auke Bay Lab; Rod Moore, West Coast Seafood Processors Association; Victoria O'Connell, Alaska Department of Fish and Game; Mike Rust, NOAA Fisheries, Northwest Fisheries Science Center; Rick Stanley, Department of Fisheries and Oceans Canada, Pacific Biological Station; and Brian Allee, University of Alaska Fairbanks, Alaska Sea Grant College Program.

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The Lowell Wakefield Symposium Series and Endowment

The 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 an important role 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. In his later years, as an adjunct professor of fisheries at the University of Alaska, Lowell Wakefield influenced the early directions of Alaska Sea Grant. The Wakefield symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries. In 2000, Lowell's wife Frankie Wakefield made a gift to the University of Alaska Foundation to establish an endowment to continue this series.

Proceedings Acknowledgments

This publication presents twenty-eight symposium papers. Each paper was reviewed by two peers, and was revised according to recommendations by associate editors who generously donated their time and expertise: Jonathan Heifetz, Jane DiCosimo, Anthony Gharrett, Milton Love, Victoria O'Connell, and Richard Stanley.

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Age-Modulated Variation in Reproductive Development of Female Pacific Ocean Perch (*Sebastes alutus*) in Waters off Oregon

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Abstract

We investigated the maturity of female Pacific ocean perch (*Sebastes alutus*) in waters off Oregon. Visual and histological methods produced similar results during the months of December to March; however, neither method provided reliable determinations of reproductive maturity in other months. Evidence of abortive maturation, characterized by mass atresia of the developing class of oocytes, was observed in 7.1% of the fish sampled during December to March, with a strong age-related decline in prevalence. Fish older than 18 (N = 73) showed no evidence of abortive maturation regardless of size, further supporting the higher reproductive value of older rockfishes. Abortive maturation was associated with adolescence (age 5-9 years), but was also observed in post-adolescent fish, especially in 2001 samples. Rates of abortive maturation varied between the years 2001 and 2003, suggesting an environmental influence on successful egg development in younger fish. Pacific ocean perch off Oregon were 50% mature at a length of about 31 cm and an age of six, two years younger than assumed in recent stock assessment models for the West Coast population.

Introduction

The age and length at maturity for female fish is a critical parameter in many stock assessment models. For example, Clark (1991) and Lunsford (1999) have shown that changes in the age at 50% maturity (A_{50}), espe-

cially in relation to the median age of fishery recruitment, can have a strong influence on estimated target fishing rates. Target fishing rates are used by the Pacific Fishery Management Council (PFMC) to manage most groundfish stocks (Clark 1991, PFMC 2000). One example of a target fishing rate would be $F_{40\%}$, the fishing mortality rate that would reduce spawning stock biomass per recruit to 40% of the unexploited level. The importance of errors in estimating the median age of female maturity was illustrated by Lunsford's (1999) study of maturity of Pacific ocean perch (*Sebastes alutus*), where a shift in the estimated median age of maturity for female fish from 7.5 to 10.5 years decreased the $F_{40\%}$ value from 0.110 to 0.076, a decrease of 31%. Correct estimation of target fishing rates is especially critical for U.S. West Coast rockfish (*Sebastes* spp.) stocks, as they are considered to be some of the least resilient (Leaman 1991, Clark 2002).

For many species of rockfish, especially those found on the upper continental slope, age and length at 50% maturity (L_{50}) are not well established (Love et al. 2002). Some information on L_{50} has been gathered for most slope rockfish species over the last several decades (Westrheim 1975, Wyllie Echeverria 1987, Barss 1989). These early studies, however, either did not collect age data (Westrheim 1975, Barss 1989), or they based ages on surface readings rather than the more accurate "break and burn" technique (Chilton and Beamish 1982, Wyllie Echeverria 1987). For some West Coast rockfish species, including Pacific ocean perch, the most extensive maturity data available have been from samples collected during the triennial National Marine Fisheries Service summer abundance surveys (Hamel et al. 2003). These data cover a wide geographic range and generally include a wide size range of fish, unlike commercial fishery samples that often lack adequate numbers of smaller, immature fish. However, these data are also based on a simple visual assessment of maturity, so they suffer from a different, but potentially serious, problem. In summer, maturity status of ovaries from winter spawning species like Pacific ocean perch can be very difficult to determine accurately—ovaries of mature, "resting" fish are macroscopically identical to ovaries of immature fish (Wallace and Selman 1981). The problem is best addressed by collecting a wide size range of fish during seasonal time periods when visual maturity determinations are more accurate. However, even within an optimal sampling period, the possibility remains that visual assessment of female rockfish maturity could be an inaccurate assessment of actual or "functional" maturity, meaning the successful production of larvae. Nichol and Pikitch (1994) evaluated maturity of darkblotched rockfish (*S. crameri*) microscopically and found that some ovaries with evidence of vitellogenesis also showed mass atresia and resorption of oocytes. Their findings underscore the importance of using histological evidence of maturity over visual assessment, as the difference between a func-

Table 1. Visual maturity stages and descriptions for rockfish ovaries from Westrheim (1975).

Stage	Condition	Description
1	Immature	Small, translucent
2	Maturing	Small, yellow, translucent or opaque
3	Mature	Large, yellow, opaque
4	Fertilized	Large, orange-yellow, translucent
5	Ripe	Large, translucent yellow or gray, with black dots (contain embryos or larvae)
6	Spent	Large, flaccid, red. A few larvae may be present
7	Resting	Moderate size, firm, red-gray, some with black blotches

tionally immature and a functionally mature individual can depend on attributes visible only microscopically, even during the period of reproductive growth. The primary objective of this study was to collect maturity samples from female Pacific ocean perch and evaluate the benefits of using histological sections to determine maturity as opposed to visual assessment. An additional objective was to develop age and length at maturity data specific to U.S. West Coast Pacific ocean perch that could be used in stock assessment.

Maternal age has been suggested as a potentially important predictor of reproductive success in rockfish (Leaman 1988, Berkeley et al. 2004). However, supporting data for individual species are very limited. Recent studies of larval quality in black rockfish (Berkeley et al. 2004) suggest a maternal-age effect on larval survival. A third objective of this study was to evaluate the effect of maternal size and age on reproductive success and the seasonal timing of ovarian development in Pacific ocean perch.

Methods

Maturity data for female Pacific ocean perch were collected from two sources, dockside sampling of Oregon's commercial fishery landings and chartered research trawl trips. Each fish was measured (cm fork length). An ovary was removed and assigned a macroscopic maturity stage (Table 1) following the criteria of Westrheim (1975). Only experienced samplers were used to assign macroscopic maturity stages to minimize errors in visual staging. One ovary was then preserved from each female fish for histological examination, except for fish with an unambiguous maturity status, such as those with developed larvae or recently spent ovaries. Sagittal otoliths were removed for subsequent age determination. Ages were determined using the break and burn technique (Chilton and Beamish 1982).

Ovaries were collected from all female fish that were not visually assigned stage 4 (fertilized eggs), 5 (eyed larvae) or 6 (recently spent). Ovaries in these three stages were considered to be unequivocally mature. Ovaries were preserved in 10% buffered formalin, and later transferred to 70% ethanol for storage. Tissue samples from the midsection of the ovary were then embedded in paraffin, sectioned at 5 µm, and stained with Harris's hematoxylin and eosin Y (West 1990). We measured the diameter of the five largest, spherical, non-atretic oocytes in each stained thin-section with an ocular micrometer (100 ×) and calculated a mean maximum oocyte diameter (MMOD) for each sample (West 1990). MMOD was compared for mature and immature fish to determine the appropriate period to evaluate samples to determine maturity. The samples were classified as mature or immature based on the presence or absence of vitellogenin, post-ovulatory follicles, and level of atresia. If the majority of the developing class of oocytes was atretic, maturation was considered abortive and the individual was considered functionally immature. The accuracy of visual examination of ovaries was then evaluated by comparing the maturity status from visual examination with status determined from histological sections.

Logistic regression was used to fit sigmoid length-maturity and age-maturity curves to microscopically verified maturity data. The model fitted had the general form,

$$p_{x_1} = e^{(b_0+b_1x_1)} / \left(1 + e^{(b_0+b_1x_1)}\right)$$

where p is the probability that a fish is mature in a given length (cm) or age category x_1, and b_0 and b_1 are parameters that define the shape and location of the fitted curve. The predicted length or age at 50% maturity was calculated as,

$$L\left(\text{or } A\right)_{50} = b_0 / b_1$$

We used the non-parametric Mann-Whitney U test and graphic methods to look for evidence of age- or size-related differences in reproductive timing as shown for darkblotched rockfish (Nichol and Pikitch 1994), yellowtail rockfish (*S. flavidus*) (Love et al. 1990), and black rockfish (*S. melanops*) (Bobko and Berkeley 2004). This analysis was applied to mature fish only, within individual months during the active spawning period, using macroscopic stage (3-7) as the dependent variable. For these tests, "old" and "large" Pacific ocean perch were defined as those 16 years of age or older and those 36 cm in length or larger. The choice of age 16 and 36 cm to split the data was somewhat arbitrary, but was chosen to maintain adequate sample sizes of fish in each group. We also evaluated how the timing of the onset of vitellogenesis varied with fish length and age by graphically examining the relationships between MMOD, developmental stage and fish length and age for the months prior to fertilization. We evaluated age- and size-related changes in the

Table 2. Summary of female Pacific ocean perch sampled for maturity, by month and year, 2000-2003.

Month	2000	2001	2002	2003	Total
January	0	45	0	57	102
February	0	182	0	0	182
March	0	0	0	100	100
April	0	0	0	0	0
May	281	0	0	0	281
June	0	0	0	0	0
July	0	0	0	0	0
August	1	0	0	0	1
September	123	0	0	0	123
October	0	0	76	0	76
November	0	0	0	0	0
December	99	0	0	0	99
Total	504	227	76	157	964

frequency of abortive maturation, as indicated by mass atresia within the developing class of oocytes, using a simple graphical approach, comparing the frequency of abortive maturation with the numbers of fish sampled, by size and age.

Results

Visual assessments of maturity stage for 964 female Pacific ocean perch (Table 2) showed highly synchronous reproduction (Fig. 1), with fertilization occurring in January to February. Based on the high frequency of ripe fish and increasing frequency of spent fish in February to March, this is the time of parturition for this species off Oregon. In May samples, many females were in the resting stage, and by September, development of mature ovaries had begun again. The timing of female reproduction, as determined from histological sections, was very similar, with most mature females being heavily vitellogenic in December and in a fertilized state by January to February. By May, most of the ovaries examined were either spent, in a resting stage, or in the early stages of vitellogenesis for the following year. Nonparametric tests for differences in mean maturity stage by month did not show any significant age- or size-related differences in the timing of parturition ($P > 0.05$), further supporting strong synchrony of spawning for this species in waters off Oregon (Fig. 2). Analysis of MMOD versus length for September and December samples (Fig. 3) showed that mature females

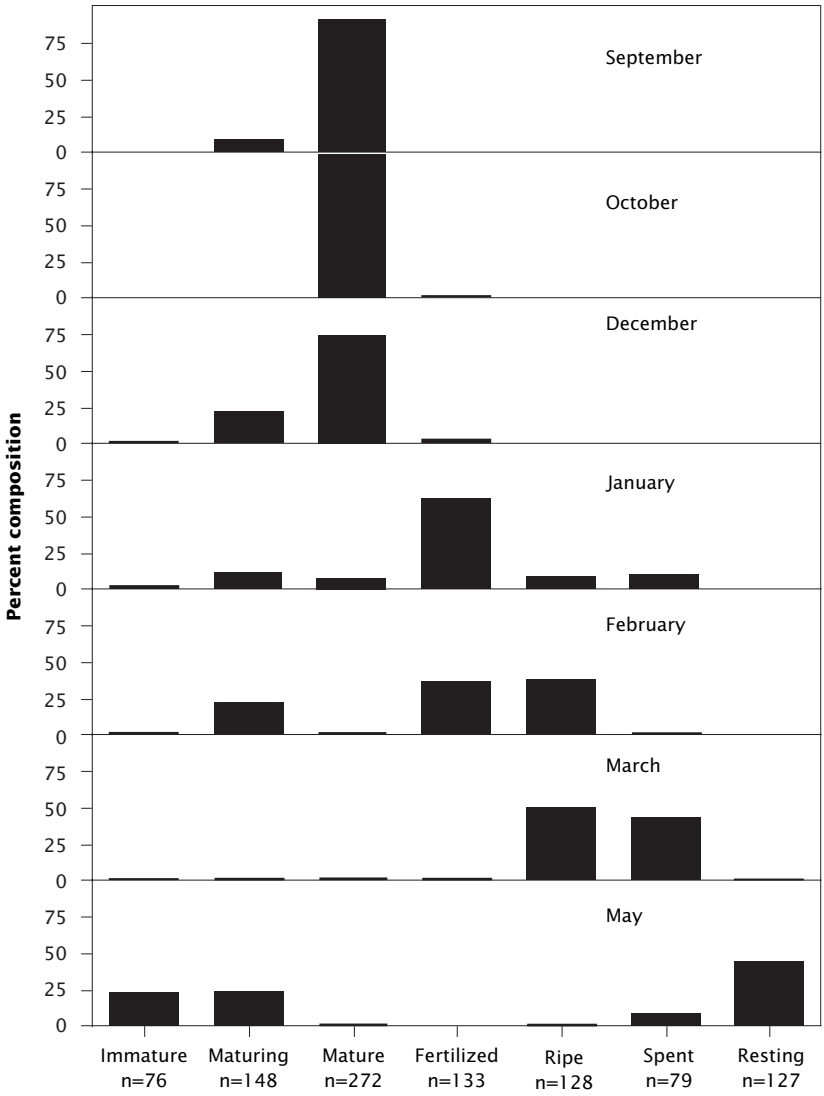


Figure 1. Relative frequency of visual maturity stages for female Pacific ocean perch, by month, 2000-2003.

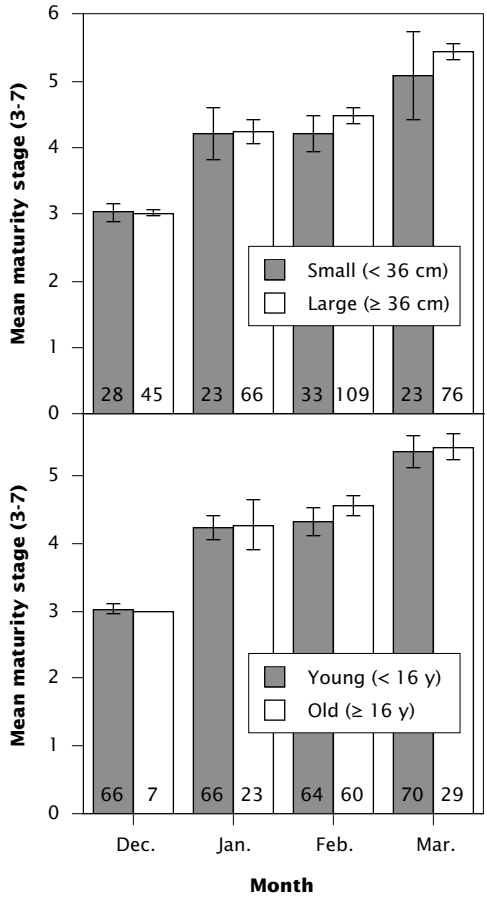


Figure 2. Comparison of mean macroscopic maturity stage (mature females only) by month for small (<36 cm) and large, and young (<16 years) and old, Pacific ocean perch. Error bars show 95% confidence intervals. Samples sizes are shown at the base of each bar.

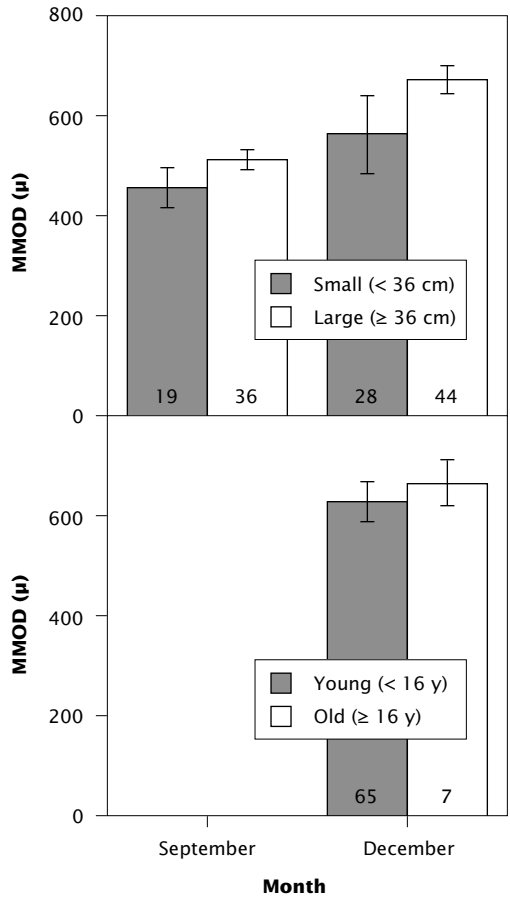


Figure 3. Comparison of mean maximum oocyte diameter (MMOD, µ) by month for small (<36 cm) and large, and young (<16 years) and old, Pacific ocean perch, for selected months. Error bars show 95% confidence intervals. Samples sizes are shown at the base of each bar.

less than 36 cm had smaller developing oocytes than the rest of the population of mature fish in these months (ANOVA, $P < 0.01$). No trend in MMOD with length was evident for fish larger than 35 cm, however. Young and old Pacific ocean perch did not have significantly different MMOD in December samples (ANOVA, $P > 0.05$), however December sample size was very low for older fish (N = 7). Taken together, these results suggest similar timing of parturition for Pacific ocean perch of different

Table 3. Comparison of macroscopic and microscopic determination of maturity in female Pacific ocean perch collected by trawl in waters off Oregon in the months of December-March, 2000-2003.

	Macroscopic classification		Microscopic classification	
Sample month	Condition	Number	Number evaluated	Number reclassified
December	Immature	24	22	1
	Mature	75	72	3
January	Immature	13	13	0
	Mature	89	16	0
February	Immature	43	43	4
	Mature	139	4	0
March	Immature	3	3	2
	Mature	97	3	0
Total		483	176	10

sizes and ages, but later onset of oocyte development or smaller final egg size for small fish.

During December-March, macroscopic maturity determinations agreed well with determinations derived from microscopic examination of ovarian thin-sections. Of the 176 ovaries examined microscopically, most of which were macroscopically classified as stages 1 (immature), 2 (maturing), 3 (mature) or 7 (resting), only 10 (5.7%) were reclassified to either mature or immature (Table 3). In December samples, most re-classified ovaries were originally stage 3 (mature) ovaries found microscopically to be in the early- or late-perinucleolus stage, with evidence of prior atresia but no vitellogenesis. In January samples, no fish were reclassified, however only 29 fish were evaluated microscopically, because most fish examined were in unambiguous visual maturity stages, either fertilized or ripe (Fig. 1). In February and March samples, most of the errors were visually "immature" (stage 1) or "maturing" (stage 2) ovaries that microscopically showed post-ovulatory follicles, found only in mature ovaries. In months other than December-March, unambiguous determinations of maturity status could not be made, either visually or microscopically, because the most advanced oocytes of both immature fish and mature fish in the resting stage were in the early- and late-perinucleolus stages.

Although microscopic assessment of maturity status offered only a small benefit in accurately determining maturity status of female Pacific ocean perch during December-March, it was useful for identifying fish going through abortive maturation. These Pacific ocean perch were

mostly classified visually as stage 1 or 2, but microscopically showed evidence of vitellogenic oocytes undergoing mass atresia and resorption. In December-March samples, 34 (7.1%) of 480 female Pacific ocean perch sampled showed evidence of abortive maturation, while another 50 (10.4%) showed evidence of minor atresia; a moderate percentage of atretic cells mixed in with many other vitellogenic oocytes that were developing normally at that time. The prevalence of abortive maturation declined weakly with size but more directly with increasing age (Fig. 4), however the phenomenon clearly extends to older age fish than normally associated with an adolescent phase lasting a year or two (Fig. 5). No fish over age 18 (N = 73) showed evidence of abortive maturation, regardless of size, providing no support for senescence in this species. There was evidence from these samples that the prevalence of abortive maturation may vary interannually. Of the 226 female Pacific ocean perch with known maturity status from the 2001 December-March samples (1 ovary sample proved unusable, Table 2), 23 or 10.2% showed evidence of abortive maturation. In the 157 samples from 2003, only one fish (0.6%) showed evidence of abortive maturation. Samples from both years contained adequate numbers of fish for a valid comparison across the age classes most likely to show abortive maturation. In 2001, 95 fish between age 6 and 13 were sampled, while in 2003, 64 fish were sampled from this age range.

Abortive maturation caused asymmetry in the relationship between the proportion mature and both length and age (Table 4 and Fig. 6), in the sense that the proportion mature increased rapidly with length or age at small sizes and young ages, but then approached the upper asymptote very gradually. The very gradual approach to 100% maturity was caused by a few larger, post-adolescent fish with abortive maturation that were classified as immature. This effect created a very poor fit to the logistic curve and derived estimates of length and age at 50% maturity that may be biased. The fitted logistic curves (Table 5) suggest a length at 50% maturity of 31.1 cm and an age at 50% maturity of 5.2 years. Simply inspecting the data on proportion mature (Fig. 5) suggests the estimate of L_{50} from the fitted curve is approximately correct, but that an A_{50} of about 6 years would be a better choice than the estimate of 5.2 years from the fitted curve.

Discussion

Pacific ocean perch are found across a broad range of latitude in the eastern Pacific and across the North Pacific Rim (Love et al. 2002) and demonstrate significant spatial heterogeneity in life history parameters, some of it possibly attributable to exploitation history (Westrheim 1975, Gunderson 1977, Leaman 1988). The synchronous spawning of Pacific ocean perch shown in this study agrees with previous maturity

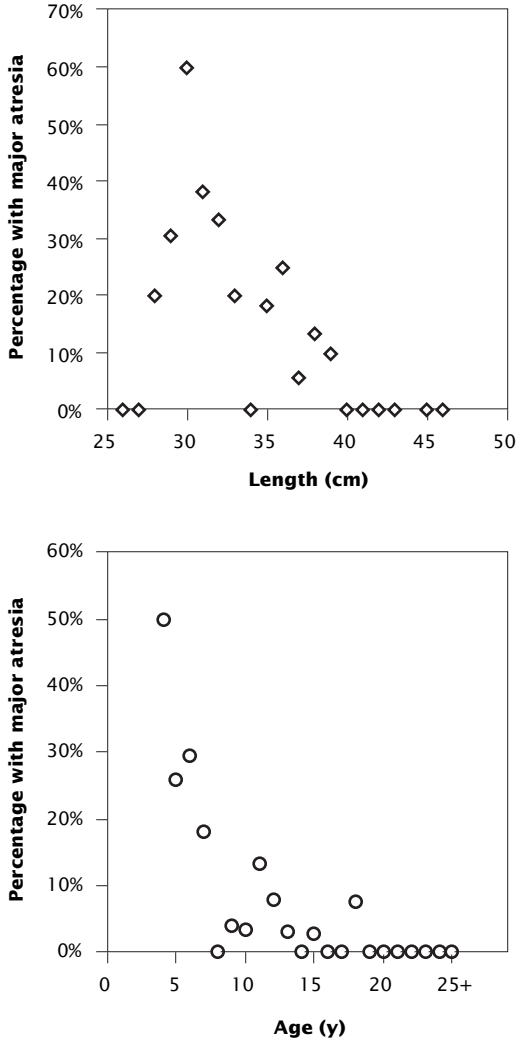


Figure 4. Percentage of female Pacific ocean perch with major atresia (N = 34) of oocytes, by length (cm, N = 468) and age (years, N = 464) class, 2000-2003.

Table 4. Number of female Pacific ocean perch sampled and proportion mature, by length (cm) and age (y). Fish showing abortive maturation were treated as functionally immature.

Length (cm)	Number sampled	Proportion mature	Age (y)	Number sampled	Proportion mature
26	1	0.00	4	2	0.00
27	2	0.00	5	21	0.24
28	5	0.00	6	27	0.48
29	13	0.15	7	22	0.68
30	15	0.53	8	13	1.00
31	14	0.43	9	25	0.92
32	20	0.75	10	28	0.96
33	13	0.85	11	45	0.78
34	25	0.84	12	51	0.82
35	56	0.79	13	33	0.79
36	51	0.82	14	35	0.94
37	62	0.92	15	36	0.94
38	61	0.97	16	20	0.95
39	53	0.94	17	17	1.00
40	40	0.97	18	13	0.85
41	19	1.00	19	9	1.00
42	14	1.00	20	10	1.00
43	7	1.00	21	6	0.83
44	3	1.00	22	6	1.00
45	3	1.00	23	7	1.00
46	3	1.00	24	2	1.00
			25+	33	1.00
Total	480			461	

Table 5. Results of logistic regression analysis of histologically determined maturity status of Pacific ocean perch versus length (cm) and age (December-March samples).

Independent variable		Coefficients	Standard error	*P*-value	L_{50} or A_{50}	95% confidence limits
Length					31.11 cm	31.02-31.21
	Constant	–12.818	1.593	0.0001		
	Length	0.412	0.046	0.0001		
Age					5.20 yrs	5.12-5.28
	Constant	–1.399	0.409	0.0006		
	Age	0.269	0.039	0.0001		

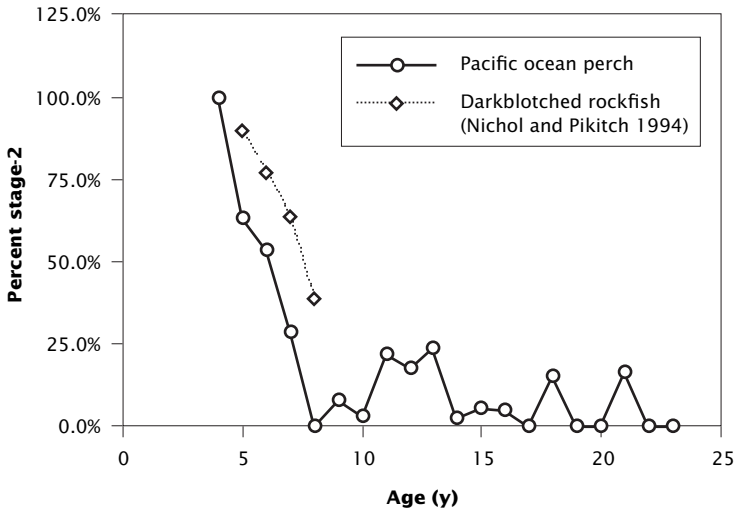


Figure 5. Percentage of ovaries of female Pacific ocean perch (this study) and darkblotched rockfish (Nichol and Pikitch 1994) identified visually as stage 2 (maturing), by age.

studies for this species, however the more northerly stocks may release larvae somewhat later in the year (Gunderson 1977) and the timing of parturition and degree of synchrony may vary somewhat from area to area within similar latitudes (Leaman 1988). Interannual variation in the timing of parturition has been shown for other species of *Sebastes* (Lenarz and Wyllie Echeverria 1986). In our study, synchrony extended across age and size groups, as we found no evidence for earlier parturition of larger or older female Pacific ocean perch. This finding contrasts with the work of Nichol and Pikitch (1994) and Bobko and Berkeley (2004) showing earlier parturition in larger darkblotched rockfish and older black rockfish, respectively. Similarly, our findings differ from the observations of Eldridge et al. (1991) that older yellowtail rockfish reproduced earlier in the season than younger fish and larger yellowtail rockfish reproduce earlier than smaller fish (Love et al. 1990). The smaller oocyte diameters we observed for the smallest mature Pacific ocean perch could be interpreted as evidence that ovaries of larger fish develop earlier each season, but may not be associated with differences in timing of fertilization or parturition. Differences in oocyte size have been reported previously for sub-stocks of Pacific ocean perch, but have not been linked to fish size or differences in the final size of eggs at fertilization (Leaman 1988). Our data show that the smaller oocytes were evident only in the smallest mature fish, and did not show a general

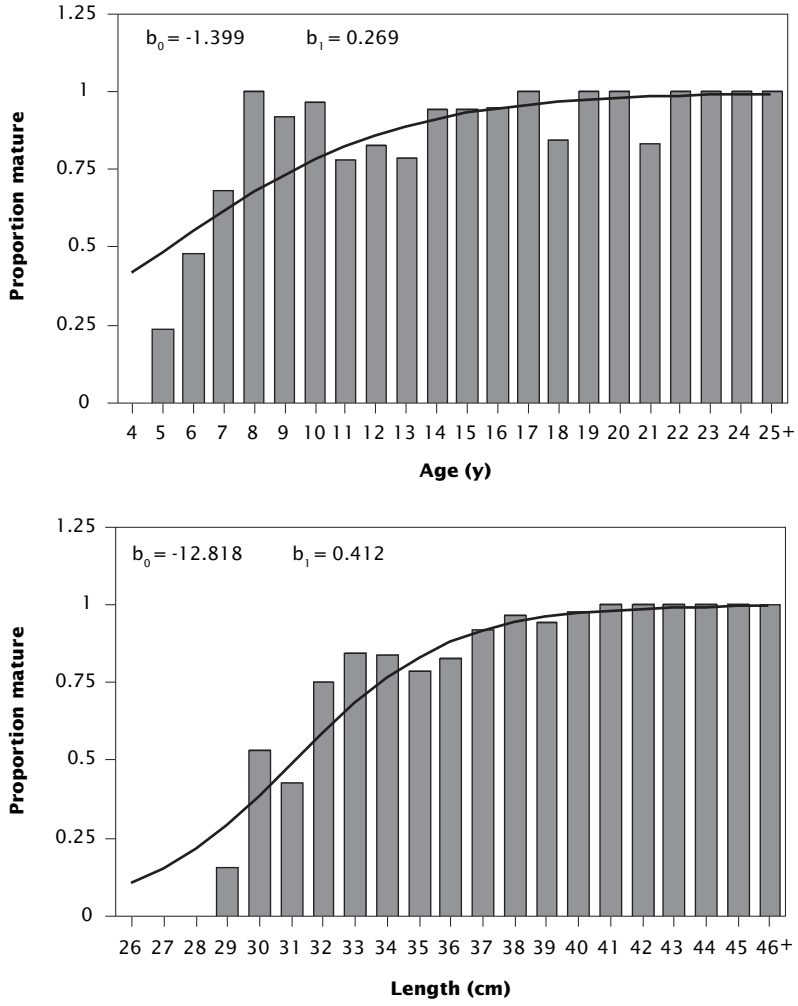


Figure 6. Proportion of mature Pacific ocean perch, by age (years) and length (cm), with fitted logistic curves.

trend towards size- or age-modulated differences in timing of ovarian development. It's possible that young Pacific ocean perch that fail to meet some energetic threshold needed to successfully develop larvae show abortive maturation via mass atresia, while in the other rockfish stocks studied, these same "energetically challenged" young fish show delayed ovarian development or parturition.

The length at 50% maturity estimated in this study fits in reasonably well with other studies showing larger L_{50} to the north and smaller L_{50} to the south. Wyllie Echeverria (1987) estimated L_{50} for female Pacific ocean perch in California waters at 26 cm, while Barss (1989) estimated L_{50} at 34 cm for Oregon waters. Both of these studies suffered from modest sample sizes and few immature fish. More comprehensive studies conducted off Washington and Britsh Columbia estimated L_{50} for female fish at 33-39 cm (Leaman 1988) and 35-38 cm (Gunderson 1977). Our estimate of an A_{50} of six years for female Pacific ocean perch off Oregon is harder to place in context due to limitations of earlier studies. Barss's (1989) study of fish off Oregon did not collect age data. Wyllie Echeverria (1987) estimated an A_{50} for Pacific ocean perch off California of 7 years while Gunderson's (1977) data suggests an A_{50} of about 11 years for fish off Washington and British Columbia, both using the "surface reading" technique for determining ages. Leaman (1988) reported an A_{50} of 7-10 y for Pacific ocean perch off British Columbia, using the "break and burn" technique to determine ages. Our estimate of six years is considerably younger than the A_{50} reported for more northern stocks, as would be expected. For example, Lunsford (1999) examined length and age at maturity for Pacific ocean perch in the eastern Gulf of Alaska and estimated L_{50} and A_{50} at 35.9 cm and 10.6 years, respectively. However, our estimate is also younger than the A_{50} reported for California and a full two years younger than the estimate of eight years used in the most recent assessment for U.S west coast Pacific ocean perch (Hamel et al. 2003). This difference is difficult to explain, however most prior studies of Pacific ocean perch maturity have utilized surface ages rather than the more reliable "break and burn" method for generating ages (Chilton and Beamish 1982) and have also often relied on visual staging of ovaries from fish collected in summer months, when visual maturity staging is unreliable (Wallace and Selman 1981).

For female Pacific ocean perch sampled during the active reproductive season, simple visual assessment of maturity performed nearly as well as histological methods in determining functional maturity (Table 3). Moreover, histology did not provide reliable determinations of maturity status outside this relatively narrow sampling window of December to March. The importance of sampling this species during the active reproductive season has been highlighted by most previous studies (Gunderson 1977, Leaman 1988). For rockfish species with less synchronous spawning, histology may prove more useful in determining female maturity status, by providing an accurate assessment of reproductive development at the cellular level, and reducing the number of fish in any given sample that must be classified as "uncertain maturity." Histology has proved useful in determining maturity status for petrale sole (*Eopsetta jordani*), a species which can be difficult to sample without bias during the active spawning period due to aggregation

of mature individuals (Hannah et al. 2002). In our study, histological examination of ovaries also provided insight into reproductive success in individual fish, showing that some post-adolescent, but still relatively young animals were not successfully developing eggs. Although visual assessment of these fish accurately identified them as immature, incorrect classification was a possibility, because, based on their large size, they could have been interpreted as mature fish that were simply late in developing. Histological examination clearly showed mass atresia and indicated some of these younger fish were not likely to develop eggs successfully within that spawning season.

The evidence presented here for abortive maturation of some younger female Pacific ocean perch is not explainable based on a brief adolescent phase. Prior studies investigating the adolescent or "maturing" stage in rockfish have concluded that adolescence is likely a brief transition period, probably lasting only a year for an individual fish, and spanning just a few ages at a population level (Leaman 1988, Nichol and Pikitch 1994). A comparison of the percentage of females in this "maturing" stage by age in the months December to March, with similar data on darkblotched rockfish from Nichol and Pikitch (1994), shows a similar steep decline in prevalence with age, supporting the argument that the rate at which young females become mature is relatively rapid (Fig. 5). In a species with highly synchronous development, this decline is an indicator of fish passing out of adolescence, because during the months just prior to parturition, few, if any mature fish would be found with stage 2 (maturing) ovaries, even though all mature fish pass through stage 2 briefly during egg development. Our data show an additional feature though, the presence of a long tail on the right side of the distribution (Fig. 5), caused by some older but still relatively young Pacific ocean perch (visually classified as stage 2) that began reproductive development but then resorbed the developing oocytes for unknown reasons. The interannual variation in the percentage of female Pacific ocean perch showing abortive maturation, along with the age-related decline in prevalance, suggest that female reproductive success may vary in relation to the ocean environment for this species. Studies of the seasonal cycles of fat reserves in other rockfish species have shown that female reserves are depleted during vitellogenesis and gestation (Guillemot et al. 1985, MacFarlane et al. 1993). For some rockfish species, larger fish have been shown to possess disproportionately higher fat reserves than smaller fish and a relationship with age has been hypothesized (Larson 1991). Reduced levels of fat reserves have been shown to influence female reproductive output in other fish species, such as winter flounder, but via the mechanism of reduced fecundity rather than mass follicular atresia (Tyler and Dunn 1976). Environmentally driven variation in the successful development of larvae in rockfish has been suggested (Larson 1991, Wyllie Echeverria 1987), however the minimal

available data argue for either delayed egg development or reduced gonad volume during poor years (Lenarz and Wyllie Echeverria, 1986). The long-term histological studies of ovarian development needed to evaluate the prevalence and causes of interannual variation in reproductive success in *Sebastes* have not been conducted. Most histological studies of maturity in rockfish have been short-term in nature and have focused mostly on the seasonal cycle in ovarian development and estimation of age and length at maturity (Bowers 1992, Nichol and Pikitch 1994).

The problem of properly classifying the maturity status of female Pacific ocean perch showing abortive maturation is more than just a question of how maturity is defined. If "mature" females are defined as those which have completed the short adolescent transition, then Pacific ocean perch showing abortive maturation could simply be considered mature, even though they might occasionally fail to produce a successful brood. In this study, such an approach would have generated data that provided a much better fit to the logistic curve. However, to make an accurate distinction between adolescent and post-adolescent females requires an understanding of the duration of adolescence, perhaps based on data similar to that shown in Fig. 5. If a rapid, size- or age-related decline in the percentage of ovaries in the "maturing" stage (e.g., age 4-8 Pacific ocean perch in Fig. 5) could be interpreted as defining adolescence, then larger or older females could be categorically classified as "mature." Whether such an approach would be appropriate, would depend on how the data were to be used. For comparing age and length at maturity between populations, more consistent results might be obtained if older fish with abortive maturation were considered mature. For purposes of stock assessment though, we recommend that fish with abortive maturation be considered "functionally immature". Further, if abortive maturation results in asymmetry in age and length at maturity data, use of the logistic curve, or other inherently symmetric asymptotic functions (see Quinn and Deriso 1999 or Schnute and Richards 1990) to describe maturity is not recommended. Simple "spline" fits to proportion mature by age or length may be the best way to represent these asymmetric data.

The data from this study are difficult to interpret at a population level because of historical evidence for spatial heterogeneity in life history traits of Pacific ocean perch. Although abortive maturation has been noted previously in Pacific ocean perch off Canada by Leaman (1988), it was at a lower level of incidence and found in only one of five sub-populations studied. Leaman's (1988) study also found spatial heterogeneity in rates of atresia, oocyte size, date of parturition, age composition and growth rate. None of the Pacific ocean perch maturity studies to date have incorporated extensive sampling across years to determine if the observed heterogeneity is related to persistent dif-

ferences between sub-populations or local variation in environmental conditions that also vary interannually. If longer term studies show that abortive maturation is common in younger female Pacific ocean perch in some years, this would provide support for the idea that maintaining an older average age structure in some rockfish species may bolster stock resilience and help prevent overfishing. It would also suggest that higher reproductive output in older rockfish may derive from various underlying mechanisms, including higher larval quality, differences in fecundity and also different probabilities of successfully developing eggs in a given year.

Acknowledgments

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Rockfish Trophic Relationships in Prince William Sound, Alaska, Based on Natural Abundance of Stable Isotopes

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Abstract

About two dozen rockfish species coexist within Prince William Sound (PWS). According to ecological theory these species should reduce competition by minimizing diet overlap. This was verified by using ecological metrics based on the natural abundance of carbon and nitrogen stable isotopes. Carbon source dependency was based on a regional carbon isotope gradient whereas trophic level was based on trophic enrichment of ^{15}N. There was a gradient in carbon source dependency among rockfish slope, pelagic, and demersal eco-groups. Pelagic rockfishes had the greatest dependency on Gulf of Alaska (GOA) derived carbon. Within demersal rockfishes, copper rockfish were most dependent on PWS derived carbon. Rockfishes did not respond to a strong pulse in GOA subsidies, like forage groups, confirming that their stable isotope composition reflected relatively longer time-integration. Yelloweye and quillback rockfish shifted concordantly in carbon source dependency but separated in terms of relative trophic level. Relative trophic level (TL), based on the nitrogen isotope value of a herbivorous copepod for reference TL = 2.0, ranged from 3.2 (juveniles) to 5.1 (shortspine thornyhead). Another slope species, the shortraker rockfish, had the second highest TL = 4.9. Dark rockfish was the lowest adult TL = 3.6. Alternative nonlethal sampling for isotope values using blood is possible given normalization of the data for lipid isotope effects.

Introduction

In the northeast Pacific Ocean, the scorpaenid fishes of the genera *Sebastes* and *Sebastolobus*, commonly called rockfishes, comprise more

Table 1. Twenty-five rockfishes found in PWS from the literature and this study.

Species	Common name	Meyer 1992	Rosenthal 1980	This study
Sebastes melaonostomus	Blackgill rockfish			×
Sebastes melanops	Black rockfish	×	×	×
Sebastes paucispinis	Bocaccio	×		
Sebastes auriculatus	Brown rockfish	×	×	
Sebastes pinniger	Canary rockfish	×		
Sebastes nebulosus	China rockfish	×	×	×
Sebastes caurinus	Copper rockfish	×	×	×
Sebastes ciliatus	Dark rockfish[a]	×	×	×
Sebastes elongatus	Greenstripe rockfish			×
Sebastes variegatus	Harlequin rockfish	×		
Sebastes alutus	Pacific ocean perch	×		
Sebastes emphaeus	Puget Sound rockfish		×	
Sebastes maliger	Quillback rockfish	×	×	×
Sebastes babcocki	Redbanded rockfish			×
Sebastes proriger	Redstripe rockfish	×		×
Sebastes helvomaculatus	Rosethorn rockfish	×		
Sebastes aleutianus	Rougheye rockfish	×		×
Sebastes zacentrus	Sharpchin rockfish	×		
Sebastes borealis	Shortraker rockfish	×		×
Sebastes brevispinis	Silvergray rockfish	×	×	×
Sebastes diploproa	Splitnose rockfish	×		
Sebastes nigrocinctus	Tiger rockfish	×	×	×
Sebastes ruberrimus	Yelloweye rockfish	×	×	×
Sebastes flavidus	Yellowtail rockfish	×	×	×
Sebastolobus alascanus	Shortspine thornyhead		×	×

[a]For nomenclature see Orr and Blackburn 2004.

than 60 species. Twenty-five of these species have been found in Prince William Sound (PWS), Alaska, a subarctic marine ecosystem of about 100 by 100 km (Table 1). Because much of PWS is north of 60ºN, this is the northern limit for some rockfish species, while others are also found in the higher latitude portions of the Bering Sea. PWS has depths to about 800 m thus providing a good range of depths accommodating the varying depth range preferences among the many rockfish species (Love et al. 2002).

Ecological theory, which suggests rockfish species coexisting within PWS reduce would compete by minimizing diet overlap, was tested

for adults of twelve rockfish (*Sebastes* and *Sebastolobus*) species and juvenile *Sebastes* using stable isotope analysis (SIA) as a metric of diet overlap (Welch and Parsons 1993, Murie 1995).

Application of SIA methods was enhanced by an existing isotopic context of potential prey sampled at the same time as most of the rockfishes (Fig. 1). A regional stable carbon isotope gradient can be used to differentiate the relative dependency of autochthonous production sources (from PWS) versus allochthonous sources assumed to be from the Gulf of Alaska (GOA; Kline 1999). Trophic level (TL) can be estimated based on nitrogen stable isotope values assuming a consistent nitrogen isotope trophic enrichment (Kline and Pauly 1998; Kline 2001, 2002; Wada et al. 1991).

The mean $\delta^{13}C'$ value (see Materials and methods for definition) of whole individual *Neocalanus* copepods analyzed from GOA was –22.7 (SD = 2.6, SE <0.1, N = 1,590) during 1995-2004; whereas that from PWS was –19.8 (SD = 2.0, SE <0.1, N = 758) (Kline 1999, 2001, 2002, and unpubl. data for post-1996). Carbon $\delta^{13}C'$ values less than about –20.5 were hypothesized to reflect allochthonous carbon with respect to PWS, reflecting GOA production sources. In contrast, the $\delta^{15}N$ gradient is much weaker (Kline 1999). The decadal mean $\delta^{15}N$ for PWS was 8.9 (SD = 1.9, SE <0.1, N = 752); whereas GOA was 7.3 (SD = 2.5, SE <0.1, N = 1,588). Because of the gradient, though small, when a $\delta^{15}N$ value of 8.4 is used as the reference for calculating TL, the uncertainty is about 0.3 TL (Kline 2001). Nevertheless, there was good agreement between TL based on $\delta^{15}N$ and TL based on predictions made by the Ecopath model (Kline and Pauly 1998). Furthermore, TL of juvenile herring, which is possibly the most important forage fish in PWS, based on $\delta^{15}N$ was consistent, about 3.2 ± <0.2 over a four-year period (Fig. 1).

A goal of this study was to determine whether PWS rockfishes partition food resources in terms of carbon source and relative trophic level with respect to species as well as the three depth range eco-groups: demersal (shelf species associated with substrates), pelagic (shelf species associated with the upper water column), and slope (deep-dwelling species, generally found deeper than 200 m). Accordingly, synoptic mean $\delta^{13}C'_{TL}$ and mean $\delta^{15}N$ values of eco-groups or species should differ.

Rockfishes are long-lived with relatively slow growth. The stable isotope values of adults were thus expected to reflect or integrate longer time spans than fishes with short life spans (cf. the 2 to 6 years of Pacific salmon species). Accordingly, their isotope values were not expected to vary much over times of less than ~1 year (Hesslein et al. 1993). For example, the large shifts in $\delta^{13}C'$ value were not expected, in response to a hypothesized pulse of GOA carbon during late 1995 (Kline 1999) observed in several taxa of fast-growing, lower trophic level organisms (Fig. 1).

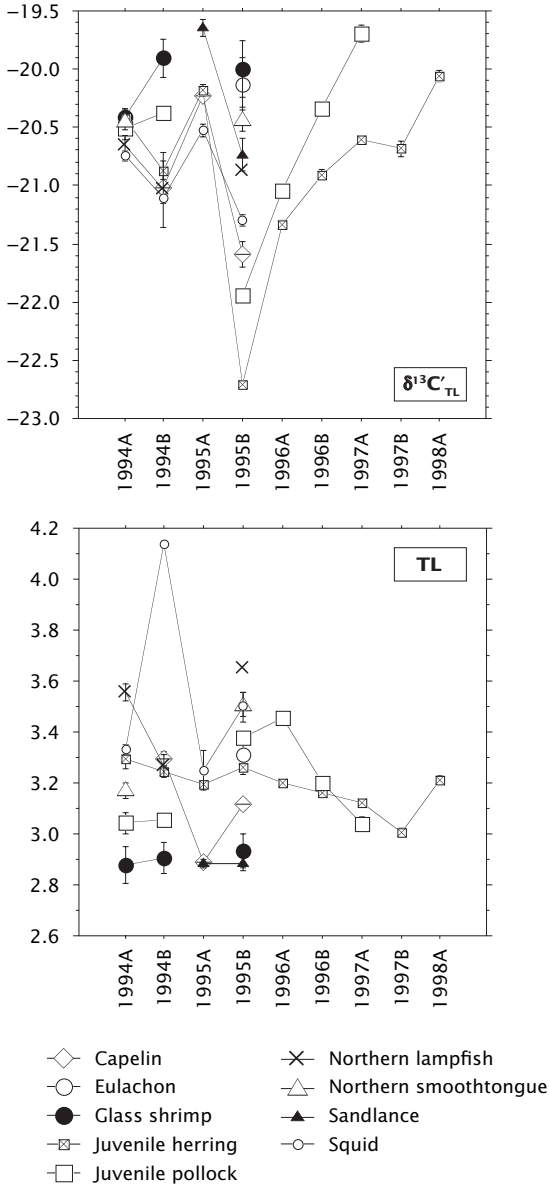


Figure 1. Trophic level and lipid normalized stable carbon isotope values ($\delta^{13}C'_{TL}$, upper panel) and nitrogen stable isotope value–based trophic levels (TL, lower panel) of forage taxa sample in PWS, 1994-1998. See text for explanation of how years were split. Error bars indicate standard error.

Rockfishes prefer rocky, high relief habitats. Western Prince William Sound (W-PWS) is characterized by deep fjords with depths reaching 800 m within 2 km of shore. Depths are <300 m in eastern Prince William Sound (E-PWS), the portion of PWS east of the tanker lanes exclusive of the area near (<30 km) this boundary. Nevertheless, there are locations with rocky habitats in E-PWS with populations of shallow-dwelling rockfish species. A secondary objective was to ascertain if carbon or TL differed qualitatively across PWS.

A long-term goal is to recover tagged rockfishes and resample over time for SIA to detect ecosystem shifts. A nonlethal sample would thus be required. The potential for this was tested by tagging and recovering rockfishes and by comparing SIA of blood with SIA of muscle tissue. Muscle is typically sampled in most SIA studies after killing the organism being sampled.

Materials and methods

Rockfishes and potential prey taxa were sampled incidentally during the Sound Ecosystem Assessment (SEA) project that focused on pink salmon, Pacific herring, and walleye pollock during 1994-1999 (Cooney et al. 2001). Samples were obtained on SEA cruises by seines, trawls, gillnets, and hook and line. Additional rockfish samples from the PWS longline fishery were obtained from Cordova fish processors during SEA. Samples for blood were collected by hook and line or by hand-nets during scuba diving as part of the Oil Spill Recovery Institute Sentinel project in 1999. Rockfish samples were organized according to the following three depth-based ecological categories: demersal, pelagic, and slope favored by each species based on their distribution in Alaska (Kramer and O'Connell 1995; Table 3). Rockfishes newly recruited from the plankton have a different appearance from adults and were simply classified as juveniles for the purposes of this study.

Rockfish samples were opportunistic and thus not systematic in terms of sampling date or location. Samples came from a range of sites in PWS, which were divided into E-PWS and W-PWS. Data were temporally aggregated to match that of forage data described below.

Approximately 1 g of anterior epaxial muscle tissue was collected from each adult rockfish (except for a single ~20 cm long copper rockfish sampled only for blood), frozen, freeze-dried, then ground to a fine powder. Juvenile rockfish and forage taxa were treated similarly except that the entire organism was ground due to their size (length ≤15 cm). Blood samples taken of fishes collected during July 1999 via caudal vein puncture using non-heparin 3.0 ml syringes were centrifuged, then plasma and cell fractions were frozen and later freeze-dried and agitated to a fine power with a dental amalgamator. Blood and muscle samples were obtained from eight rockfishes (seven dark rockfish and

Table 2. Sample sizes and sample timing of forage taxa used for Fig. 1.

Forage taxa			Sample periods									δ^{15}N		TL	
Common name	Scientific name	N	1994A	1994B	1995A	1995B	1996A	1996B	1997A	1997B	1998A	Mean	SE	Mean	SE
Capelin	*Mallotus villosus*	103		11	28	64						12.0	0.07	3.1	0.02
Eulachon	*Thaleichthys pacificus*	18				18						12.9	0.26	3.3	0.08
Glass shrimp	*Pasiphaea pacifica*	65	38	11		16						11.4	0.16	2.9	0.05
Juvenile Pacific herring	*Clupea pallasii*	1,839	69	86	129	250	717	172	288	59	69	12.5	0.01	3.2	<0.01
Juvenile walleye pollock	*Theragra chalcogramma*	596	121	45		175	80	92	83			12.6	0.04	3.2	0.01
Northern lampfish	*Stenobrachius leucopsarus*	10	7	2		1						13.5	0.16	3.5	0.05
Northern smoothtongue	*Leuroglossus schmidti*	39	15			24						13.1	0.14	3.4	0.04
Pacific sand lance	*Ammodytes hexapterus*	52			25	27						13.1	0.14	2.9	0.02
Squid	*Berryteuthis magister*	124	81	1	22	20						13.0	0.08	3.4	0.02

Mean δ^{15}N and calculated TL with standard errors confirm forage taxa have TL ~3. Higher TL values likely reflect consuming zooplankton with δ^{15}N values higher than *Neocalanus* such as euphausiids and amphipods (Kline 1999, 2001).

one black rockfish) and from three salmon sampled at the same time, two coho salmon (*Oncorhynchus kisutch*) and one chinook salmon (*O. tshawytscha*). One 20 cm long copper rockfish was sampled for blood (1.5 ml) and released live following overnight recovery.

Powdered samples were shipped to the University of Alaska Fairbanks Stable Isotope Facility (SIF) where duplicate subsamples of ~0.4 mg were weighed to the nearest 1 µg and loaded into combustion boats for mass spectrometric analysis. A mass spectrometric analysis (using either a Europa 20/20 or a Finnegan Delta Plus unit; both equipped with continuous flow sample preparation units) generated the following data: $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios expressed in standard delta units, $\delta^{13}C$ and $\delta^{15}N$, respectively, and %C and %N. The delta notation used to express stable isotope ratios is reported as the per mil (‰) deviation relative to an international standard, air for nitrogen, and Vienna Peedee belemnite (VPDB) for carbon. The conventional delta notation used to express stable isotope ratios relative to international standards is defined by the following expression:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1{,}000‰ \qquad (1)$$

where $R = {}^{15}N/{}^{14}N$ or $^{13}C/^{12}C$. By definition, the isotope standards have delta values of zero, i.e., $\delta^{15}N = 0$ for atmospheric N_2. Mass spectrometric analysis quality assurance protocols consisted of running laboratory standards before and after groups of five "unknowns" and duplicate analyses of each sample. Samples were run again when duplicate analyses differed by more than 0.6 ‰.

Normalization for lipid (DeNiro and Epstein 1977) and trophic level effects of $\delta^{13}C$ values of fish makes it possible to assess carbon source (Kline 1997, 1999). The method of McConnaughey and McRoy (1979) was used to calculate lipid-normalized $^{13}C/^{12}C$ while the method of Kline (1997, 1999) was used to normalize for trophic level. Details of these protocols are described in Kline (1997, 1999) and Kline et al. (1998). In general, normalization reduces sources of ^{13}C variability, enabling comparisons among fishes without the confounding effects of trophic level and lipid content. The expressions $\delta^{13}C$, $\delta^{13}C'$, $\delta^{13}C_{TL}$, or $\delta^{13}C'_{TL}$ are used to denote $^{13}C/^{12}C$ abundance in relation to the international standard, normalized for lipid content, normalized for trophic level, and normalized for lipid content and trophic level, respectively. Whereas $\delta^{13}C'$, $\delta^{13}C_{TL}$, and $\delta^{13}C'_{TL}$ is used in accordance to a particular data analysis context, "^{13}C" is used to reflect generic $^{13}C/^{12}C$ isotopic trends irrespective of normalization. Cross-taxon comparisons of carbon isotope values were made using $\delta^{13}C'_{TL}$.

$^{15}N/^{14}N$-based trophic levels in the northern GOA are accurate to within ±0.3 trophic levels (TL; Kline 2001). Trophic level was determined

by comparing $\delta^{15}N$ values to a reference value (Cabana and Rasmussen 1994.). The $\delta^{15}N$ of higher trophic levels were calculated by adding the trophic enrichment factor, 3.4 (Minagawa and Wada 1984; Kline 2001, 2002), to the reference value. Using a single herbivore species as the reference eliminated the compositional (taxonomic and ecologic) variability, and therefore TL uncertainty associated with particulate organic material or bulk zooplankton often used as a TL reference proxy (Kline 1999). The herbivorous copepod *Neocalanus cristatus*, in diapause, was chosen as the reference herbivore (TL = 2.0) based on observations that their carbon isotope values corresponded with those of PWS fishes (Kline and Pauly 1998; Kline 1999, 2001, 2002).

The following formula was used to calculate trophic level:

$$TL_i = \left(\delta^{15}N_i - \delta^{15}N_H / 3.4\right) + 2 \qquad (2)$$

where TL_i is the trophic level of organism i, $\delta^{15}N_i$ is the mean $\delta^{15}N$ value of organism i, and $\delta^{15}N_H$ is the mean reference herbivore $\delta^{15}N$ value.

The Statview (version 5.0.1; SAS Institute, Inc.) computer program was used for data analyses and to generate all figures. Standard errors were used to qualitatively assess differences among mean values.

The forage taxa data (Table 2) have been previously published (Kline 1997, 1999, 2001, 2002), but in different formats. The relatively narrow standard errors of $\delta^{15}N$ data and therefore TL (Table 2) provided additional baseline references to that of *Neocalanus*. Because the intention here is to qualitatively assess the effect of the GOA carbon pulse inferred to have taken place in late 1995 (Kline 1999), data from each year were divided into two parts: A for data collected through August, and B for data collected after August. Data for rockfishes were treated similarly to show temporal trends.

Results and discussion

The $\delta^{13}C'_{TL}$ values of demersal rockfishes either at the species level (Fig. 2) or collectively as a group (Fig. 3) were generally higher than other rockfishes. This is consistent with their consuming more PWS carbon relative to other rockfishes that had more negative values, which suggested a dependency, in part, on GOA carbon. Juvenile $\delta^{13}C'_{TL}$ values approximated those of demersal rockfishes. The $\delta^{13}C'_{TL}$ values of slope species were the same or more negative than demersals but not as negative as pelagics, suggesting a lower dependence on GOA carbon than pelagics but a greater dependence on GOA carbon compared to demersals (Fig. 3). There were slight differences in $\delta^{13}C'_{TL}$ values among the demersals for which there were relatively good sample sizes (copper, quillback, and yelloweye) with copper rockfish having the least negative values (Fig. 4). The $\delta^{13}C'_{TL}$ values of yelloweye and quillback rockfishes shifted concordantly with slight species differences that may reflect

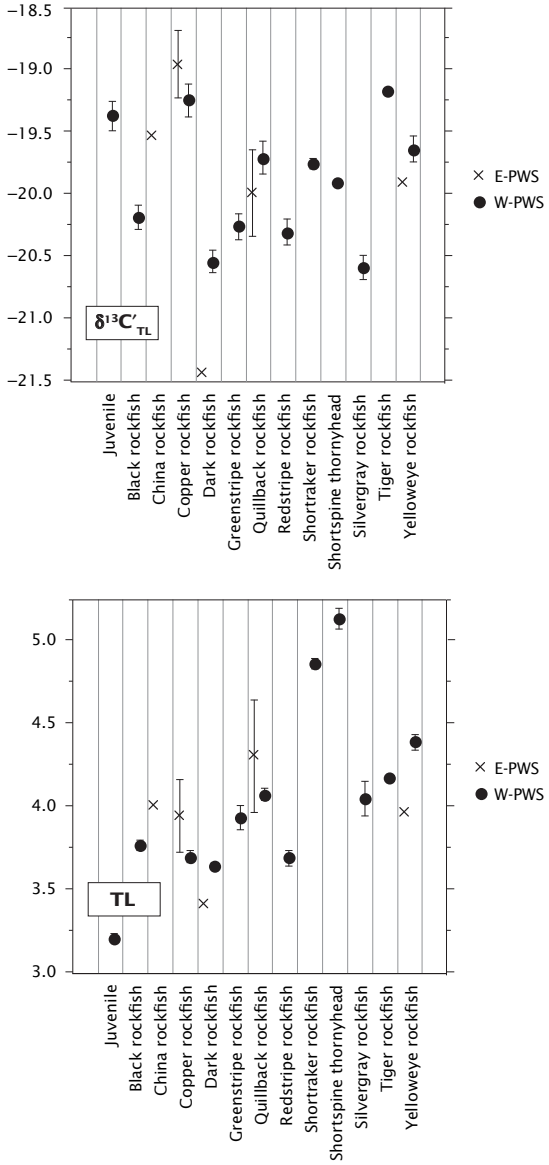


Figure 2. Trophic level and lipid normalized stable carbon isotope values ($\delta^{13}C'_{TL}$, upper panel) and nitrogen stable isotope value–based trophic levels (TL, lower panel) of PWS rockfishes by species by eastern and western PWS. Error bars indicate standard error.

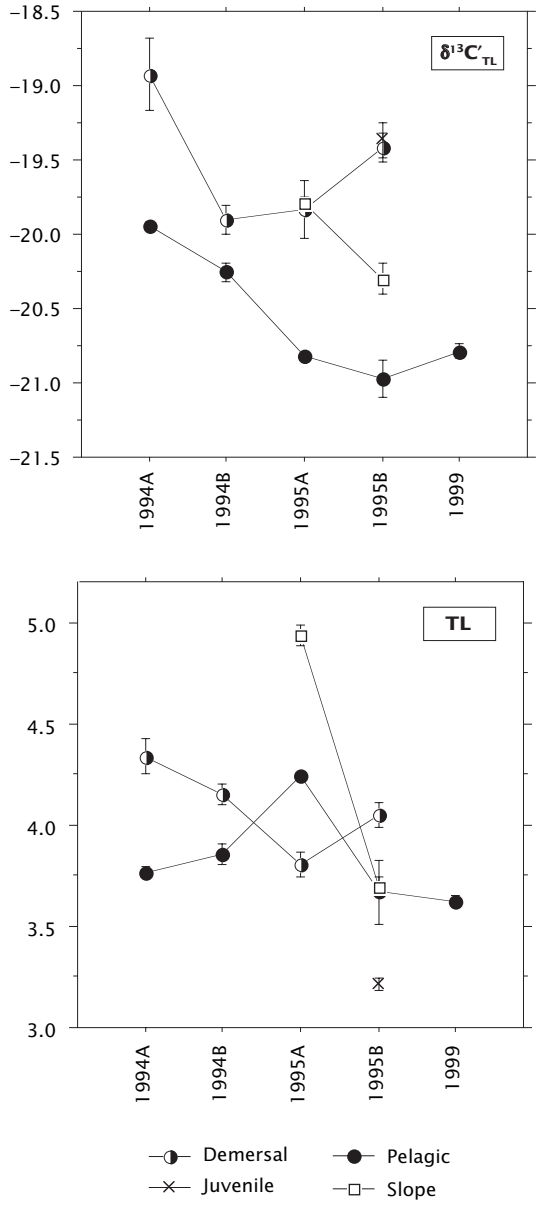


Figure 3. Trophic level and lipid normalized stable carbon isotope values ($\delta^{13}C'_{TL}$, upper panel) and nitrogen stable isotope value–based trophic levels (TL, lower panel) of PWS rockfishes by eco-group and year periods as in Fig. 1. Error bars indicate standard error.

sample size at some of the sample times (Table 3). Dark rockfish were significantly more negative than the three demersals during late 1995. In late 1995 demersal rockfishes had $\delta^{13}C'_{TL}$ values falling within the range of values observed the previous 1.5 years, unlike forage taxa that had shifted systematically. The temporal variation of ~2‰ observed in the three demersal rockfish species shown in Fig. 4 was similar to the range observed collectively for demersals and may reflect variation among individuals due to opportunistic feeding. For example, there was a 1 to 2‰ range among potential forage taxa at any one time (Fig. 1). Cross-PWS $\delta^{13}C'_{TL}$ differences within species (Fig. 2) were small, suggesting no apparent strong east-west gradient in effect of GOA carbon subsidies in rockfishes. Species $\delta^{13}C'_{TL}$ differences were greater than these geographic differences (Fig. 2). Overall, pelagic rockfishes had lower $\delta^{13}C'_{TL}$ values collectively and by species, confirming that the PWS pelagic system depends in part on GOA subsidies (Kline 1999). GOA subsidies are hypothesized to vary over long time spans according inter-decadal variations in oceanic zooplankton populations (Kline 1999). Accordingly, rockfish $\delta^{13}C'_{TL}$ values are expected to shift over inter-decadal spans while having less short-term variation. Measurable rockfish response to such ecosystem variation may thus have less intrinsic "noise" (response to short-term pulses) compared to lower trophic levels and thus be good sentinel species.

Whereas there were no group-specific $\delta^{15}N$, and thus TL, trends among the three groups, there were very large differences among species (Figs. 2 and 4). Rockfishes occupy TL from slightly greater than TL = 3 or primary carnivore, to about TL = 5 or tertiary carnivore. However, most species were within 0.5 TL of TL = 4 or secondary carnivore. Comparing the same three species, with good sample sizes as above, suggests an apparent TL difference spanning almost 1 TL (Fig. 4). Shortspine thornyhead and shortraker rockfish with TL ~5 are suggested to be among the highest trophic level organisms observed thus far in PWS based on $\delta^{15}N$ value (Kline unpubl.). The high TL cannot be explained directly by stomach data (Table 3). However, these are some of the largest rockfishes found in PWS and consequently may be able to prey upon carnivores of TL ~4.

Whereas quillback and yelloweye rockfish concordantly shifted their carbon source, differences in TL suggest that their food chains were of different length and thus they did not compete directly, supporting the concept of separate niches. Copper rockfish TL was lower than either and $\delta^{13}C'_{TL}$ was higher when observed at the same time. Dark rockfish TL may be more similar to that of copper rockfish but $\delta^{13}C'_{TL}$ was lowest among the four species shown in Fig 4. Thus isotopes of C and N when used together provide two dimensions of ecological niche conferring ecological separation among these congeners. Food chain length of a given species appears to be more conservative than carbon source (Fig.

Table 3. Sample sizes and sample timing of rockfish samples by eco-group.

Common name		Sample periods									Locations		Pelagic diet		Demersal diet	
		May-94	Jul-94	Sep-94	Mar-95	May-95	Jun-95	Oct-95	Nov-95	Aug-99	Western PWS	Eastern PWS	Fishes	Invert.	Fishes	Invert.
Eco-group	N	1994A		1994B		1995A		1995B		1999						
Juvenile	12							12			3			*		*
Demersal																
China rockfish	1							1				1			*	*
Copper rockfish	32						9	10	13		4	4			*	*
Greenstripe rockfish	4			4							1		*	*	*	*
Quillback rockfish	36	5		8	5			7	11		4	1			*	*
Tiger rockfish	1								1		1				*	*
Yelloweye rockfish	23		4	7	1			9	2		6	1	*		*	*
Slope																
Redstripe rockfish	11							11			1		*	*	*	*
Shortraker rockfish	3					3					1		*	*		
Shortspine thornyhead	1					1					1				*	*
All slope rockfishes																
Pelagic																
Black rockfish	7	3		3						1	3		*	*		*
Dark rockfish	19		7					3	1	8	3	1				*
Silvergray rockfish	9			6	1			1	1		4					

Number of sampling sites in E-PWS and W-PWS for each species is given. Literature food habit taken from Love et al. (2002) summarized in terms of presence (*) or absence (no symbol) of fish or invertebrate diet and whether prey is demersal or pelagic. Both pelagic and demersal fish indicated in cases when diet was described simply as fish.

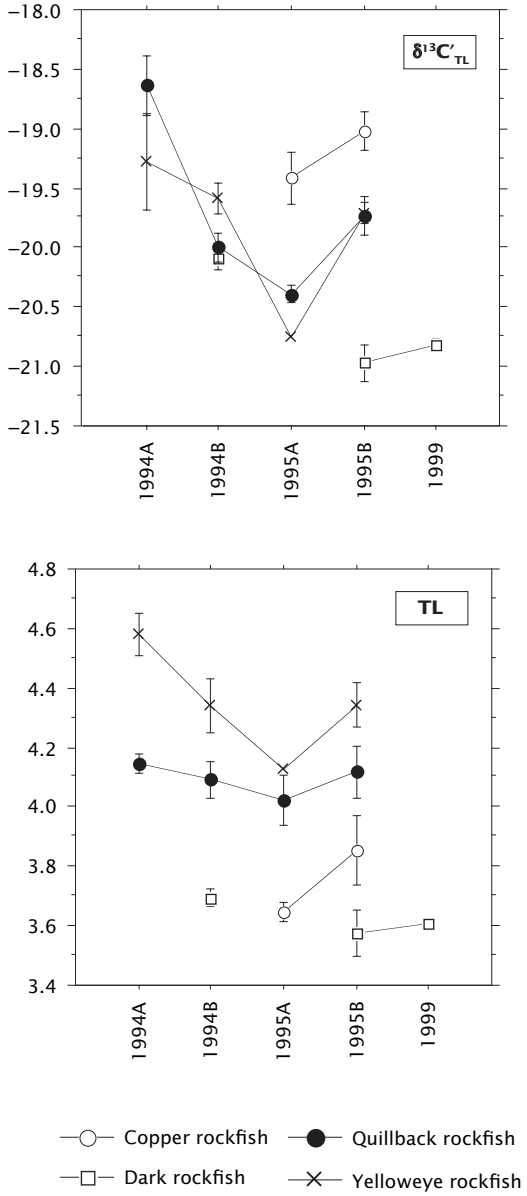


Figure 4. Trophic level and lipid normalized stable carbon isotope values ($\delta^{13}C'_{TL}$, upper panel) and nitrogen stable isotope value–based trophic levels (TL, lower panel) of four PWS rockfishes by year periods as in Fig. 1. Error bars indicate standard error.

Table 4. Blood isotope data from 1999 samples with statistics. See text.

Tissue	C/N atoms		%N	%C	$\delta^{15}N$	$\delta^{13}C$	$\delta^{13}C'$	$\delta^{13}C'_{TL}$	TL
Rockfish (N = 8)									
Muscle	Mean	3.8	14.9	48.3	13.9	–18.9	–19.2	–20.8	3.6
	SD	0.1	0.3	1.3	0.3	0.2	0.2	0.2	0.1
Blood plasma	Mean	6.1	8.9	46.1	13.3	–21.2	–19.7	–21.1	3.5
	SD	0.7	1.2	5.9	0.5	0.3	0.1	0.1	0.1
Blood cells	Mean	4.2	13.7	49.1	13.1	–19.5	–19.3	–20.7	3.4
	SD	0.3	0.7	1.2	0.5	0.3	0.2	0.2	0.1
Copper rockfish (N = 1)									
Blood plasma		4.7	10.3	41.6	14.6	–17.4	–16.7	–18.8	3.8
Blood cells		4.0	13.7	47.5	14.6	–17.0	–16.9	–18.5	3.8
Salmon (N = 3)									
Muscle	Mean	4.0	14.1	47.8	13.2	–19.4	–19.4	–20.8	3.4
	SD	0.2	0.3	2.2	0.6	1.4	1.2	1.1	0.2
Blood plasma	Mean	6.5	9.2	51.7	13.4	–22.1	–20.3	–21.8	3.5
	SD	0.4	0.3	1.7	0.4	0.3	0.1	<0.1	0.1
Blood cells	Mean	4.0	14.7	50.8	12.4	–20.0	–19.9	–21.1	3.2
	SD	0.1	0.1	0.9	0.2	0.1	0.2	0.1	0.1

4). However when aggregated by eco-group, carbon source appears to be more conservative than TL (Fig. 3). TL is thus a property of species whereas carbon source is more of an eco-group property.

Blood isotope data were qualitatively similar to muscle tissue (Table 4). The higher C/N ratio of plasma was indicative of relatively high lipid content and when used to correct for lipid effects resulted in $\delta^{13}C'_{TL}$ values much closer to those of other tissues. Differences among tissue type may reflect differences in turnover time. Each type thus reflects more or less recent versus past feeding (Hobson and Clark 1993). Blood plasma should reflect the most recent feeding. The greatest disparity between blood plasma and muscle $\delta^{13}C'_{TL}$ of ~1‰, for salmon, may have reflected that much of the muscle tissue was attained while feeding in the GOA prior to entering PWS. Salmon and pelagic rockfish plasma $\delta^{13}C'_{TL}$ were similar whereas that of the copper rockfish was enriched. Copper rockfish blood in terms of TL and $\delta^{13}C'_{TL}$was similar to copper rockfish sampled four to five years earlier. Dusky rockfish muscle values from 1999 were also comparable to those from 1995 (Fig. 4). The relatively small spatial home range of shallow demersal species such as copper and quillback rockfishes (Richards 1987) (suggested to be 10 km or less in PWS based on ultrasonic pinger data [Kline unpubl.]), their capture

ease with scuba, and their ability to be nonlethally sampled for blood, leads to their potential as sentinels for environmental change using SIA of blood. A test that could be performed over long-term (e.g., multi-decade) observations would be to ascertain if ecological niche separation in terms of isotope values was reduced or expanded, a possible result of climate-driven ecosystem shifts.

Acknowledgments

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Movement Patterns of Black Rockfish (*Sebastes melanops*) in Oregon Coastal Waters

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Abstract

We studied the movement patterns of black rockfish (*Sebastes melanops*) in Oregon coastal waters to estimate home range over daily to annual time scales, determine if females relocate during the reproductive season, and evaluate the influence of environmental variation on movement. We moored 18 acoustic receivers in a 3×5 km array south of Newport, Oregon, at depths from 9 to 40 m. We then surgically implanted 42 black rockfish (34-48 cm total length [TL]) with coded, pressure transmitters having an approximate lifespan of 6 months. Fish were tagged in August (n = 6), September (n = 13), October (n = 7), and February (n = 8 depth and 8 non-depth). Fish were temporarily absent from the monitored area for short periods (usually <7 days) indicating limited travel outside the monitored area. Seven fish left the area permanently. During one full year of monitoring, home ranges were relatively small (55±9 ha) and did not vary seasonally. Absences of females >39 cm (likely mature) from the array were longer in duration than for mature males, especially during the reproductive season (November, January, and February), but both sexes had the longest absences during April through July. These data indicate that black rockfish in open coastal waters live in a very restricted area for long periods as adults, but may relocate periodically. A small home range could make them susceptible to local depletion from targeted fishing, but also make them good candidates for protection using marine reserves.

Introduction

Understanding movement patterns and behavior is fundamental to understanding the ecology of a species. Defining an area of normal activity or home range and determining home range size stability is critical in developing strategies to manage local populations (Vincent and Sadovy 1998). In the nearshore environment along the northeast Pacific coast (<50 m depth), black rockfish (*Sebastes melanops*) are the primary target of the recreational groundfish fishery. Managers need to know the scale of daily, seasonal, and annual movements of these fish to define population boundaries and interpret catch statistics. Fisheries scientists must also know mixing rates to validate experiment assumptions (e.g., mark-recapture studies) and to understand if variable catch rates are the result of fish movement among local reefs or the result of changes in behavior. Some earlier tagging studies have been conducted using external visual tags, providing location information for only two points in time (Coombs 1979, Gowan 1983, Mathews and Barker 1983, Culver 1987). Even with a multiyear design, both location points often occur during the seasonal fishing months, providing no information on locations at other times. For example, lower catch rates for female rockfish during the reproductive season have led to speculation that they may move to deeper water to release larvae in areas favorable for larval retention (Welch 1995; Worton and Rosenkranz 2003; Farron Wallace, Washington Department of Fish and Wildlife, pers. comm.). Managers also need to understand the scale and timing of movements if they are to use closed areas or marine protected areas (MPAs) as conservation tools to limit the impact of fishing on local populations (Kramer and Chapman 1999, Parker et al. 2000).

High resolution, medium- and long-term movement studies of rockfishes in temperate environments are challenging to conduct. The experimental design needed to monitor fish locations frequently and for relatively long periods in the marine environment requires the use of remote sensing. The tool of choice is often acoustic telemetry, which is expensive and requires an intensive monitoring and data management effort (Arnold and Dewar 2001). Weather restricts access to nearshore environments along the exposed Pacific coast year-round, but especially in winter months when storms generate strong wind and wave action (>7 m). In addition to logistical challenges, most rockfish suffer barotrauma when captured due to the expansion of gas in their physoclistic swim bladder (Parker et al. 2006). This trauma makes choosing an individual likely to survive capture more risky, makes surgical tagging more difficult, and requires additional studies to conclude that the barotrauma has no significant impact on subsequent movement behavior. Few acoustic telemetry studies of rockfish exist for these reasons. These telemetry studies have typically addressed only a few of these constraints, often by facing great logistical hurdles (Matthews 1990; Pearcy 1992; Starr et

al. 2000, 2002). Our study used receiver moorings specifically designed to withstand wave and current action for long periods, yet be periodically retrievable by boat. We also removed excess swim bladder gas at the surface and used surgical implantation of transmitters.

Our objectives were to document annual, seasonal, and diel movement patterns of black rockfish, estimate home range size under different environmental conditions, and evaluate female movement during the reproductive season off the Oregon coast. Understanding black rockfish movement patterns with high resolution on both short and long time scales will provide fundamental information necessary to define local population characteristics, movement patterns and pathways, make habitat associations, and aid in the design of MPAs.

Materials and methods

Study area and acoustic array

This study was conducted in the Pacific Ocean near Newport, Oregon, at depths of 9-40 m, within an area normally fished by the recreational groundfish fishery (Fig. 1). We monitored the study site using a rectangular array of 18 VR2 69-kHz omni-directional acoustic receivers (Vemco Ltd., Nova Scotia, Canada) designed to monitor for transmitters in a 1,500 hectare area. The receivers were individually anchored on single buoy lines according to manufacturer specifications, approximately 5 m off bottom. The receivers recorded tag code, receiver number, date, time, and depth of the transmitter (for depth transmitters) at a known location. Range testing showed a normal detection range of 350-500 m radius, and receivers were spaced 700 m apart to allow tags to be detected by more than one receiver. Some receivers were moved slightly to avoid shielding by observed bathymetric features. If during the study, a receiver was lost, it was replaced as soon as possible. We also moored a tag within the array for 27 days to provide an indication of horizontal positioning accuracy and precision.

Tagging

Fish were captured by barbless hook and line fishing throughout the study area using typical recreational fishing gear periodically from August 2004 through February 2005. We attempted to catch and tag fish throughout the monitored area to minimize transmission interference from multiple tags in the same area and to gather data on fish living at different depths. Coded acoustic V-13 HP transmitters (69 kHz, pressure sensitive [0-50 m] 155 dB output, 13×42 mm) were programmed to transmit at a random period of between 30-90 seconds, giving an expected battery life of 6 months (Vemco Ltd.). Black rockfish (34-48 cm TL) were vented to release excess pressure from the expanded swim bladder using an 18 gauge hypodermic needle. No anesthesia

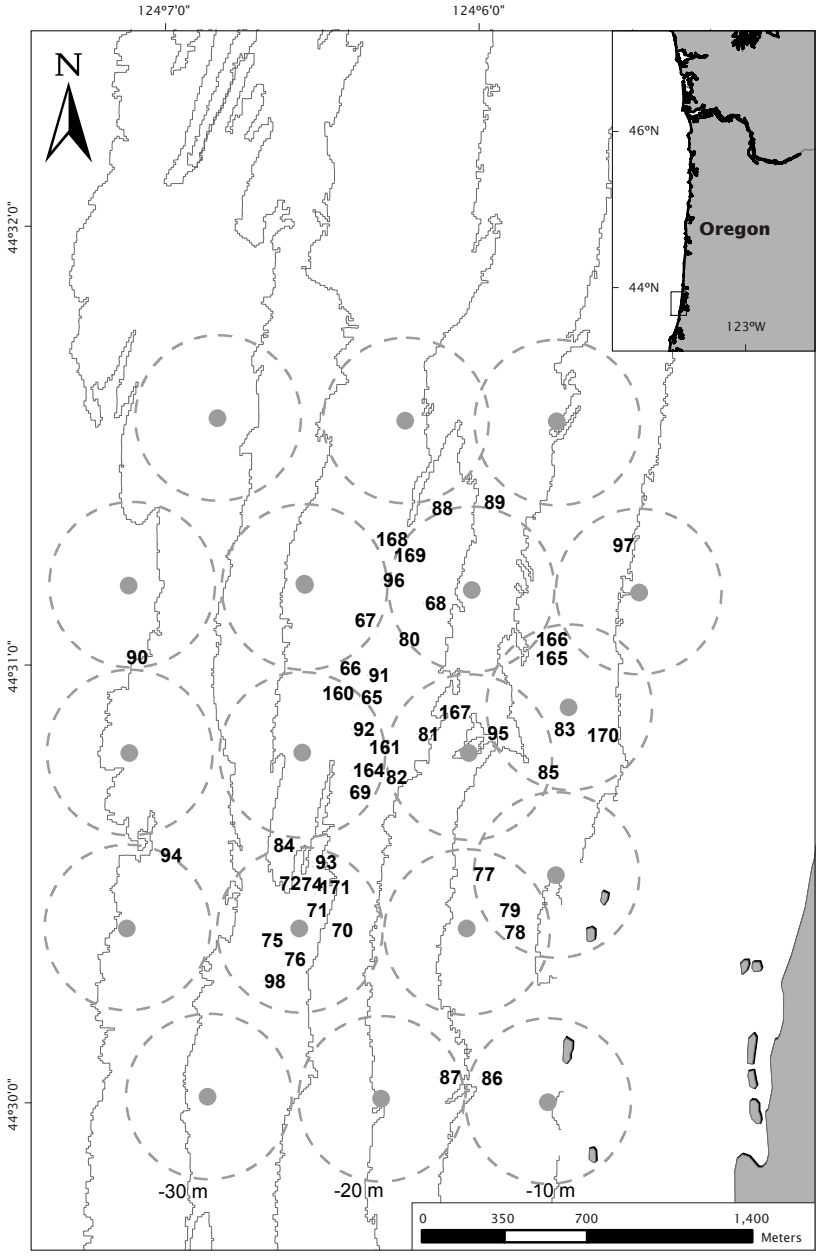


Figure 1. Map of study area showing locations of 18 acoustic receivers off Seal Rock, Oregon, and 5 m bathymetric contours. Dashed circles show expected detection range from range tests. Initial locations of released fish are shown by tag ID number. Inset shows study area location on Oregon coast. ID 84 is a moored positive-control tag.

was used. Length and sex (based on external genitalia) were recorded. Only fish with few visible barotrauma symptoms were tagged (Parker et al. in press), except for ID 67. After venting, the fish was held ventral side up in a tagging cradle so that its gills were partially immersed in oxygenated seawater. Several scales were then removed on the midline, anterior to the anus. A 2 cm incision was made and a disinfected tag was inserted into the peritoneal cavity. The incision was closed with 2 to 3 sutures using PDS II 3-0 monofilament absorbable suture thread (Ethicon, New Jersey), and a small smear of Neosporin® ointment was applied to the wound as a temporary barrier to water and bacteria. The fish was allowed to recover briefly in a darkened tank until oriented, and was then released at the surface at the location of capture.

Analysis

Periodically, when weather allowed, we downloaded data from the receivers and replaced any missing receivers. Data files from each receiver were appended to a master file, and any non-project or spurious transmitter codes were removed. Fish were assumed to be alive if some evidence of vertical movement beyond a continuous tidal rhythm was apparent in the depth data (tidal range ≈ 3 m, tag precision < 0.5 m). Environmental observations at the time of each transmitter detection were added (e.g., photoperiod, tide stage, wave height) from standard tables, formulas, or acquired from Oregon State University (hmsc.oregonstate.edu/weather), or the NOAA National Weather Service (ndbc.noaa.gov).

Periods of absence were determined for each tag, and the mean number of days absent was analyzed by month and sex using ANOVA of log-transformed data. The analysis of seasonal absences was restricted to fish that were likely to be mature based on the size at maturity relationship (Bobko and Berkeley 2004). We also examined periods just prior to and following absences to determine if the fish was likely outside the array, or was not detected due to other factors (e.g., storms, loss of receiver).

Fish locations were interpolated within the receiver array as described by Simpfendorfer et al. (2002). Briefly, to calculate a mean location for a given period, the numbers of detections from multiple receivers with known locations were used as weighting factors to generate a mean position for that period. Fish positions were plotted using GIS (ArcGIS 9.1 or ArcView 3.3, ESRI, Redlands, California). We used the 5% outlier removal method from the Animal Movement Analysis Extension (Hooge and Eichenlaub 2000) to remove the effect of sample size on home range size and to remove spurious locations (Schoener 1981). This method yields a more conservative estimate of home range size given the bias in position densities determined when only two

receivers detected a tag during a period, resulting in positions along a straight line between the receivers (Simpfendorfer et al. 2002).

A maximum home range for any given period was determined using the minimum convex polygon (MCP) function from ArcGIS (Beyer 2004). We calculated a site fidelity index as the ratio of distance between the first and last positions, and the total distance moved, where 1 equals a straight line (no fidelity) and a value close to zero implies strong site fidelity. Home range sizes were compared statistically with a paired *t*-test (diel comparisons). The relationship between fish size and home range size for each sex was examined with linear regression and a student's *t*-test.

Results

Forty-two black rockfish were tagged and released within the array on seven different days within a seven-month period (August 2004 to February 2005) (Table 1, Fig. 1). Fish were tagged in August (n = 6), September (n = 13), October (n = 7), and February (n = 8 depth and 8 non-depth transmitters). From the appearance of external genitalia, we determined that 20 of these fish were females (one was equivocal). Based on length at maturity curves, it is likely that only 11 females were reproductively mature (>39 cm) (Bobko and Berkeley 2004). Total surgical time (removal from water to recovery chamber) was less than 10 minutes and total time from capture to release was less than 18 minutes.

We recorded more than 2.4 million detections between August 4, 2004, and August 16, 2005. Fish locations were interpolated based on all observations occurring within a 2 hour period. This period was determined by comparing the number of detections per receiver for periods from 1 to 6 hours for each tag (Simpfendorfer et al. 2002). Longer periods utilize more detections when generating a position estimate. However, if the animal is moving, longer periods can yield a less accurate position. The moored tag indicated that the position averaging method was accurate to within 227 m of the known location.

We observed no evidence in the pressure data or horizontal position patterns to suggest that any fish had died within the array. However, a number of fish (7 of 42) left the array and did not return during the six-month period that the transmitter was expected to be functional (Fig. 2). Most of these fish left between March and May (IDs 80, 87, 92, 93, 98, 166, 167). The loss of a receiver was not correlated with any fish leaving the array for the duration of the study. The fates of these individuals are unknown, but include leaving the area volitionally (relocation), capture in the recreational fishery, tag malfunction, or predation by an animal that subsequently left the area. Although transmitters were expected to

last six months, most lasted 10 months and some provided information for up to 340 days (Table 1).

The distribution of cumulative days without detection (n = 575 absences > 1 day) shows that for all fish combined, the median number of days absent was only 2.00, and 90% of the absences were less than 7.78 days duration. This indicates that if fish left the array, they did not range far and were usually detected again within a few days. Multiple long absences outside the monitored area were observed, some lasting more than one month, and one lasting almost four months. The fact that many fish left the array for extended periods but returned to the same sub-area within the array suggests some ability to home to a specific area. There was an overall pattern of fish temporarily leaving the array area for longer periods from April through July (Fig. 3). Females of reproductive size (>39 cm) were absent from the array for longer periods than mature males overall ($F = 6.458$, df = 1, $P = 0.012$) and the duration of absences varied by month ($F = 2.73$, df =11, $P = 0.002$). Within a month females were absent for longer periods than males during the reproductive months; October, November through February ($P < 0.05$), though not in December ($P = 0.186$).

Some recorded absences were due to acoustic noise from storm events. Several brief periods with few detections were correlated with storm events having combined seas of more than 4.5 m (Fig. 2). We were not able to discern differences between lack of detection due to movement or due to storm events, except that storm events typically affected many fish simultaneously, and that the fish were usually detected in the area soon after the storm passed (Fig. 2, see early December). Furthermore, storms were relatively short in duration and did not impact detection for more than a few days.

For the fish that remained in the study area, horizontal movements were typically restricted to a small area. Fish had an average home range for the entire period of 55 ± 9 ha (n = 41), ranging from 2 to 271 ha (Table 1, Fig. 4). One fish (ID 80) was only detected at a single receiver for a short period, so a home range could not be determined. The site fidelity index was low (0.017 ± 0.008) indicating overall nondirected movement. There were a few instances of fish spending considerable time along the edge of the array, potentially biasing home range size because the scale of movement outside the monitored area is unknown (e.g., IDs 86 and 97 in Table 1). However, mean home range of fish with locations completely within the array was not significantly different from the home ranges of fish with many locations along an edge of the array ($P = 0.819$). We detected no relationship between fish length and overall home range size for either sex (females: df = 18, $P = 0.917$; males: df = 21, $P = 0.768$). There was no difference in overall home range size between sexes (df = 39, $P = 0.952$).

Table 1. Summary data of black rockfish tagged and released off Seal Rock, Oregon, from August 4, 2004, through August 16, 2005.

Fish ID[a]	Date range	Fork length (cm)	Sex	Duration (days)	Number of 2 h blocks	Number of absences >1 d	Linearity index	Home range MCP (ha)
65D	08/04-04/19	36	M	259	1448	33	0.004	37
66D	08/04-04/11	42	F	251	1498	23	0.002	39
67D	08/04-07/09	40	M	340	3148	5	0.002	14
68D	08/04-06/03	40	M	304	2904	7	0.008	59
69D	09/21-08/16	45	M	330	2253	26	0.004	89
70D	09/21-08/16	43	M	330	2961	12	0.001	88
71D	09/21-08/01	42	M	315	2470	9	0.003	18
72D	09/21-05/21	41	F	243	1909	6	0.002	130
74D	09/21-07/12	43	M	295	2216	15	0.003	9
75D	09/21-07/13	41	M	296	3176	3	0.001	13
76D	09/21-03/31	46	F	192	1523	5	0.006	3
77D	09/21-05/29	45	F	251	822	40	0.022	21
78D	09/21-08/16	39	M	330	2392	30	0.001	89
79D	09/21-03/28	36	M	189	988	27	0.003	7
80D	09/23-10/06	38	F	14	16	1	NA	NA
81D	09/23-07/12	34	M	293	432	38	0.012	271
82D	09/23-07/25	34	M	306	725	64	0.001	33
83D	10/04-07/16	39	M	286	2634	3	0.008	36
85D	10/04-08/15	40	F	316	827	28	0.005	59
86D	10/04-07/22	35	F	292	1981	4	0.003	18
87D	10/04-01/30	40	F	119	269	17	0.006	2
88D	10/04-08/16	40	F	317	1087	53	0.008	57
89D	10/04-08/08	46	F	309	1902	30	0.001	49
90D	10/04-08/16	45	F	317	2563	19	0.001	53
91C	02/15-08/16	38	F	183	1836	0	0.009	94
92C	02/15-05/07	38	F	82	336	6	0.217	28
93C	02/24-03/18	48	F	23	135	3	0.012	108
94C	02/24-08/16	36	F	174	1839	0	0.001	15
95C	02/15-08/16	36	M	183	1969	0	0.002	16
96C	02/25-08/16	38	M	173	1708	0	0.001	16

[a]The letter after each tag number indicates if the tag was a depth transmitter or a simple coded transmitter.

Date range is from date tagged to last day ID was detected. Duration is the total number of days ID was detected during the study. Number of 2 h blocks is the total number of 2 h average positions for each tag. Linearity index is a measure of site fidelity with little site fidelity approaching one, and strong site fidelity approaching zero. MCP is minimum convex polygon home range area.

Table 1. (Continued.)

Fish ID[a]	Date range	Fork length (cm)	Sex	Duration (days)	Number of 2 h blocks	Number of absences >1 d	Linearity index	Home range MCP (ha)
97C	02/25-08/16	38	M	173	1650	1	0.072	60
98C	02/25-07/08	36	M	134	39	6	0.228	15
160D	08/04-12/19	41	F	138	1268	5	0.004	35
161D	08/04-12/16	40	M	135	1202	4	0.000	54
164D	02/15-08/16	37	M	183	1384	16	0.004	121
165D	02/24-08/16	38	M	174	1542	2	0.003	30
166D	02/24-05/13	37	F	79	810	0	0.003	40
167D	02/15-07/02	38	F	138	215	6	0.035	232
168D	02/25-08/16	37	F	173	1757	1	0.002	17
169D	02/25-08/16	38	F	173	1117	2	0.004	33
170D	02/15-08/16	35	M	183	1092	12	0.003	26
171D	02/25-08/16	44	M	173	704	13	0.001	117
Mean		39.6		218.29		15.5	0.017	55
SEM		0.6		132.66		2.5	0.008	9

The 12 month period examined in this study did not exhibit the typical seasonal cycle in environmental conditions with long periods dominated by upwelling or downwelling conditions (Hickey 1989). The typical seasonal pattern in the study area shows upwelling beginning in May and continuing through September. 2005 was atypical in that the upwelling did not begin until the end of June and then became stronger than normal. Downwelling was weaker than normal throughout the study period as well. We observed no difference in home range size associated with periods of upwelling, downwelling, or transition using the monthly upwelling index at 45ºN, 125ºW (www.pfeg.noaa.gov/products/las.html), ($F = 0.520$, df = 3, $P = 0.670$).

We recorded a distinct shift in location within the array for 11 individuals during the study. These shifts occurred on various dates and although discrete, they were not large distances (<1 km). Several fish showed repeated shifts between two sites approximately 1 km apart (Fig. 5). These relocations lasted various periods, from a few days to several months and occurred in different directions. We did not find any evidence of fish movement away from the surf zone during storm events, even though the shallow region of the array was only 9 m deep and sometimes subjected to waves more than 6 m. These repetitive relocations also suggest the ability to home over short distances.

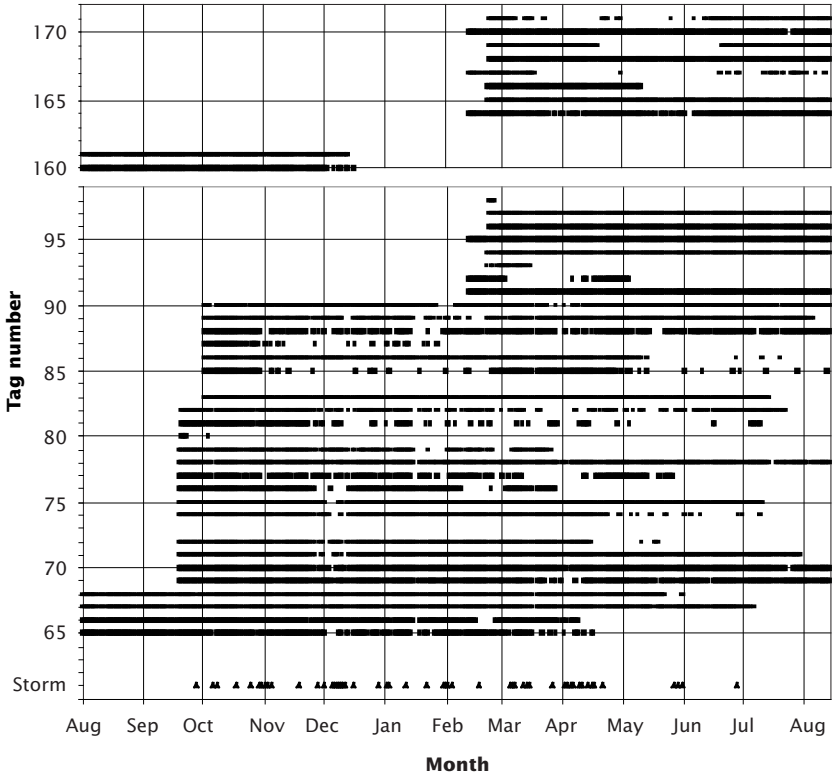


Figure 2. Presence-absence diagram showing which tags were detected in the array each day between August 4, 2004, and August 16, 2005. Days when mean overall wave height was >4.5 m are indicated by filled triangles on the line labeled "Storm".

Some examples of individuals making short forays within the array but returning to a core area were observed, usually lasting just a few days. These infrequent movements were typically removed by the outlier removal process, but three individuals made multiple short forays resulting in the largest home range estimates (Table 1).

Diel movements were minor and usually not associated with a particular direction. However, four fish did show obvious directional and repetitive movements with a diel pattern (Fig. 6). Each fish moved in a different direction and the spatial shift did not appear to be directed to a specific bathymetric feature, but rather to a broader region covering a considerable portion of the home range.

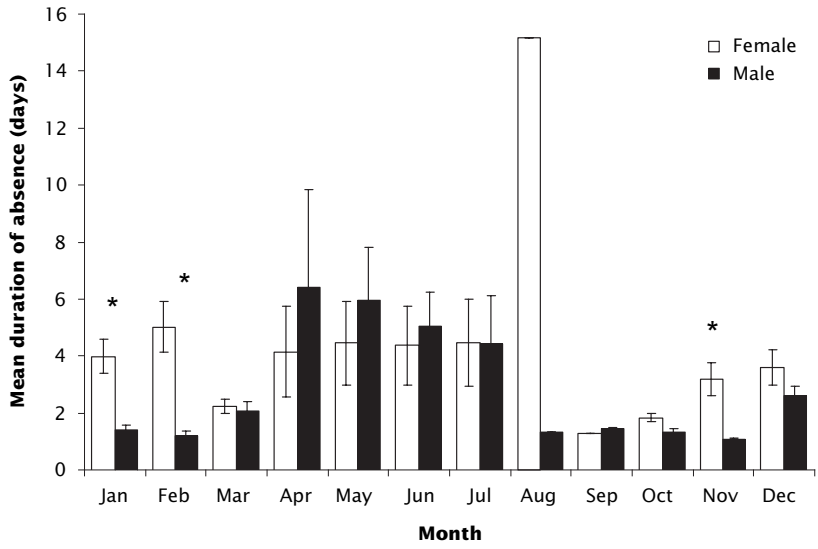


Figure 3. Mean number of consecutive days a tag was not detected within the array for males and females of reproductive size (>39 cm) for each month. Error bars are ± standard error of the mean. Months with significant differences between sexes are indicated with *. Note: N=1 for August females, males, and September females.

Discussion

Our array design allowed us to monitor the movements of 42 black rockfish at a high temporal resolution (minutes) spanning a full year for the group as a whole. Our study also provides detailed behavioral information on black rockfish from a previously unstudied environment; exposed rocky coastline in a temperate ocean. The low frequency and duration of absences observed indicate that the fish remained within the monitored area essentially for the entire period with a few exceptions, which were usually forays lasting less than 7 days, or some fish that left the monitored area permanently.

On average, black rockfish showed restricted daily movements and a relatively small home range size. However, the variation in home range size was large. Our ability to determine larger scale movements was limited, but presence-absence data allowed us to determine that most movements outside the array were of short duration and no evidence of mass seasonal movements north or south following prevailing currents was detected. Any underestimation of home range size due to edge effects was obscured by the large variability in movements among

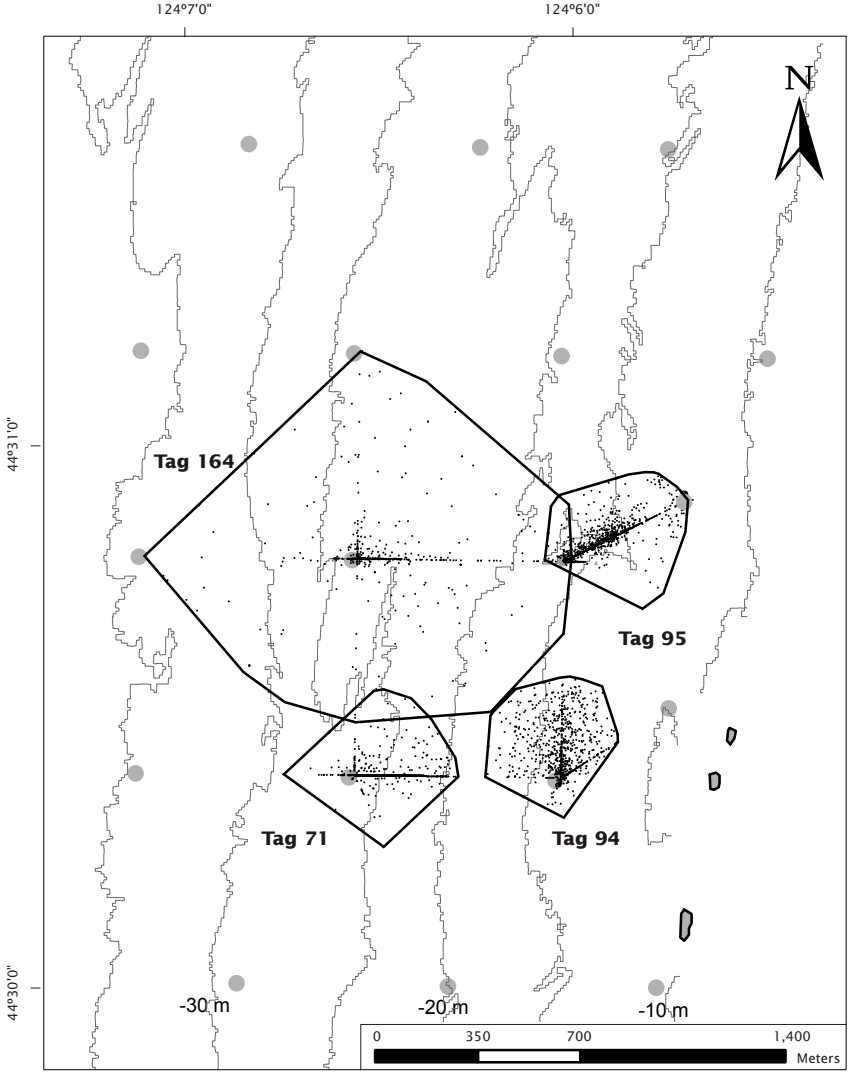


Figure 4. Examples of overall minimum convex polygons (MCPs) for black rockfish off Seal Rock, Oregon, showing small (IDs 71, 94, 95), and large (ID 164) home range sizes and the corresponding distribution of locations for each ID.

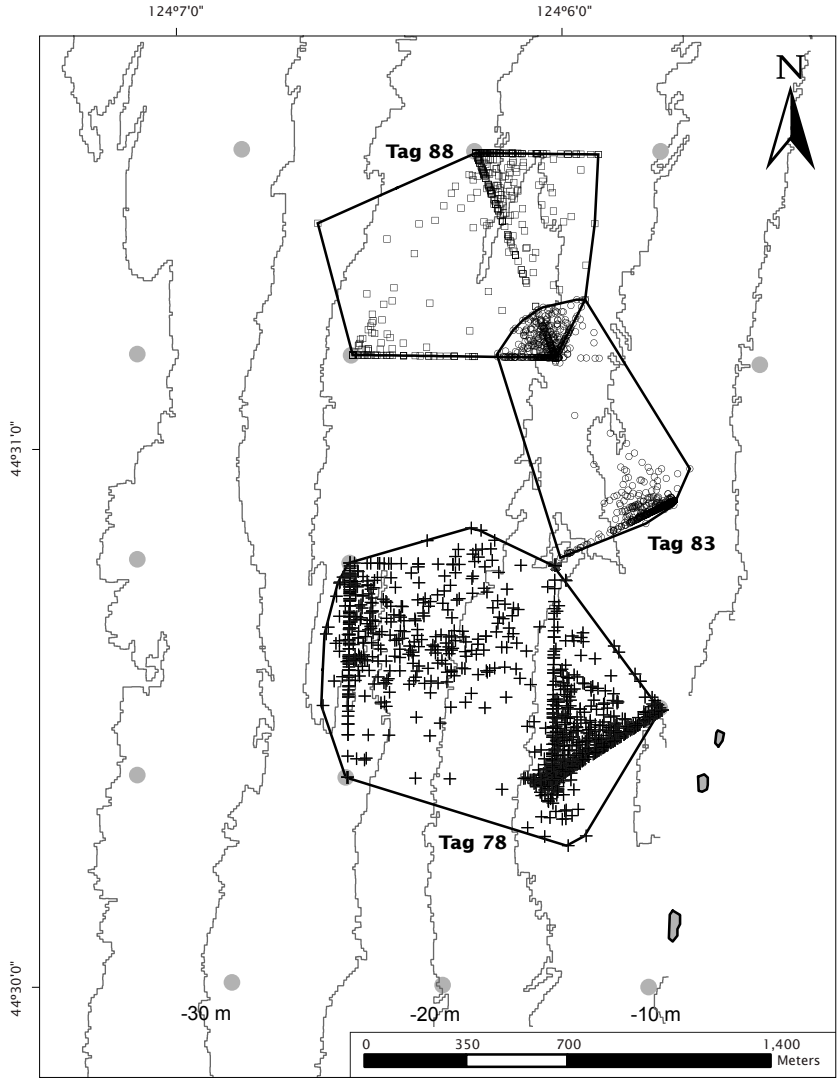


Figure 5. Examples of discrete relocations of activity areas for three black rockfish from August 2004 through August 2005. IDs 78, 83, and 88 showed repetitive movements between their two respective areas, with stays lasting several days to several months at each site.

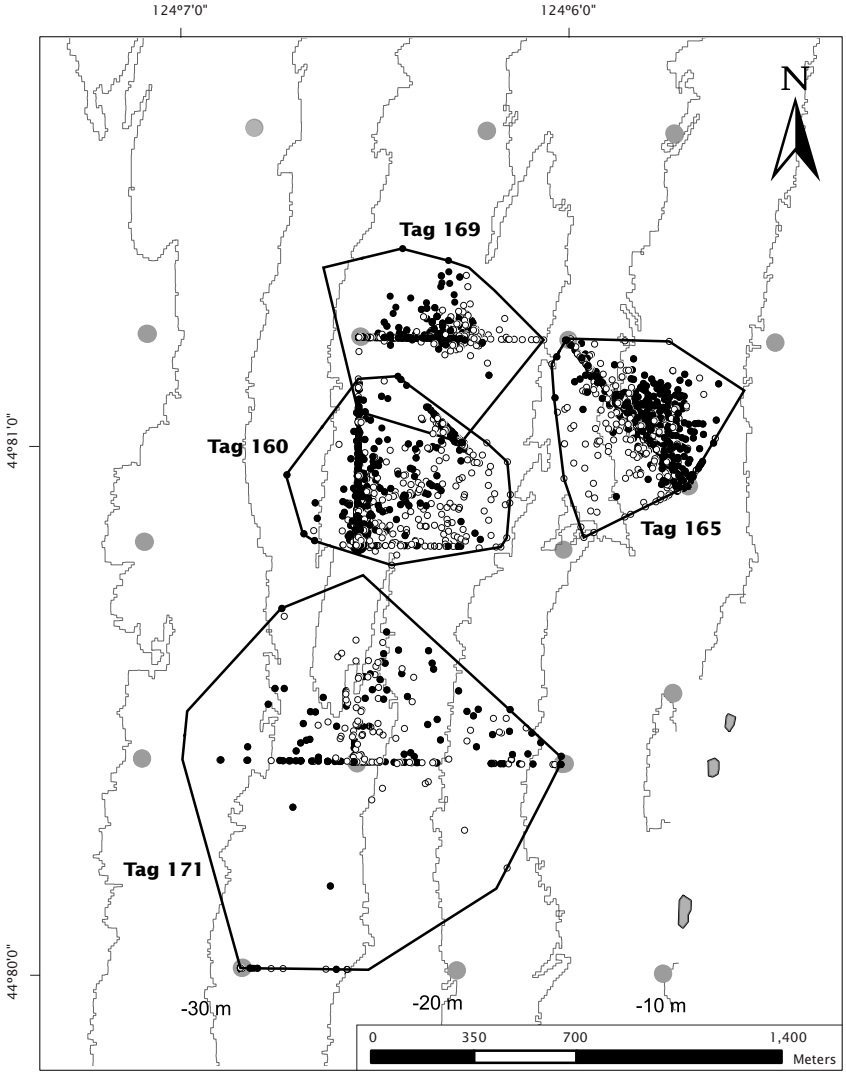


Figure 6. Examples of segregation in location during day (white circles) and night (black circles) for four fish (IDs 160, 165, 169, 171).

individuals. Small home range areas have been typical for rockfishes studied to date, although most telemetry studies have been of short duration (Matthews 1990, Starr et al. 2002).

Previous tagging studies of black rockfish using visual marks showed that the vast majority of recoveries were from the local tagging area during the same or following season, but the degree of movement was on short time scales, and the pattern of movements throughout the annual cycle could not be described (Culver 1987). Our results suggest that most adult black rockfish live primarily on the same reef, and although their home ranges are large compared with some rockfish species studied in Puget Sound (Matthews 1990), they are relatively small given the dynamic environment along the open coast, especially through the winter months. If home range size was affected by ocean currents, then a more elongated north-south home range would be expected due to prevailing along-coast currents.

The size of the home range has been shown to be correlated with fish size in several tropical species, but not for rockfishes (Kramer and Chapman 1999). This relationship has been attributed to the ability of larger males to traverse larger areas, or the relative lower energy requirements for larger fish to patrol larger areas. But there is no evidence that black rockfish males actually defend a territory given their schooling nature (Hallacher 1977). The few extended absences we detected (i.e., over 1 week) suggest some ability for black rockfish to relocate a small activity area after a foray on the scale of at least several kilometers. Although Coombs (1979) displaced 50 tagged black rockfish, she did not recapture any individuals to address the possibility of homing. Studies of some other rockfish species have demonstrated homing through classic displacement techniques (Carlson and Haight 1972, Matthews 1990). Maintaining position in a small area while living semi-pelagically in a dynamic environment with strong currents, and turbid water would likely require some degree of navigation even over short distances.

We observed no distinct seasonal movement pattern or shift in distribution within an individual's home range associated with seasonal oceanographic conditions. Eleven individuals showed a distinct shift in activity centers during the study, but these were not correlated in time or direction in any discernable way. Those shifts in activity centers may be related to a home range relocation, where an individual makes a definite shift to a new location (Kramer and Chapman 1999). The most distinct seasonal movement pattern was the longer mean absence time for both sexes from April through June compared with the rest of the year, and the longer absences for females only during the winter reproductive season. Individuals may range farther during April through June as food availability changes seasonally with the start of upwelling. The absence of pregnant females in the catch during the reproductive

season has generated the hypothesis that females leave their normal home range and move to an area in deeper water for gestation and parturition (Welch 1995, Worton and Rosenkranz 2003). Fisheries in the winter months are typically limited to nearshore waters close to ports. Recreational catch shows that these females are prevalent by the end of March, but not in February (Oregon Department of Fish and Wildlife, unpubl. data). An alternative hypothesis is that the females remain on the reefs but cease to actively feed, which is supported by observations of scuba-collected fish in Oregon (S. Berkeley, pers. comm.). Although not conclusive, our data suggest that females of reproductive size may leave their usual area between copulation and parturition for longer periods than males or smaller females. More directed studies of this phenomenon are needed to show that these absences are related to reproduction and to determine where these individuals go during that period. We suspect they do not travel excessive distances because the duration of their absences was relatively short.

Marine protected areas are being considered as conservation tools to protect a portion of a population from exploitation, generate and maintain a natural age structure, or serve as a research area (Murray et al. 1999). The effectiveness of an MPA relative to these objectives depends on the temporal and spatial scale of movements of animals in and near the reserve (Kramer and Chapman 1999). The degree of exposure an individual has to exploitation outside the reserve, especially in the long term, will determine the effectiveness of any protection offered within the reserve. Other factors, such as the degree of home range relocation, or the degree to which fish density is determined by habitat type, density-dependence or environmental conditions will also affect the stability of the population inside the reserve (Chapman et al. 2005). Preference for habitat types not included in the reserve can result in fish leaving the reserve, especially if the habitat is occupied through competitive interaction. Conversely, if adult fish never leave the reserve area (no spillover), any reserve contribution to outside populations and local fisheries would be limited to export of larvae or juveniles.

Movement patterns and presence-absence data from this experiment show that although black rockfish have relatively small home ranges, these home ranges may be ephemeral and open to relocation over various distances. We observed eleven fish that shifted to a new activity center within the array, and seven fish that left the array completely, for a total of 18 fish (43%) exhibiting some type of relocation. The distance outside the array that the seven traveled is not known, but likely not more than a few kilometers given the scale of the movements within the array and information from other tagging studies. In addition to these individuals, others left the array for more than two weeks at a time. Scaling a protected area's size as a function of the home range size to achieve a specified reduction in fishing pressure still may not

provide sufficient protection for a species that relocates periodically if the relocations are outside the protected area (Kramer and Chapman 1999). This is especially important in that this study monitored individual fish for more than six months. The vast majority of telemetry studies span much shorter periods, from weeks to two months, and therefore may not detect such relocations. The distances some fish moved outside the monitored area are not known and the proximal cause for the relocation is not known. Therefore, with these data it is not possible to determine a minimum reserve area that would provide a prescribed degree of protection for black rockfish. The home ranges we calculated incorporate any observed relocations, but not those leaving the monitored area. Tagging studies conducted by the Oregon Department of Fish and Wildlife and the Washington Department of Fish and Wildlife indicate that a significant portion of the population remains in the same general area for long periods, often moving less than one kilometer in two years (Oregon Department of Fish and Wildlife unpubl. data; Culver 1987). The overall pattern appears to be reef-specific dwelling with occasional relocations to nearby reefs, possibly returning to some reefs over time. This amount of mixing would allow individuals to identify and take advantage of better habitats as environment, natural mortality, and fishing pressure slowly modify the size and sex composition on nearby reefs.

Perhaps most important is the observation that black rockfish movement patterns (and scale of movement) change seasonally, and do so differently for each sex. The implications are that the design of protected areas should incorporate long-term monitoring data and that different population segments may behave differently (Chapman et al. 2005, Heupel and Simpfendorfer 2005). Therefore, caution should be used to apply our data to describe the movement patterns of black rockfish juveniles, or even black rockfish adults in different habitats. Understanding the ecology that drives movement patterns will ultimately lead to more effective protection methods.

Acknowledgments

This field project required extensive fieldwork and the help of many people to deploy and maintain the array. J. Scott Malvitch managed the challenging database and tracked the status of individual fish for the entire year. We especially thank Zeb Schobernd, Troy Buell, Keith Matteson, Steve Kupillas, Jon Nottage, and Stephen Jones for their assistance in catching fish, maintaining the array, and downloading the receivers. Christopher Romsos provided GIS assistance. We also thank the fishermen and beachcombers that found and returned receivers that were lost during storm events or fishing mishaps.

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New Data on Distribution and Biology of Gray, Angry, and Northern Rockfishes from the Northwestern Pacific

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Abstract

Despite relatively small numbers of rockfish species inhabiting the western North Pacific and quite intensive studies conducted recently in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka, the distribution patterns and biological features of gray rockfish *Sebastes glaucus*, angry rockfish *S. iracundus*, and northern rockfish *S. polyspinis*, remain poorly understood. On the basis of data collected during 1993-2000 bottom trawl surveys and 1992-2002 commercial fishing operations within the depth range of 83-850 m, some quantitative indices of occurrence of gray, angry, and northern rockfishes in the study area are provided. In addition, their spatial and depth distributions are analyzed, bottom temperature preferences are shown, size composition and length-weight relationships are considered, and the diurnal, seasonal, and multi-annual changes of catch rates and occurrence in catches are analyzed.

Introduction

Rockfishes (Sebastidae) in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, with at least 12-13 species, are less diverse than in the northeastern Pacific (Fedorov 2000, Sheiko and Fedorov 2000). Many of them are common or abundant and several

species, such as Pacific ocean perch *Sebastes alutus*, shortraker rockfish *S. borealis*, rougheye rockfish *S. aleutianus*, broadbanded thornyhead *Sebastolobus macrochir,* and shortspine thornyhead *S. alascanus* are commercially important targets of bottom trawl, longline, and gillnet fisheries. The distribution and biology of these species in the study area are rather well-studied. Despite quite intensive research conducted recently in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka the distribution patterns and biological features of three rockfish species (gray rockfish *Sebastes glaucus*, angry rockfish *S. iracundus*, and northern rockfish *S. polyspinis*) remain poorly understood. The angry rockfish is believed to be a temporary migrant from southern areas (Orlov et al. 1998), northern rockfish recently penetrated the study area from the neighboring Aleutian Islands waters (Orlov 2004), while the status of gray rockfish is still uncertain. Until now, most publications dealing with these species in the northwestern Pacific contain data on their taxonomy or general information regarding zoogeography, depth ranges, and maximum size (Moiseev 1937; Snytko and Fedorov 1974; Barsukov 1981, 2003; Masuda et al. 1984; Lindberg and Krasyukova 1987; Amaoka et al. 1995; Fedorov and Parin 1998; Borets 2000; Fedorov 2000; Sheiko and Fedorov 2000; Snytko 2001; Chereshnev et al. 2001; Novikov et al. 2002; Parin et al. 2002; Fedorov et al. 2003).

The main purpose of this paper is (1) to provide some quantitative indices of the occurrence of three insufficiently studied rockfish species in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, (2) to consider patterns of their spatial and depth distributions, (3) to analyze their catch rates and occurrence depending on bottom temperature, time of the day, season, and between years, and (4) to show their size compositions and relations between length and body weight.

Materials and methods

This paper is based on materials sampled in the framework of the scientific program for species that had not been studied adequately, or were not being sufficiently utilized on the continental slope of the Russian Far Eastern seas. This paper presents the results of analysis of catches from about 1,500 bottom trawl survey hauls (19 bottom trawl surveys, 1993-2000) and over 10,000 commercial fishing operations (about 50 cruises, March-December 1992-2002) in Pacific waters off the northern Kuril Islands and southeastern Kamchatka (between 47°50' and 52°00'N, depths 83-850 m). Positions of bottom trawl stations were randomly selected. Commercial fishing efforts varied by depth, season, and areas depending on targeted species. However, since trawlers fished for a variety of species (from shallow-water flatfishes and Pacific cod to deepwater rockfishes, thornyheads, and sablefish), the whole study

area was covered by a dense grid of trawlings, and between-year maps of distribution of survey stations and commercial trawlings were quite similar (Orlov 2003). These research cruises were conducted jointly by the Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) with Kamchatka (KamchatNIRO) and Sakhalin (SakhNIRO) where the distribution and biology data on three rockfish species were collected. That study was done aboard the Japanese trawlers (*Tomi-Maru 53, Tomi-Maru 82* and *Tora-Maru 58*) specially equipped for ground hauls on the parts of the continental slope having rough relief. The bottom temperature was measured during most of the hauls. Trawls were made over 24 hours, with the bottom trawls having vertical (5-7 m) and horizontal (25 m) openings and 100 mm mesh size in codend. The trawl opening parameters were monitored instrumentally and the mean speed was 3.6 knots. Since the duration of hauls during the cruises varied between 0.5 and 10 hours, all catches were subsequently recalculated into standard 1 hour hauls. The distribution of individual species by depth and bottom temperature was analyzed according to the percentage of their occurrence calculated by average 1 hour haul catches. Analysis of species occurrence, spatial and vertical distributions, bottom temperature preferences, composition of species co-occurring, diurnal, seasonal and multi-annual changes of catch rates, and frequency of occurrence are based on 251 captures of gray rockfish, 32 captures of angry rockfish, and 77 captures of northern rockfish. Length frequency distributions are based on measurements of 282 specimens of gray rockfish, 119 specimens of angry rockfish, and 162 specimens of northern rockfish. Length-weight relations are analyzed using measurements and weights of 281 gray rockfish, 38 angry rockfish, and 88 northern rockfish. The relation between fish fork length (FL, cm) and weight (W, g) is described by the following equation: $W = aFL^b$, where a and b are linear and exponential coefficients respectively. Limited data (62 specimens of gray rockfish, 31 specimens of angry rockfish, and 27 specimens of northern rockfish examined) were analyzed to obtain some information about sex ratios, size differences between males and females, and stomach fullness. Stomach fullness index (SFI) was determined on a five number scale (0 = empty, 4 = full).

Results and discussion

General information and occurrence in the study area

Gray rockfish

The gray rockfish is distributed in the North Pacific mostly within Asian waters (Sea of Japan, Sea of Okhotsk, Bering Sea, Pacific waters off Japan, Kuril Islands, and Kamchatka). Its range is limited in the north by the Bering Sea while in the south the species reaches Japanese waters off Iwate Prefecture (northern Honshu). In the Sea of Japan off the conti-

nental coast, the gray rockfish is distributed northward to Tatar Strait and to Peter the Great Bay southward; off the Japanese coast it reaches Toyama Bay in the south (Masuda et al. 1984, Snytko 2001). Recently this rockfish was found off Attu Island, in the Aleutian Islands (Orr and Baker 1996). The abundance of gray rockfish in the majority of areas of its range is rather low. It is most abundant in the northern Sea of Okhotsk where it is a commercially important fishery target (Chereshnev et al. 2001, Fedorov et al. 2003). Its biology is little known (Novikov et al. 2002, Love et al. 2002). The gray rockfish probably plays a certain role in trophic webs being consumed by fin whales (Barsukov 2003). The data on life history of the gray rockfish to the present were limited to waters off Kamchatka, northern and southwestern Sea of Okhotsk, where this species is considered a prospective target of longline and bottom trawl inshore fisheries (Panchenko 1996, Kondratiev 1996, Chetvergov 1998, Nemchinov 2001).

In the study area, gray rockfish is believed to be abundant (Fedorov and Parin 1998, Sheiko and Fedorov 2000). Among the three rockfishes this species was taken most frequently (251 captures). However, while it was caught most frequently (Table 1) the average catch rate was the lowest of the three species. This may be evidence of the fact that gray rockfish in some periods is able to form dense concentrations. However, during most of the year this species is very scarce in the study area and is caught only occasionally. In addition, during summer months this species in Kamchatkan waters primarily inhabits inner shelf waters (Chetvergov 1998). Since the studies were limited to depths no shallower then 80 m, our observation based on bottom trawl catches probably provides an underestimate of its real abundance in the study area.

Angry rockfish

At present, there is no common point of view regarding the taxonomic status of the angry rockfish (Barsukov 2003). The majority of authors suggest the existence in the northwestern Pacific of two congeneric rockfish species, *Sebastes flammeus* and *S. iracundus* (Snytko and Fedorov 1974, Masuda et al. 1984, Nagasawa and Torisawa 1991, Amaoka et al. 1995) differing in size, depth range, and spawning grounds. Other researchers (Barsukov 1981, Snytko 2001) consider them subspecies, *Sebastes iracundus iracundus* and *Sebastes iracundus flammeus*. The information regarding their range is also very controversial. The angry rockfish is distributed from the Pacific coast of Japan (Chiba Prefecture) along the Kuril Islands to Emperor Seamounts (Masuda et al. 1984), in the Sea of Japan off Moneron Island and in the southwestern Sea of Okhotsk (Snytko and Fedorov 1974, Romanov 1999) and off Tennou seamount (Nagasawa and Torisawa 1991). Snytko (2001) states that this species also inhabits waters of southeastern Kamchatka, the Commander Islands, and the Aleutians as far as Amchitka Strait and Bowers Ridge in

Table 1. Some quantitative indices of occurrence of gray, angry, and northern rockfishes in catches within the Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002.

Species	Proportion in catches %	Number of fish caught		Weight of fish caught		Depth, m	Bottom temperature, °C	Length, cm	Weight, g	Number of hauls with species
		Total	Per hour trawling	Total	Per hour trawling					
Gray rockfish	0.001-9.433	1-944	0-251	0-2830	0-395	83-390	–1.0-3.5	19-57	140-3300	251
	0.176	10.15	3.66	20.68	5.54	185.6	1.40	44.78	1780.7	
Angry rockfish	0.008-5.571	1-210	0-38	1-462	0-84	370-650	3.1-3.55	26.67	470-3700	32
	1.163	24.15	4.61	44.97	8.44	473.4	3.41	46.55	1462.6	
Northern rockfish	0-8.769	1-524	0-123	0-90	0-67	101-466	–0.2-3.6	15-48	80-1200	77
	0.212	18.70	7.69	5.90	3.59	209.4	1.91	32.38	602.7	

Note: above the line minimum and maximum values are given, while under the line average values are provided.

the Bering Sea. However, some authors (Sheiko and Fedorov 2000) doubt whether angry rockfish live in Kamchatkan waters. It is most probable that the suggestion is correct and angry rockfish does not inhabit waters off Kamchatka and the northern East Pacific, because it was not included in recent taxonomic reviews of Alaska and northeastern Pacific rockfishes (Kramer and O'Connell 1995, Orr et al. 2000, Love et al. 2002, Mecklenburg et al. 2002).

The flesh of angry rockfish is very delicious (Snytko 2001); it has high demand at fish markets in Japan where it is used for cooking traditional Japanese dishes such as sushi and sashimi and for frying as well. Angry rockfish probably plays a certain role in food webs since it is the most abundant rockfish species in the Pacific waters off Japan (Nagasawa and Torisawa 1991), and is known to be eaten by sperm whales (Barsukov 2003). The publications dealing with this species contain some data on its morphology (Sasaki 1976, Romanov 1999) and general information on life history aspects in Japanese waters (Nagasawa and Torisawa 1991).

In Pacific waters off the northern Kuril Islands, the angry rockfish was rarest among the species considered (32 captures) though the data provided are probably understated due to difficulties of species identification. In catches angry rockfish co-occurred most frequently with the similar-appearing shortraker rockfish (Barsukov 1981).

Northern rockfish

The northern rockfish inhabits primarily North American waters from British Columbia (Graham Island) in the south to the eastern Bering Sea (to 60ºN) in the north, including the Gulf of Alaska and waters off the Aleutian Islands (Allen and Smith 1988, Snytko 2001). In Asian waters, this species is known from occasional captures in the western Bering Sea, off southeastern Kamchatka and the northern Kuril Islands as far as Onekotan Island in the south (Snytko and Fedorov 1974, Fedorov and Parin 1998, Snytko 2001, Parin et al. 2002). The northern rockfish is believed to be one of the most abundant rockfishes of the North Pacific (Moiseev and Paraketsov 1961). It is most abundant in the Gulf of Alaska, off the Aleutian Islands and in the eastern Bering Sea (Harrison 1993, Ronholt et al. 1994, Martin 1997, Snytko 2001) and off the Commander Islands as well (Mecklenburg et al. 2002). The species is very important in the U.S. bottom trawl fisheries in the Gulf of Alaska and off the Aleutians as an export to Japan and Korea (Love et al. 2002, Clausen and Heifetz 2002). The majority of published data on the biology of the northern rockfish comes from the northeastern Pacific (Westrheim and Tsuyuki 1971; Mito 1974; Brodeur and Livingston 1988; Yang 1993, 1996; Cailliet et al. 2001; Clausen and Heifetz 2002). The life cycle of this species in Asian waters is little known. Until the present, there were only few data on its occurrence and some biological characters in the

western Bering Sea and Pacific waters off the northern Kuril Islands and southeastern Kamchatka (Moiseev and Paraketsov 1961; Skalkin 1964; Orlov 2000, 2001).

Some authors (Sheiko and Fedorov 2000, Parin et al. 2002) consider the northern rockfish in the study area to be abundant while others (Fedorov and Parin 1998) suggest it is rare. Our results show that the northern rockfish was rather rare in the study area (77 captures). Its maximum catches exceeded 500 individuals per haul (mean 18.7 individuals), with an average of 7.7 specimens or 3.6 kg per hour of trawling. These data show that northern rockfish catch rates are very low for most of the year, but this species may form increased concentrations during some periods.

Spatial distribution

The gray rockfish in the study area was most abundant opposite the First Kuril Strait and off the western slope of the underwater plateau in the southern part of the area surveyed (Fig. 1a), where catches exceeded 250 kg per hour trawling. The majority of captures occurred north of the Forth Kuril Strait though most catches had several specimens only. The existence of dense concentrations opposite straits suggests that the majority of gray rockfish are able to migrate to the study area from the Sea of Okhotsk, mostly through shallow First and Second Kuril Straits. However, it will be further shown that the gray rockfish inhabits this area permanently. We speculate that the relatively dense concentrations opposite straits are probably related to better feeding conditions within these areas due to higher water exchange with the Sea of Okhotsk. The persistence of dense concentrations off the underwater plateau, where the quasi-stationary eddy exists, may be evidence of transport of pelagic juveniles here from the north and of their further dwelling within eddy waters until settlement. In the Sea of Japan and southwestern Sea of Okhotsk, the gray rockfish inhabits sludgy and sandy grounds (Lindberg and Krasyukova 1987, Panchenko 1996, Novikov et al. 2002). However, Chetvergov (1998) pointed out that this species in the waters off Kamchatka and the Commander Islands preferred areas with complex bottom relief. Apparently, in this study area, gray rockfish exhibits more plasticity regarding bottom type preference, since it forms dense concentrations on rather soft grounds north of the Forth Kuril Strait and off the underwater plateau which is characterized by rocky relief and rough bottom.

The angry rockfish occurred exclusively within the southern part of the study area (Fig. 1b). At the same time, almost all captures were off the eastern slope of the underwater plateau; only a single record was observed outside this area, opposite Onekotan Island. The data obtained confirm previous suggestions that this species migrates to the northern Kurils from southern areas (Orlov et al. 1998), and also

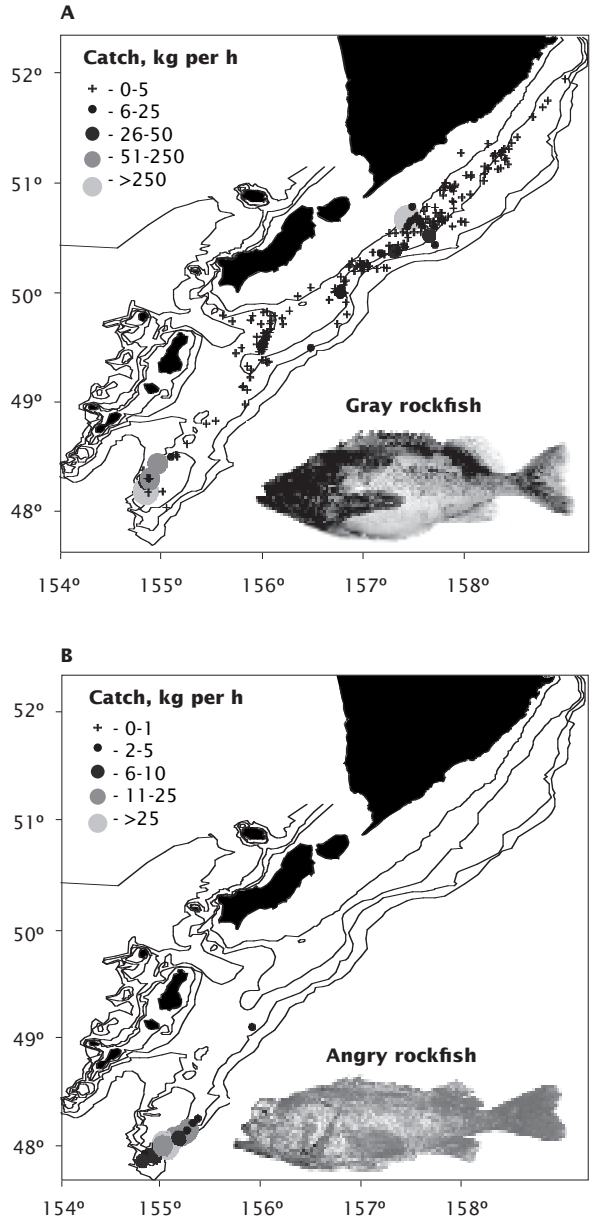


Figure 1. Spatial distribution and relative abundance of (a) gray, (b) angry, and (c) northern rockfishes in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002.

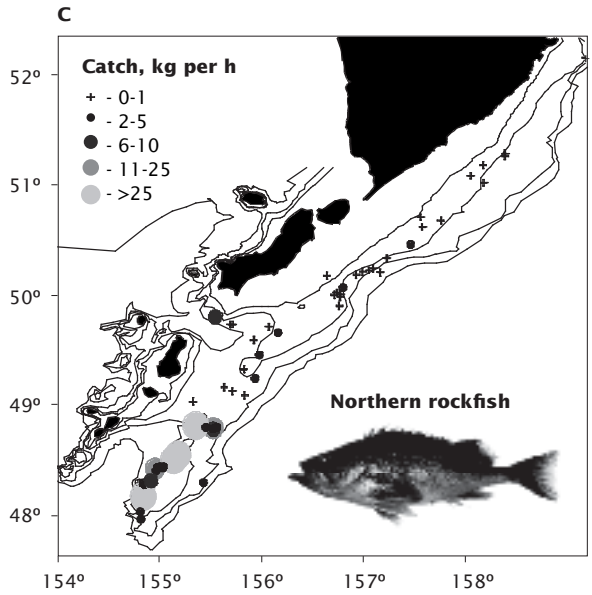


Figure 1. (Continued.)

that no angry rockfish inhabit Kamchatkan waters (Sheiko and Fedorov 2000). There are no data on spatial distribution of species considered in other areas.

The northern rockfish occurred within the entire area surveyed from 48ºN in the south to 52ºN in the north (Fig. 1a), though its maximum catches (over 25 kg per hour trawling) were registered in the southeastern part of the study site. Previous to the mid 1990s, northern rockfish were not captured in this area. It was in May 1996, that a few fish (spawning females) were first captured. It is possible that the northern rockfish migrated to the Kurils and Kamchatka from the Aleutians (Orlov 2004) and found favorable conditions for spawning within the southern part of the study area, where a quasi-stationary eddy exists (Orlov 2003). In waters off the Aleutian Islands and in the western Gulf of Alaska, northern rockfish are also most abundant off seamounts where they prefer hard and rough bottoms (Ronholt et al. 1994, Martin 1997, Clausen and Heifetz 2002).

Bathymetry

According to recent data, the gray rockfish within its range occupies depths of 2-550 m (Orr et al. 2000; Love et al. 2002) though some authors believe that the maximum depth of its occurrence is 370 m with

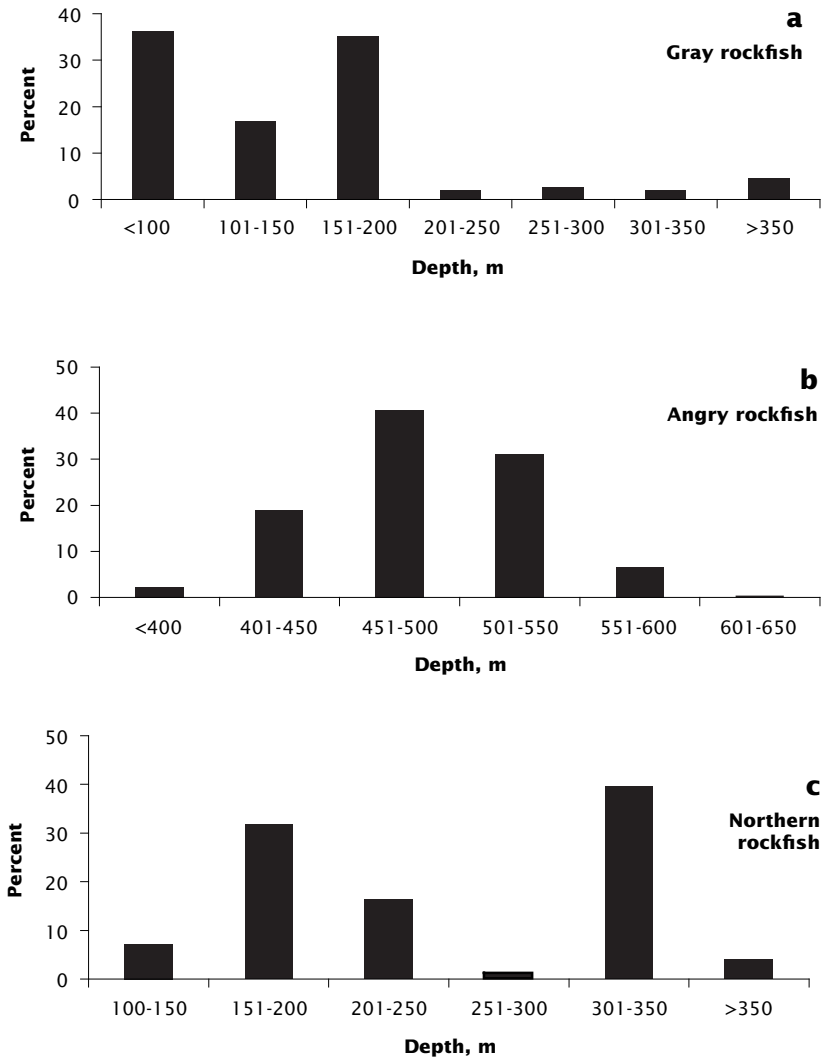


Figure 2. Vertical distribution of (a) gray, (b) angry, and (c) northern rockfishes in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002.

an optimum at 20-40 m (Fedorov 2000, Sheiko and Fedorov 2000). In this study, gray rockfish were found within the depth range of 83-390 m with mean depth of 186 m (there were no hauls shallower than 80 m). Maximum catches were made from less than 100 m to about 200 m (Fig. 2a). This probably reflects seasonal changes of depths inhabited. The gray rockfish during periods of mating (autumn) and larval release (spring-summer) occupies shallower depth in comparison with the rest of the year (Kondratiev 1996, Nemchinov 2001). Our observations (Fig. 3c) do not conflict with these data. However, the pattern of vertical distribution presented might be incomplete due to lack of trawling in shallow waters where the bulk of the population may exist.

The angry rockfish is the most deepwater species among rockfishes considered. It inhabits a depth range of 200 to 1400 m (Sheiko and Fedorov 2000), with optimal depths believed to be either 450-1,000 m (Fedorov 2000) or 400-800 m (Amaoka et al. 1995). In the study area, angry rockfish occurred in catches at depths of 370-650 m (mean 474 m). The maximum catch rates were registered within the depth range of 450-550 m and the diagram of vertical distribution had one peak only (Fig. 2b) which may be associated with the fact that this species is caught in the study area predominantly in the summer period. It is known that during the summer the angry rockfish migrates from feeding areas in deeper waters to shallower depths. In addition, it is known that this species inhabits shallower depths in the northern parts of the range as compared to the southern ones (Nagasawa and Torisawa 1991).

The northern rockfish within its range occupies depths of 73 to 740 m (Sheiko and Fedorov 2000) with an optimum between 95 and 190 m (Fedorov 2000), although optimal depths vary with location. According to data of Snytko (2001), maximum abundance of the northern rockfish occurred at 100-120 m in the western Bering Sea, at 100-400 m in its southeastern part, at 235-250 m off the Bowers Ridge, at 100-320 m off the Aleutians, and at 70-250 m in the Gulf of Alaska. According to other data (Clausen and Heifetz 2002), the northern rockfish is most abundant off the Aleutians at depths of 75-175 m, and in the Gulf of Alaska at 75-150 m. Off the Kurils and Kamchatka the maximum abundance of this species was registered at depths of 150-200 and 300-350 m (Fig. 2c). The existence of two peaks of vertical distribution is probably related to seasonal changes of depths inhabited since northern rockfish feed during summer months in shallower waters in comparison with the rest of the year (Love et al. 2002). Our observations (Fig. 3c) also showed that, overall, northern rockfish were distributed in slightly shallower waters in the summer months.

The relationship between capture depth and average body weight showed that gray rockfish tended to be larger in shallower waters, because juvenile fish lived in deeper waters (Fig. 3a). Such size-depth differentiation may serve to decrease intraspecific feeding competition.

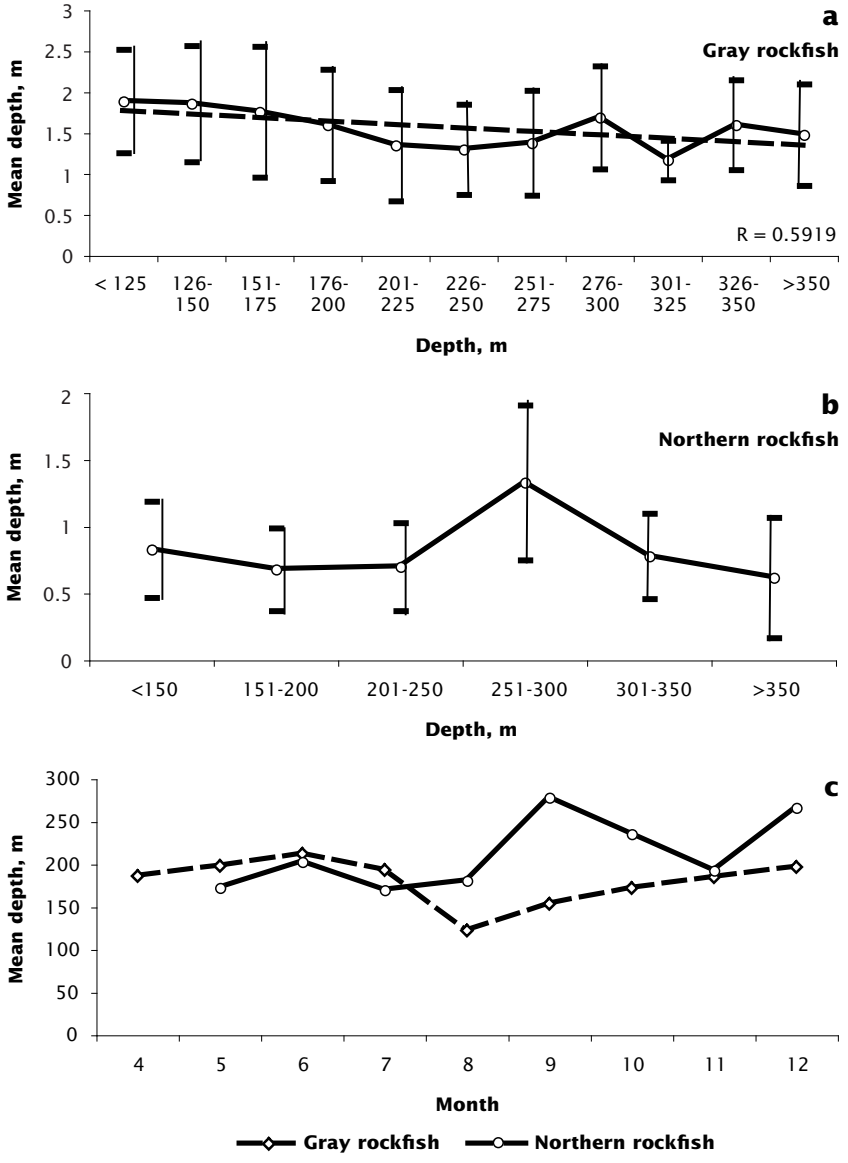


Figure 3. Relation between average body weight and capture depth of (a) gray and (b) northern rockfishes, and monthly changes of their mean capture depth in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002 (dashed lines indicate linear trend, *R* = correlation coefficient).

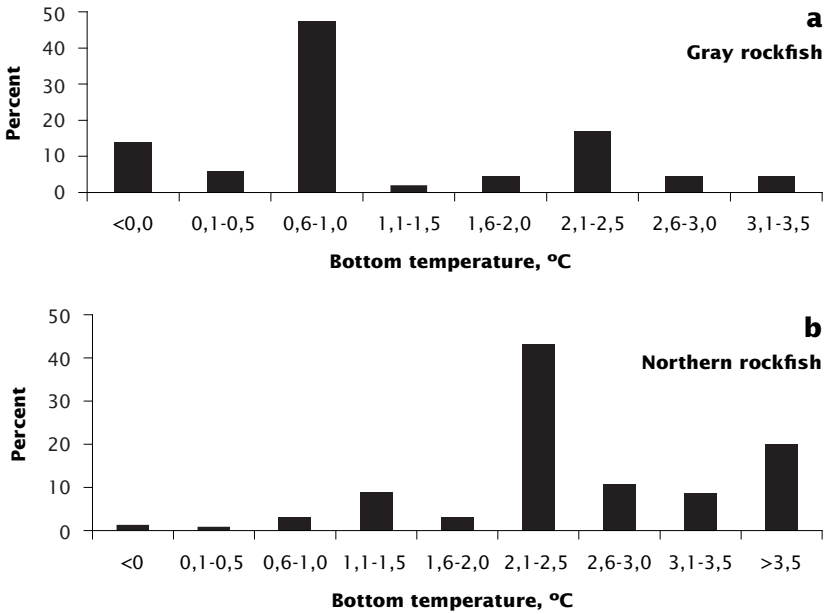


Figure 4. Distribution of (a) gray and (b) northern rockfishes in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002, depending on the bottom temperature.

The smallest northern rockfish was registered at depths less than 250 m and over 300 m (Fig. 3b) while the largest fish was caught within 250-300 m depth range (differences are statistically invalid). However, similar size-depth distribution of this species were observed in the Gulf of Alaska and off the Aleutians (Harrison 1993, Ronholt et al. 1994, Martin 1997).

Bottom temperature preference

The gray rockfish in the Sea of Japan occupies a very wide range of bottom temperatures, from 1.5 to 15ºC (Novikov et al. 2002). In the study area, this species dwelled in the coldest water among the three rockfishes considered (Table 1). It was registered in catches at bottom temperatures from –1 to 3.5ºC (mean 1.4ºC); about half of these fish were caught within the range of 0.6 to 1ºC (Fig. 4a).

There are no data on temperature preferences of the angry rockfish. Our insufficient observations showed that this species occurred in relatively warm waters (Table 1). In the catches, it occurred within a very narrow range of bottom temperatures of 3.1 to 3.55ºC (mean 3.41ºC).

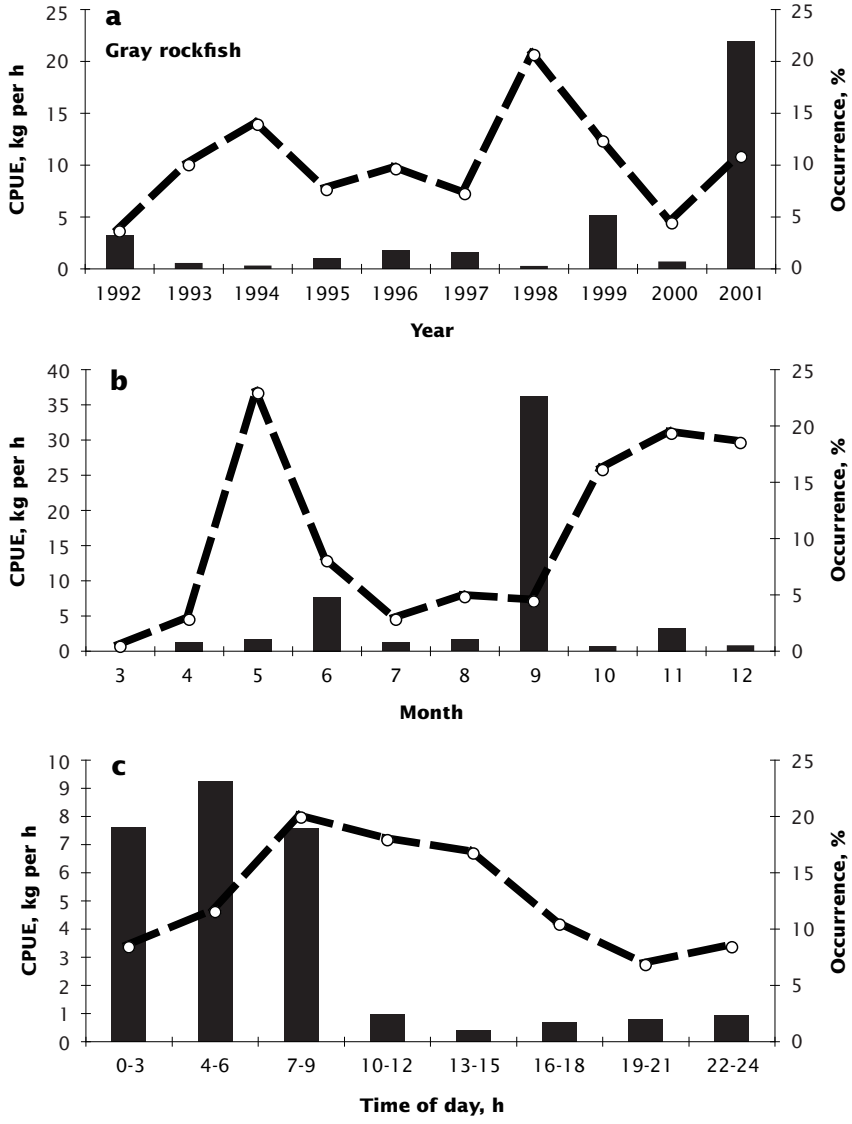


Figure 5. (a) Multi-annual, (b) seasonal, and (c) diurnal changes of catch rates and occurrence of gray rockfish in Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002 (bars are average catch, dashed line is occurrence).

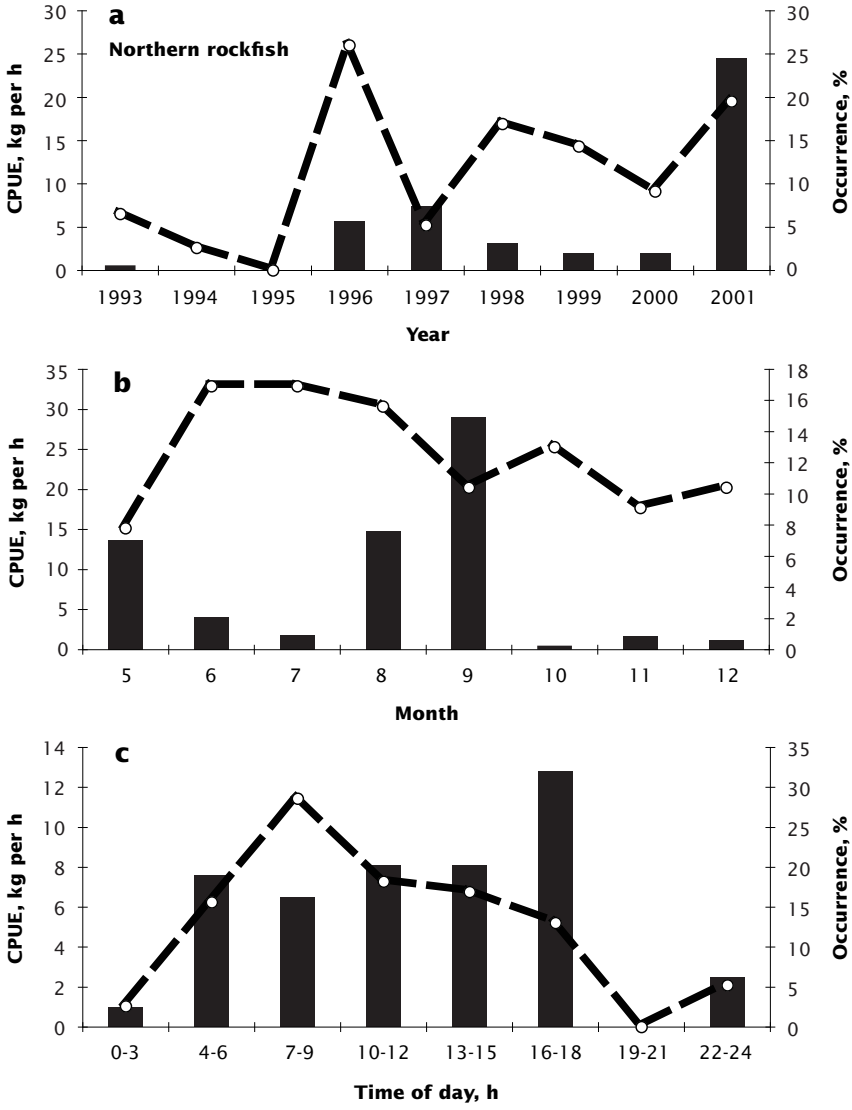


Figure 6. (a) Multi-annual, (b) seasonal, and (c) diurnal changes of catch rates and occurrence of northern rockfish in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002 (bars are average catch, dashed line is occurrence).

The preference by angry rockfish of bottom temperatures over 3ºC confirms earlier suggestions (Orlov et al. 1998) that this species penetrates this area from the south during seasonal or long-term warming only.

The temperature ranges at which the northern rockfish occurred off the bottom differ in various areas. According to data of Snytko (2001), they are 3.1-4ºC in the southeastern Bering Sea, 2.1-4.4ºC off the western Aleutians, 2.9-5.8ºC off the eastern Aleutians, and 4.1-5.3ºC in the western Gulf of Alaska. By comparison, in the Pacific waters off the northern Kurils and southeastern Kamchatka, this species occurred at considerably lower bottom temperatures that varied from –0.2 to 3.6ºC (mean 1.9ºC). At the same time, more than half the specimens were caught within the temperature range of 2.1-2.5ºC (Fig. 4b).

Multi-annual changes of occurrence and catch rate

The occurrence and catch rate of species varied during the year. For most of the study period, catches of gray rockfish were rather low (Fig. 5a). Its occurrence slightly increased in 1999 and reached a maximum in 2001. All the captures of angry rockfish occurred in 1998, 1999, and 2000 though there were only two records of this species in 2000. There were no captures observed of the angry rockfish during other years. The captures of the northern rockfish in the area surveyed prior to 1996 were incidental (Fig. 6a). After 1997 its catches were very low but rates increased dramatically in 2001. It should be noted that catch dynamics of gray and northern rockfishes are very similar. That may be related to long-term changes of thermal conditions in the study area and also to similar temperature preferences of both species. The captures of angry rockfish in the study area were registered in 1998-2000, when other rockfish species occurred only occasionally. In 2001 catch rates of gray and northern rockfishes increased while angry rockfish disappeared from the catches.

Seasonal changes of occurrence and catch rate

The catch rate and occurrence of rockfish species exhibit seasonal dynamics that may be associated with different phases of their life cycles. The maximum catches of gray rockfish in the study area were registered in June and September while its maximum occurrence was in May-June and October-December (Fig. 5b). The density of gray rockfish concentrations increases during the mating and larvae release periods, which in the southwestern Sea of Okhotsk occurred respectively in September-October and May-June (Panchenko 1996, Nemchinov 2001). In the northern Sea of Okhotsk gray rockfish releases its larvae from late June to early July (Kondratiev 1996) but according to other data (Chereshnev et al. 2001), it happens from the end of summer to the beginning of autumn. Thus, maximum catches of gray rockfish in the area surveyed in June and September are most probably associated with

mating and larvae release which occurred there in the same periods as in other regions. The existence of gray rockfish spawning may be evidence of a separate population in Pacific waters off the northern Kurils and southeastern Kamchatka.

The limited data on angry rockfish captures off the Kurils showed that this species occurred here predominantly during summer months (July-August), i.e. when near-bottom layers have maximum water temperatures. Its captures in November and December 2000 off the southern tip of the underwater plateau were probably related to a delay of migration of some fish, whereas the majority of gray rockfish had already moved back to the south.

Occurrence of northern rockfish during the year varied insignificantly though its maximum catches were registered in May and August-September (Fig. 6b). In the Gulf of Alaska maximum catches of this species occurred in July and October; off the Aleutians they are observed from March to May (Clausen and Heifetz 2002). According to published data the release of larvae in the Northeast Pacific occurs in spring (Love et al. 2002); in the Bering Sea it happens in April-May (Moiseev and Paraketsov 1961). The first catch peak is probably associated with spawning concentrations. There are no data on the period when the northern rockfish is mating. Judging from the catch rates, the mating of this species in the area surveyed most probably occurs in August-September when its catches are maximal. In the Gulf of Alaska mating probably occurs in October when northern rockfish form the densest aggregations.

Diurnal changes of occurrence and catch rate

The diurnal dynamics of catch rate and occurrence of these rockfishes probably reflect the changes of their distribution patterns during the day, which may be related to changes of fish behavior and physiological conditions and, as a consequence, the daily variability of fish availability for fishing gear. The maximum gray rockfish catches occurred from midnight to 9 am (Fig. 5c). Large catches during that period may reflect peculiarities of feeding behavior. Within the entire species range gray rockfish diet consists mostly of gelatinous plankton (jellyfish) and euphausiids (Kondratiev 1996, Chereshnev et al. 2001, Novikov et al. 2002). In the study area, the gray rockfish also ate mainly jellyfish and fishes. It is possible that the density of gray rockfish prey within the near-bottom layer is maximal from midnight until 9 am, and highest catch rates during this time period are related to increasing feeding activity of these fish.

The angry rockfish was registered in catches most frequently (59.4%) between 9 am and 6 pm. In Japanese waters this species feeds on crustaceans, squid, and fish (Nagasawa and Torisawa 1991). In the area surveyed it ate mysids and shrimps. It is known that the angry rockfish

during night hours goes up in the water column to feed (Nagasawa and Torisawa 1991). This is the probable reason for its higher catch rates during the light period in comparison with dark.

The maximum catches of northern rockfish were also observed during daylight from 4 am to 6 pm (Fig. 6c). The bulk of its diet within the entire range consists of copepods and euphausiids (Skalkin 1964; Mito 1974; Brodeur and Livingston 1988; Yang 1993, 1996), i.e., of crustaceans performing daily vertical migrations. In the study area, the stomachs of northern rockfish mostly contained copepods and euphausiids. Apart from these dietary components it consumed arrow worms (Chaetognatha), comb jellies (Ctenophora), nudibranchs (Nudibranchia), midwater squid *Galyteuthis phyllura,* and bigeye lanternfish *Protomyctophum thompsoni*. It seems that during dark hours the northern rockfish migrates for feeding from the bottom into the water column together with plankton, and its catches in this period decrease.

Length

The data on maximum length of the gray rockfish are controversial. Some authors believe it is 50 cm (Amaoka et al. 1995, Orr et al. 2000, Love et al. 2002, Novikov et al. 2002) while others suggest that this species attains 56 cm (Snytko 2001) and even 59 cm (Chetvergov 1998, Chereshnev et al. 2001, Mecklenburg et al. 2002). The size composition of species considered depends on fishing gear and differs in various areas. Off the southern Kurils, gray rockfish taken by gillnets varied in length between 33 and 50 cm with a mean length of 40.5 cm (Panchenko 1996). Fish caught off southeastern Kamchatka by longline were considerably larger; their maximum and mean lengths were 59 cm and 52.8 cm respectively. At the same time, longline catches taken off the Commander Islands contained significantly smaller gray rockfish (range 27-46 cm, with mean length 36.2-40.1 cm). Even smaller fish were found in bottom trawl catches taken off western Kamchatka where length varied between 11 and 51 cm with mean value of 31.3 cm (Chetvergov 1998). The smallest gray rockfish probably inhabits the northern Sea of Okhotsk where catches are represented by fish ranging in length between 8 and 38 cm, and predominately 20-28 cm (Kondratiev 1996, Chereshnev et al. 2001). In the study area, bottom trawl catches comprised gray rockfish individuals measuring 19-57 cm with mean length 44.78 cm (Fig. 7a). Fish sized 38-42 and 49-53 cm were most numerous. In bottom trawl catches off the western Kamchatka, gray rockfish of 23-29 and 33-39 cm predominated (Chetvergov 1998). Thus, size structures of species considered in the area surveyed and off western Kamchatka differ considerably. This confirms our earlier conclusions that the gray rockfish is a permanent dweller of Pacific waters off the northern Kurils and southeastern Kamchatka and doesn't migrate there from

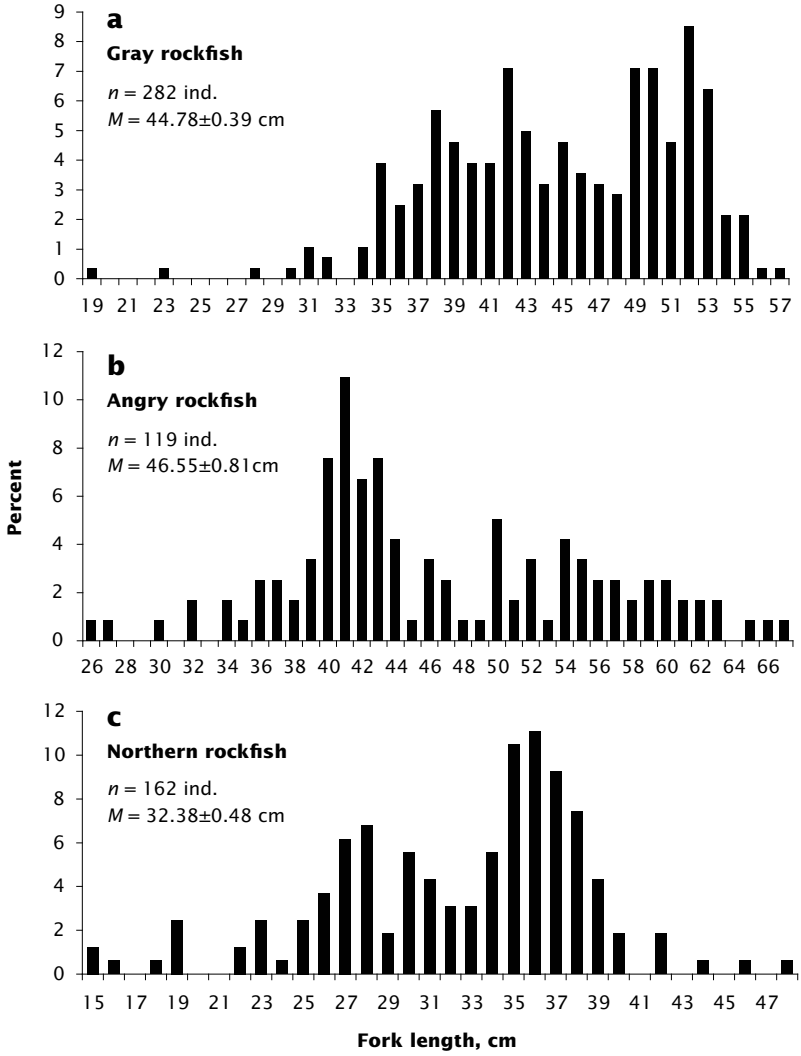


Figure 7. Length frequencies of (a) gray, (b) angry and (c) northern rockfishes in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002 (*n* = number of fish measured, *M* = mean length).

the Sea of Okhotsk. In longline catches taken adjacent to our areas off southeastern Kamchatka and the Commander Islands, gray rockfish of 47-57 cm and 37-43 cm size classes, respectively, were most abundant (Chetvergov 1998). This indicates significant similarity of size composition of fish in all three above-mentioned areas.

Previously, angry rockfish were noted to attain 60 cm in length (Masuda et al. 1984, Nagasawa and Torisawa 1991). Our catches were represented by fish of lengths between 26 and 67 cm with mean value 46.55 cm, and most individuals sized 40-44 cm (Fig. 7b).

Maximum size of the northern rockfish has been variously reported as 40 cm (Orr et al. 2000), 41 cm (Kramer and O'Connell 1995, Mecklenburg et al. 2002), 42 cm (Snytko 2001), and 48 cm (Clausen and Heifetz, Love et al. 2002). Size composition of this species differs considerably among different areas. On the whole, the fish from the Gulf of Alaska are notably larger than those off the Aleutians (Yang 1993, 1996; Clausen and Heifetz 2002). The smallest northern rockfish inhabits the southern Bering Sea (individuals sized 16-17, 20-23, and 26-27 cm prevalent, mean length 24.4 cm); off the Aleutians specimens with length 27-32 cm (mean 30.2 cm) are most numerous in catches; fish from the eastern Bering Sea (mean length 34.1 cm) are slightly larger; the largest northern rockfish are taken in the Gulf of Alaska where the mean length is 37.3 cm and most abundant are specimens having length 35-40 cm (Bakkala et al. 1992, Harrison 1993, Martin 1997). Catches in the study area were represented by fish with length ranging from 15 to 48 cm with a mean value of 32.4 cm. Individuals of two size groups, 27-31 and 34-38, cm (Fig. 7c) were most numerous, i.e., similar to the length classes in the Gulf of Alaska and off the Aleutians

Body weight

There are few data on maximum body weight of these species. It is believed gray rockfish may attain 1.9 kg (Chereshnev et al. 2001). In longline catches off southeastern Kamchatka gray rockfish body weight ranged from 0.6 to 2.95 kg (mean 2.15 kg) with most fish weighing 1.25-1.75 kg (Chetvergov 1998). The gray rockfish taken by bottom trawls in the northern Sea of Okhotsk and off western Kamchatka were significantly lighter with body weights of 5.2-874 g (Kondratiev 1996) and 20-950 g (Chetvergov 1998). Near the Commander Islands longline catches were represented by fish with body weights of 0.4-1.8 kg with mean values of 0.9-1.2 kg (Chetvergov 1998). In the study area, the gray rockfish body weight was 0.140-3.3 kg with mean 1.8 kg (Table 1). Taking into account differences between fish sizes of trawl and longline catches, it is possible to conclude that our data on body weight from the area under study is very close to those from southeastern Kamchatka waters (Chetvergov 1998).

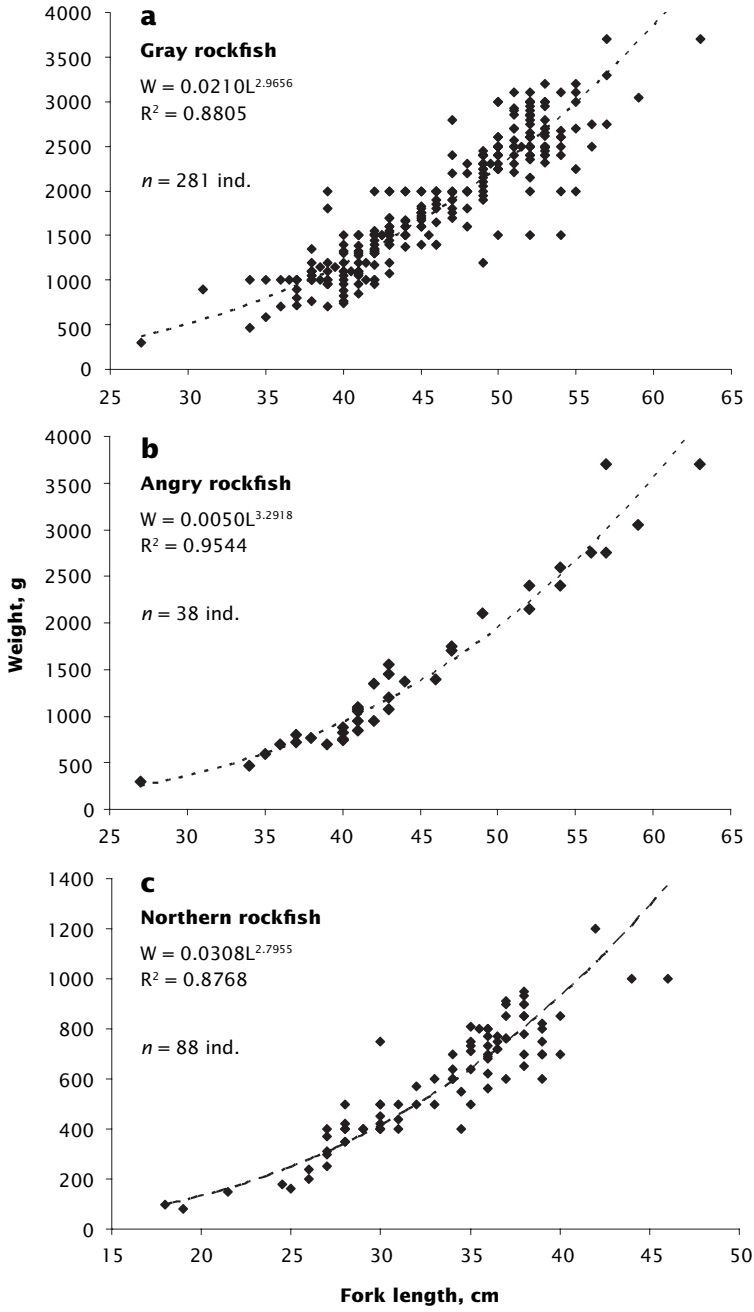


Figure 8. Length-weight relationships of (a) gray, (b) angry, and (c) northern rockfishes in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka, 1992-2002 (*n* = number of fish measured).

Published data on body weight of the angry rockfish is lacking. In the study area its individuals had body weights of 0.47-3.7 kg with mean 1.46 kg (Table 1).

It is known that the northern rockfish may attain weights of 1.8 kg (Snytko 2001). Gulf of Alaska fish are distinguished by maximum body weight; the mean values varied from 0.68 to 0.95 kg for different years (Martin 1997, Clausen and Heifetz 2002). Individuals taken in the eastern Bering Sea are characterized by a somewhat smaller body weight (mean 0.676 kg) but smallest northern rockfish (mean value range 0.35-0.59 kg in different years) are caught off the Aleutian Islands (Bakkala et al. 1992, Ronholt et al. 1994, Clausen and Heifetz 2002). In the area surveyed the species in question had body weights range 80-1200 g with a mean of 602.7 g (Table 1), and according to this pattern fish taken here and off the Aleutians were quite similar.

Length-weight relationship

There are a few published data regarding length-weight relationships of the three rockfish species. This relationship allows judging the character of fish growth (Zotina and Zotin 1967) while the power coefficient of its equation may vary among fish belonging to different populations (Vinberg 1971). There are no published data on length-weight relationships for the gray rockfish. In the study area length and weight of species considered had a well-pronounced relation ($R^2 = 0.881$). The power coefficient of this equation proved to be close to three (Fig. 8a), which is characteristic of the majority of aquatic animals (Vinberg 1971).

There are no data on length-weight relationships of the angry rockfish as well. Off the Kurils this relationship had a high correlation ($R^2 = 0.954$) and the power coefficient was notably larger than three (Fig. 8b), which may be evidence of different growth patterns of both species described.

There are some data on length-weight relations of the northern rockfish from off the Aleutians (Ronholt et al. 1994) and the Gulf of Alaska (Martin 1997). In the Aleutians the linear coefficients depending on the study year ranged from 0.0151 to 0.0314 while the power ones varied from 2.78 to 2.996. In the Gulf of Alaska respective values were 0.0124 and 3.035. In Pacific waters off the northern Kurils and southeastern Kamchatka the relationship considered was quite well expressed ($R^2 = 0.877$). Linear and power coefficient of respective equations (Fig. 8c) were very similar to those from the Aleutian Islands waters.

Sex ratio, sexual dimorphism in sizes, stomach fullness

It is known that one male gray rockfish will mate with several females (Chereshnev et al. 2001). Such a spawning feature suggests numerical predomination of females in populations. However, in the majority of areas male gray rockfish are more abundant than females. Off the

southern Kurils the sex ratio was 68% vs. 32% (Panchenko 1996); in the northern Sea of Okhotsk it was 65% vs. 35% (Kondratiev 1996); off the southeastern Kamchatka it was 69.5% vs. 30.5% (Chetvergov 1998). Near the western Kamchatka coast the sex ratio of the gray rockfish is almost equal while off the Commander Islands females are more abundant and prevailed over males 59% vs. 41% (Chetvergov 1998). In the study area, similar to many other parts of its range, female gray rockfish were also less abundant than males (33.9% vs. 66.1%).

It is also known that male gray rockfish in most areas are larger than females (Kondratiev 1996, Nemchinov 2001). Thus off western Kamchatka mean lengths and weights of males were 40.1 cm and 1.2 kg, and mean lengths and weights of females were 36.2 cm and 0.9 kg. In the area surveyed males were also larger than females. Mean values of body length and weight were 48.82 and 41.65 cm and 2,286.6 and 1,415.6 g respectively.

Feeding intensity of the gray rockfish during the year is rather low; average stomach fullness index off the southern Kurils were 0.9 in June, 1.4 in July, and 1.2 in October (Nemchinov 2001). In the study area stomach fullness of the species considered was even lower (SFI 0.16 on average). Since the maximum catches were taken in September (mating period), low feeding activity is probably related to almost no feeding in this time. It should be noted that female stomach fullness (SFI 0.47 on average) was slightly higher than in males (SFI 0.03 on average).

Sex ratio and sexual dimorphism of the angry rockfish are unstudied. In Pacific waters off the northern Kurils the number of males and females in catches was close to equal (51.6 vs. 48.6% respectively). Male angry rockfish were notably larger than females. Their mean lengths and weights were 45.88 and 42.93 cm and 1,663.1 and 1,248.7 g respectively. The feeding intensity of the angry rockfish during summer months was quite low. The average stomach fullness index was 0.67; during the same time females consumed larger amounts of food (average SFI 0.93) in comparison with males (average SFI 0.33).

According to published data (Westrheim and Tsuyuki 1971, Clausen and Heifetz 2002), in the Gulf of Alaska the sex ratio of northern rockfish in catches is almost equal with minor female prevalence (50.8 vs. 49.2%). Off the Aleutians predominance of females is considerably greater, 57.1 vs. 42.9% (Clausen and Heifetz 2002). The northern rockfish sex ratio in the area surveyed was quite similar to that described above (59.3% females and 40.7% males).

Some authors (Westrheim and Tsuyuki 1971) suggest a similar male and female size composition in the Gulf of Alaska, while others (Clausen and Heifetz 2002) noted greater female length compared to males: 34.3 and 33.0 cm in the Gulf of Alaska and 30.8 and 29.1 cm off the Aleutians. In the study area males were slightly longer than females (34.1 and 33.9 cm) though females were notably heavier than males (672.5 and

617.3 g). The northern rockfish fed little during the study period; the average value of SFI was 1.0. During the same time, females consumed food somewhat more intensively (average SFI 1.33 in females vs. 0.55 in males).

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Preliminary Results of Trans-generational Marking of Larval Marine Fish Otoliths

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Abstract

Dispersal, connectivity, and retention of larval fish are key ecological processes affecting populations of marine fishes. Quantification of these parameters is vital for effective use of marine reserves and other resource management options, and yet these determinations are among the greatest challenges facing marine ecologists today. A major impediment is the lack of a reliable technique for marking extremely small marine fish larvae. Extensive testing with captive rockfishes (*Sebastes* spp.) and surfperches (Embiotocidae) has validated that trans-generational mass marking of larvae in vivo occurs with the transfer of elemental strontium to otoliths of developing larvae via matrotrophic viviparity. The mark is induced by intramuscular injection of up to 30,000 ppm strontium chloride into gestating females in situ. The marks are permanent, and can provide unique identifiers for cohort and location. Laser ablation inductively coupled plasma mass spectrometry detects marks in juvenile otoliths as a zone of significantly increased ratio of strontium to calcium. The first field test of trans-generational marking used brown rockfish (*S. auriculatus*) on Pt. Heyer reef in Puget Sound, Washington. Post-settlement juveniles were captured for otolith recovery only from Pt. Heyer reef. To date, 127 otoliths from marked-cohort juveniles have been analyzed and one strontium-marked otolith recovered.

Introduction

Understanding the patterns of larval marine fish dispersal that result in either connectivity between distant populations, or retention in local populations, or both, is key to understanding a host of ecological factors that influence populations of marine fishes. The consequences of incorrect predictions about distant larval dispersal and population connectivity, versus local retention, can have profound implications for global, regional, and local approaches to marine fish management (Roberts 1997, Palumbi 1999, Cowen et al. 2000, Lockwood et al. 2002, Warner and Cowen 2002, Botsford et al. 2003). This information is also vital for effective resource management interventions in these natural processes, such as marine reserves, that are designed to sustain, rebuild, or enhance the populations. Some current management approaches emphasize the use of marine reserves to protect habitat, biodiversity, and spawning biomass in order to enhance progeny output that will contribute to local and/or regional stocks. Use of marine reserves assumes that natural patterns of larval dispersal will accomplish these goals. However, the dispersal of larval fish is among the least understood aspects of marine fish ecology, and the extent of larval movement away from source populations is rarely known.

The assumption, that populations of marine fish operate as "open" systems and larval recruitment into a population is independent of local production, is being reconsidered in light of increasing evidence of larval fish retention near source populations (Jones et al. 1999; Swearer et al. 1999, 2002; Jones et al. 2005). Retention of larvae is also supported by evidence that many marine fish larvae have the ability to detect and respond to environmental cues by altering their dispersal patterns, and these larvae should not be considered as passively dispersed particles (Kingsford et al. 2002). If the recruitment of marine fish larvae and pelagic juveniles represents local retention, then the design of effective marine reserves must include preservation of retention areas as well as adult habitats (Warner and Cowen 2002).

Recent applications of molecular genetic techniques (Strathmann et al. 2002, Swearer et al. 2002, Buonaccorsi et al. 2004, Hauser et al. 2007), and mass spectrometric analysis of otolith microstructure and microchemistry (Jones et al. 1999, Swearer et al. 1999, Guido et al. 2004, Miller and Shanks 2004, Warner et al. 2005), have improved knowledge of larval fish dispersal patterns. However, these techniques yield estimates of larval dispersal or retention on broad geographical and population-level scales and seldom provide information on exact larval-source locations (Hellberg et al. 2002). Definitive information is needed on larval fish dispersal that is based on direct measurements that connect the exact origins of the larvae with the subsequent recruitment of juveniles to specific locations. Such measurements are key to determining the connectivity of populations of marine fishes, and the

effects of larval retention and dispersal processes on the variability of this connectivity.

Quantification of dispersal and retention rates is a major hurdle in marine ecological studies that has been described as "one of the greatest challenges facing marine ecologists today" (Swearer et al. 2002). The difficulties in achieving this goal for marine fishes are compounded by extremely small pelagic larvae that suffer high mortality rates and that may disperse over large areas for months. Current analytical techniques are inadequate to mark the large number of larvae needed to achieve mark recoveries at later life stages (Swearer et al. 2002, Thorrold et al. 2002, Miller and Shanks 2004). The only unambiguous way to quantify dispersal and retention rates is through the recovery of artificial marks or tags that can be used to track larvae from specific origins to ultimate destinations (Jones et al. 1999, Thorrold et al. 2002).

Thorrold et al. (2002) note that the difficulties in marking large numbers of larvae may be alleviated by having "a tag that could be transferred from the female to developing eggs or embryos." In this study, we describe and test a trans-generational marking technique that uses natural processes in viviparous fishes (*Sebastes* spp., Embiotocidae) to transfer an artificial body burden of naturally occurring elemental strontium (Sr) from gestating females to their larvae. The in vivo exposure of the larvae to Sr levels well in excess of ambient induces a permanent Sr mark in the otoliths of the larvae prior to parturition.

Methods

Trans-generational marking

In this study, trans-generational marking uses intramuscular injections of elemental Sr, in a strontium chloride ($SrCl_2$) solution, in late-stage gestating viviparous female rockfishes (*Sebastes* spp.) and surfperches (Embiotocidae) to elevate the Sr level in the ovarian fluid. Strontium is a naturally occurring element in seawater that is found in all bony structures in marine fishes. The conduit for transferring the Sr to the larvae in vivo is the natural matrotrophic viviparity in these fishes, whereby the females supply nutrition to the developing embryos (Turner 1938, 1952; Dygert and Gunderson 1991; Shimizu et al. 1991). Injection dosages were 1 ml per 500 g body weight of 30,000 ppm $SrCl_2$ in an isotonic solution (0.1125 M $SrCl_2 \cdot 6H_2O$). Injections were intramuscular; half of the dose was injected into each side of the fish, near the proximal margin of the spiny dorsal between the 5th and 7th rays. Extensive testing with captive brown rockfish (*S. auriculatus*), kelp perch (*Brachyistius frenatus*), and shiner perch (*Cymatogaster aggregata*) confirmed that trans-generational mass marking of the larvae in vivo results in otoliths with permanent marks (R. Buckley and E. Volk, Washington Department of Fish and Wildlife (WDFW), unpubl. data).

Field trials of trans-generational marking could not proceed until the U.S. Food and Drug Administration (FDA) determined that injections of elemental Sr in adult rockfish, at dosages significantly higher than ambient, would not pose a threat to human health if injected rockfish were consumed post-injection. Pivotal research on Sr depuration rates in kelp rockfish (*S. atrovirens*) answered FDA concerns (D. Casper, M. Carr, P. Raimondi, and N. Grant, University of California Santa Cruz, unpubl. report to FDA), and in spring 2004 the FDA granted regulatory discretionary authority to inject and release brown rockfish, kelp perch, and shiner perch. Field trials were designed to evaluate both the utility of applying trans-generational marking procedures in situ under field conditions, and the recovery of Sr-marked otoliths from post-settlement juveniles.

Rockfish field trial

The field trial was conducted at Pt. Heyer reef, located in central Puget Sound, Washington, on the eastern shoreline of Vashon Island (47º25.2'N, 122º25.6'W). This insular reef was constructed of high-relief quarry rock and large concrete material in 1983 (2,500 m^2; Hueckel and Buckley 1987), and modified in 1991 with the addition of small rock (8-10 cm diameter; 3,000 m^2; West et al. 1995) in a low-profile design to create nursery habitat for juvenile rockfishes. The total reef coverage of 5,500 m^2 encompasses a bottom area of 7,000 m^2, and depths of –4 m to –36 m mean-lower-low-water (MLLW) on a moderately sloping sand and gravel substrate. Pt. Heyer reef is separated from other rock-reef habitat by >7 km in all directions.

Pt. Heyer reef typically had an adequate number of reproductive-sized adults (approximately 200-250 fish >20 cm total length (TL); WDFW, unpubl. data) for experimental purposes. Females with an enlarged abdomen, indicating late-stage gestation, were captured during spring-summer 2004 on the reef by divers using 30 cm diameter hand nets with 2 mm red mesh, and transferred to a holding bin placed on the bottom at capture depth. The holding bin was moved, if necessary, to a depth of 10 m for injection operations to optimize diver bottom-time constraints.

Injections of $SrCl_2$ were applied in situ within 1-2 hours post-capture in order to avoid subjecting the fish to barotraumas and to minimize handling stress. Fish were measured to the nearest cm TL to estimate weight from a length-weight table, and the upper lobe of the caudal fin was clipped to obtain a tissue sample for genetic analyses in a companion study (see Hauser et al., 2007). The caudal fin-clip also temporarily marked the injected females to avoid recapture. Injections were administered using a 1 ml dosage-adjustable, self-refilling syringe fitted with a 21-gauge hypodermic needle. The syringe was coupled with surgical

tubing to a 1.8 L hydration reservoir (Platypus™) filled with $SrCl_2$ solution. Injected fish were immediately released onto reef habitat.

Juvenile brown rockfish (i.e., young-of-the-year) were captured on Pt. Heyer reef using 15-30 cm diameter hand nets with 2 mm red mesh. Tissue samples for genetic analyses (see Hauser et al. 2007) were taken from the juveniles in the field. Otoliths (sagittae) were recovered in the laboratory, cast in resin blocks, and prepared for mark recovery analysis as described in Volk et al. (2000). Mark recovery analyses were conducted using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS; see Miller and Shanks 2004), and marked otoliths were identified by a zone that had a substantially increased ratio of strontium to calcium (Sr:Ca) near the core of the otolith.

Fecundity analysis

Gestating brown rockfish (n = 6, range 21-37 cm TL) captured in June 2004 on central Puget Sound reefs provided ovary samples with developing larvae from which estimates of fecundity were made by extrapolating weights of enumerated subsamples of larvae from each ovary to the total weight of the ovary. A length-fecundity relationship was estimated using linear regression (Neter et al. 1990).

Results

In 2004, injections of $SrCl_2$ were administered to 31 gestating brown rockfish that ranged in size from 21 to 31 cm TL and averaged 25 cm TL (Table 1). The six gravid brown rockfish used for fecundity estimates encompassed the size range of the 31 injected rockfish, and provided a preliminary length-fecundity relationship for estimating the number of larvae in the rockfish injected with $SrCl_2$ (Adj. $R^2 = 0.93$, $F_{05(1,4)} = 71.8$, $p = 0.001$). The estimated numbers of developing larvae in the injected rockfish ranged from 3,506 in the 21 cm TL female to 138,304 in the 31 cm TL female. Approximately 1.7 million larvae were exposed to Sr in vivo (Table 1), assuming 100% efficacy of the treatment.

In September and October following the summer parturition period for brown rockfish, fish that were ≤100 mm appeared in nearshore reef habitat (i.e., depths of 8-18 m). It was assumed that fish of this size range on Pt. Heyer reef had recently recruited to the reef (Fig. 1). This size-group also exhibited the "typical" new recruit behavior of being closely associated with, and often hidden in, small-sized crevice habitats in the rock substrate (see Buckley 1997). We collected 2004 cohort Pt. Heyer juveniles (n = 325, range 45-100 mm TL) for otolith samples from October 2004 through June 2005.

Limitations in the availability of the LA-ICPMS equipment resulted in Sr analysis of only 127 of the 325 otoliths. Those analyses determined that 126 of the otoliths had Sr:Ca ratios across the otolith that was

Table 1. Data for 31 gravid brown rockfish injected with 30,000 ppm $SrCl_2$ at Pt. Heyer reef in 2004, to induce in vivo trans-generational Sr marks in the otoliths of developing larvae. See text for length-fecundity estimation.

Capture date	Estimated fecundity	Total length (cm)	Capture depth (m)	$SrCl_2$ injected (cc)
May 19	124,824	30	12.8	0.96
May 19	57,426	25	12.2	0.96
May 19	57,426	25	13.1	0.96
July 9	84,385	27	7.0	0.57
July 9	57,426	25	10.7	0.57
July 9	57,426	25	10.1	0.57
July 9	70,905	26	9.8	0.57
July 9	70,905	26	10.1	0.57
July 9	57,426	25	6.4	0.57
July 9	30,466	23	11.3	0.57
July 9	70,905	26	10.7	0.57
July 9	70,905	26	10.7	0.57
July 9	16,986	22	7.0	0.57
July 12	16,986	22	13.7	0.57
July 12	70,905	26	15.8	0.57
July 12	16,986	22	18.6	0.57
July 12	57,426	25	16.2	0.57
July 12	3,506	21	13.7	0.57
July 12	57,426	25	15.2	0.57
July 12	57,426	25	14.6	0.57
July 12	57,426	25	13.7	0.57
July 12	57,426	25	11.9	0.57
July 14	30,466	23	9.8	0.57
July 14	16,986	22	17.4	0.57
July 14	16,986	22	14.6	0.57
July 15	16,986	22	7.0	0.57
July 15	16,986	22	6.1	0.57
July 15	30,466	23	8.5	0.57
July 20	97,865	28	7.6	0.96
July 20	138,304	31	15.2	0.98
August 8	111,345	29	13.7	0.98
Mean	54,817± 6010 (SE)	24.8	11.4	
Minimum	3,506	21	6.1	
Maximum	138,304	31	18.6	
Total	1,669,314			

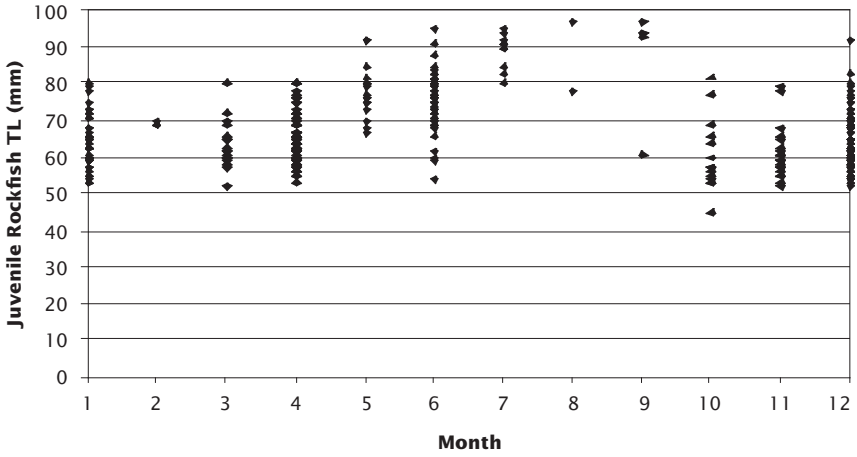


Figure 1. Length frequency distribution, by month, of 2004 cohort juvenile brown rockfish ≤100 mm total length (n = 359), collected on Pt. Heyer reef, May 2004 through June 2005. (Note: Collection months are numbered as January = 1 to December = 12, and juvenile rockfish are grouped by month regardless of collection year.)

consistent with exposure to ambient concentrations of these elements. Those otoliths were classified as non-Sr-marked otoliths (Fig. 2A). One otolith also had strong spikes in the Sr:Ca ratio on either side of the core region, which demonstrated that the larva had been exposed to a >200% increase in Sr for a short period during early development (Fig. 2B). This otolith was classified as having a definite Sr mark. The two spikes in the Sr:Ca ratio represented the laser passing through a circular band (i.e., a growth increment) around the otolith core that contained an elevated concentration of Sr.

The Sr-marked juvenile brown rockfish was 60 mm TL when it was collected on January 27, 2005. A companion genetic study to determine parent-progeny relationships of brown rockfish on Pt. Heyer reef determined that the Sr-marked juvenile was the progeny of a 22 cm TL female captured on Pt. Heyer reef on July 9, 2004, and injected with $SrCl_2$ solution as part of this study (see Hauser et al. 2007). The juvenile was collected 202 days post-injection. During the injection process, that female released a small number of premature but well developed larvae, indicating that parturition would likely occur soon and that the developing larvae would be exposed to high Sr levels in vivo for only a short period of time.

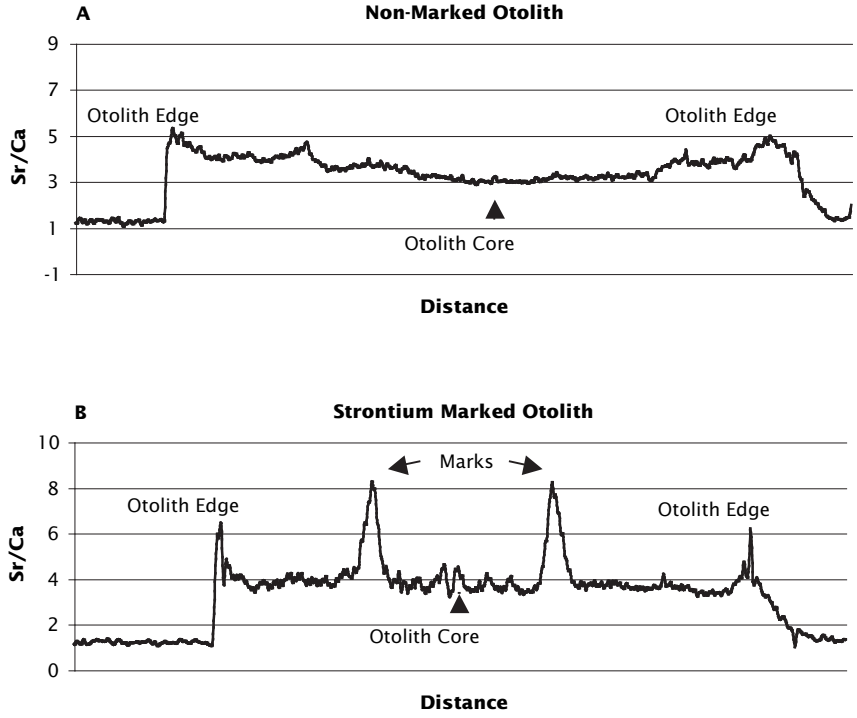


Figure 2. LA-ICPMS analysis of 2004 cohort juvenile brown rockfish otoliths from Pt. Heyer reef. A: Non-Sr-marked otolith; B: Sr-marked otolith. (Note: The laser moves across the otolith (from left to right) recording Sr:Ca ratios in the matrix of the otolith. A: Sr:Ca ratios show exposure to ambient concentrations of these elements; B: Sr:Ca ratios show marks from exposure to high Sr concentrations for a short period early in larval development, and exposure to ambient concentrations of these elements over the remainder of the otolith.)

Discussion

Rockfishes and surfperches are ecologically important species in temperate marine reserves, and it is critical to quantify the dispersal and retention rates of their larvae to determine the efficacy of current marine reserve designs and locations. Trans-generational mass marking provides the first method for using a specific manipulation of gestating viviparous fishes to induce a specific mark in the otoliths of the larvae in vivo. The larvae are born carrying a benign permanent artificial "tag" that can be used to identify different cohorts and marking locations over the life of the fish.

The field trial with brown rockfish demonstrated the utility of this method when applied in situ, and that it is likely applicable to all rockfishes. The recovery of one Sr-marked otolith from 127 juveniles further demonstrated that trans-generational marks in larvae can be recovered from post-settlement juveniles. These validations are reinforced when the relatively small sizes of the experimental groups are considered. Only 31 brown rockfish females were injected, and approximately 1.7 million larvae were exposed to Sr in vivo assuming 100% efficacy. The latter is not an enormous number considering the potentially high natural mortality rates of rockfish larvae, and that post-settlement juveniles were the earliest development stage examined for Sr marked otoliths. The underwater injection protocols likely enhanced the potential for success by minimizing stress to the females, and reducing possible mortality or alteration of behavior due to handling. It was common to see females on the reef that had been injected with $SrCl_2$ many days earlier (identified by the genetic sample fin-clip in the upper lobe of the caudal) demonstrating the same behaviors as non-injected fish.

The field trial did not prove that all the injected females proceeded to term and released viable larvae. Validating these parameters would require tracking injected females and observing parturition of live larvae under natural conditions. This would be an extremely difficult task. The next best, albeit indirect, proof that trans-generational marking with $SrCl_2$ does not affect the development or survival of viviparous fish larvae comes from studies done with rockfishes and surfperches held in captivity to develop the marking technique. Captive brown rockfish commonly progressed through parturition and released live larvae after being injected with $SrCl_2$ at 30,000 ppm, and larvae could be reared for several weeks. However, the small size of the larvae (5-6 mm TL) precluded definitive analyses of the otoliths to verify exposure to Sr during development, as well as accurate assessments of meristics for comparisons of larval development in control and experimental groups. Better information can be gained from kelp perch, which release "early-stage" juveniles (35-45 mm TL) at parturition that readily feed in captivity and can be reared. Juveniles from female kelp perch injected

with $SrCl_2$ at 30,000 ppm during gestation had strong Sr marks in their otoliths (Buckley et al., WDFW, unpublished data). Also, comparisons of meristics of these juveniles from control and experimental groups detected no significant differences in paired structures within groups, or in single and paired structures between groups. These comparisons are commonly used indicators of abnormal development.

In the field trial it was assumed that all of the larvae developing in the ovary of a female injected with $SrCl_2$ are adequately exposed to the high Sr levels, both in duration and at concentrations to induce a detectable mark in the larval otolith. The physiological work on ovarian fluid dynamics and related larval development needed to validate this assumption remains to be done. However, Sr-marking the otoliths of early development stages of other species has demonstrated that a brief exposure to a relatively low concentration of Sr is sufficient to induce a detectable mark in the otolith (Schroder et al. 1995).

Given these potential sources for reduction in the number of Sr-marked juvenile brown rockfish available for recovery, it is an even more remarkable and conservative result that one mark was found in 127 otoliths. These potential reductions were offset somewhat (although to an unknown degree) by the potential for local larval retention and self-recruitment at. Pt. Heyer reef. The configuration of the shoreline, tidal current gyres, and prevailing wind directions in the area may have created good conditions for retention of pelagic larvae. The potential for recruitment of brown rockfish larvae back to Pt. Heyer habitat is also enhanced if the late-stage larvae and early stage pelagic juveniles have the ability to alter their dispersal patterns and actively seek rocky-reef settlement habitat (see Kingsford et al. 2002).

More juvenile brown rockfish otoliths from Pt. Heyer reef, and from other locations, need to be analyzed, and more Sr-marked otoliths recovered, before the rate of local retention of larvae at Pt. Heyer can be determined. However, this preliminary field trial represents the first known recovery of a trans-generationally marked fish from the wild. This technique shows great potential for providing direct assessments of local retention and dispersal in marine fish larvae. Quantification of these parameters is critical for the marine ecological studies needed to design effective systems of marine reserves.

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Genetic Identification of Progeny of Reef-Resident Brown Rockfish (*Sebastes auriculatus*)

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Abstract

The extent of larval retention and natal homing in demersal fish is a topic central to the design and the efficacy of marine protected areas (MPAs). Unfortunately, little is known about effective larval dispersal in many marine species. The duration of the pelagic phase in many species suggests extensive dispersal, and population genetic studies indicate large-scale exchange of migrants, though there is also recent evidence for surprisingly limited realized dispersal. Here, we use genetic markers (microsatellites) to identify the offspring of resident adult brown rockfish (*Sebastes auriculatus*) among incoming settling juveniles on an isolated artificial reef at Point Heyer in Puget Sound, thus directly estimating rates of self-recruitment on the reef. Due to low marker variability, unambiguous identification of these offspring from empirical data was not possible. Nevertheless, comparison between parent-offspring matches in observed and simulated genetic data suggested that self-recruitment was less than 10%. One of the juveniles genetically matching an adult was confirmed as its offspring by larval otolith marking, which confirms that self-recruitment does occur. Our data suggested

some, but limited, self-recruitment, that corresponded well to expectations at this scale from mean dispersal distances in brown rockfish.

Introduction

The extent of dispersal in marine species has attracted great interest among ecologists, evolutionary biologists, and resource managers alike, not only because data on dispersal and retention mechanisms provide powerful insights into the distribution, phylogeography (Feral 2002), and evolution of marine species (Palumbi 1996, Lessios et al. 2001), but also because assumptions about self-recruitment of marine stocks underlie many of the commonly used strategies in fish stock assessment (Cowan and Shaw 2002) and conservation (Planes et al. 2000). With the emphasis on marine protected areas (MPAs) as a tool for marine conservation, the question of realized dispersal of pelagic larvae has found renewed significance, because the function of MPAs in a regional context depends critically on the demographic exchange between the MPA and surrounding areas (Botsford et al. 2003, Palumbi 2003). At one extreme, retention of all life history stages within an MPA negates any positive effects on surrounding areas, while at the other extreme, total export of larvae or juveniles from the MPA may limit the conservation value of the protected area (Palumbi 2003). Some information on realized dispersal from MPAs is therefore required; and, although data on adult migration are accumulating (Pittman and McAlpine 2003), little is known about the effect of larval dispersal, which most likely dominates the level of demographic connectivity of protected areas with surrounding regions.

Unfortunately, there is little information on realized dispersal of marine larvae, and most estimates have been derived indirectly by inferences from current speeds, larval duration, or the genetics of adult populations (Bohonak 1999, Palumbi 2003). Such estimates are inherently imprecise; and, although cross-species correlations between genetic population differentiation (estimating migratory exchange) and larval duration could be demonstrated (e.g., Doherty et al. 1995, Bohonak 1999), the predictive value of such indirect inferences for MPA design remains limited. Furthermore, while some more direct evidence, such as the occurrence of larvae of coastal species in the open ocean (Scheltema 1986) and the rapid spread of marine invasive species with pelagic larvae (e.g., green crab, *Carcinus maenas*, Geller 1994) clearly demonstrate the occurrence of long-distance dispersal, its frequency and thus ecological significance in the short term, especially for MPA design, remains questionable (Palumbi 2003).

Indeed, recent evidence from larval biology suggests that long distance dispersal, although important evolutionarily (Strathmann 1978, Duda and Palumbi 1999), may be rare (Palumbi 2001) and that at least

some of the recruitment in demersal fish and benthic invertebrates may stem from local sources. Oceanographic features such as currents or eddies play an important role in dispersal and retention of pelagic larvae and may also strongly affect larval mortality (Bailey et al. 1997, Withler et al. 2001). Furthermore, behavioral mechanisms, such as vertical migrations exploiting currents at different depths, can greatly influence the direction and extent of horizontal advection (Bilton et al. 2002). Evidence for localized self-recruitment comes from unexpected genetic subdivisions in marine species (Avise 1992, Taylor and Hellberg 2003), the persistence of demersal fish with pelagic larvae on isolated oceanic islands (Hourigan and Reese 1987, White 1998), and information on larval distribution (Bailey et al. 1997, Hay and McCarter 1997) and behavior (Bilton et al. 2002). However, although such evidence suggests predominantly localized recruitment, the quantification of larval export vs. self-recruitment, which is so important for MPA design, remains elusive.

Two major approaches to the estimation of larval dispersal are particular noteworthy; both have striking results, but they also have some complications. First, chemical signatures within the otoliths, either natural or artificial, can be used to track down the origin of juvenile fish. For example, by marking eggs of coral reef damselfish, *Pomacentrus amboinensis*, with tetracycline, a compound producing fluorescent marks in larval otoliths, Jones et al. (1999) demonstrated that 15-60% of larvae originated from the local adult population on Lizard Island, Great Barrier Reef (about 20 km^2 area). Although that paper clearly demonstrated a relatively high degree of self-recruitment, the confidence limits of the quantitative estimate were wide, mainly due to the large size of the adult population, which limited the proportion of marked eggs to 0.5-2%. A similar approach that exploited natural differences in otolith microchemistry was used to estimate self-recruiting rates of 60-81% to natal spawning sites in weakfish (*Cynoscion regalis*), an estuarine spawning fish in the eastern United States (Thorrold et al. 2001). The estimates of self-recruitment were more precise for weakfish, though the technique relied on differences in chemical composition of the water in natal habitats and may have been limited to estuarine species or more large-scale investigations.

The second main approach used for the estimation of effective larval dispersal is based on genetic differentiation among populations. Most genetic studies find only slight, if any, genetic differentiation among populations of marine species, which greatly complicates the interpretation of data in an applied context, because populations that exchange very few migrants (<10 individuals per generation) cannot be distinguished from a single larger randomly interbreeding population. Under such circumstances, classical population genetic analyses based on Wright's F_{ST} statistic are inadequate to estimate dispersal on

ecological timeframes (Waples 1998). However, new approaches to data analysis that used more realistic models now allow the estimation of mean dispersal distances from low but significant genetic differentiation (Palumbi 2003). Available genetic data suggest mean dispersal distances of 25-150 km in many marine invertebrate and fish species, an estimate that is consistent with observations from invasive species (Shanks et al. 2003). Although this approach revolutionized our perception of large scale or even ocean-wide random interbreeding, it is limited to species with a detectable increase in genetic divergence with geographic distance. In many species, sharp genetic breaks can be detected (Avise 1992, Taylor and Hellberg 2003), but in others there is no clear geographic pattern of genetic divergence (Hauser and Ward 1998). Furthermore, dispersal distance estimates are derived as a mean over wide geographic areas; and, although currents can be incorporated into the models (Palumbi 2003), the prediction of dispersal patterns at specific MPAs is still difficult.

An alternative and potentially very powerful approach to evaluate larval dispersal and retention is the use of molecular markers for parental assignment, which allows identification of recruits originating from local adult fish. Until recently, such parental identification was not feasible because of low variability of markers, lethal sampling, and time-consuming analysis of samples. However, the development of microsatellites as high-variability molecular markers now allows parental identification in wild populations. Microsatellites consist of 1-5 base pair (bp) repeats that form tandem arrays up to 300 bp in length and exhibit high levels of allelic variation in repeat number. Polymorphism exhibited by specific microsatellites is readily detected by amplification of the microsatellite by the polymerase chain reaction (PCR) and estimation of length variation on automated systems. Microsatellites have recently come into widespread use in kinship analyses (reviewed in Wilson and Ferguson 2002) because they offer three critical advantages: opportunities for nonlethal sampling, rapid analysis of samples, and high variability. The approach is currently used extensively in salmonid populations (Bentzen et al. 2001) mainly to estimate reproductive success (Dickerson et al. 2002, Seamons et al. 2004), interactions between wild and hatchery fish (McLean et al. 2003), and the evolution of life history strategies (Garant et al. 2003). A similar approach is also possible for marine fishes, provided that a large proportion of resident adults can be sampled, which increases the chance of detecting at least some offspring with practical sample sizes. That way, offspring could be assigned not only to adults on a specific reef or MPA, but in contrast to otolith tagging studies, also to individual adult fish. By selecting a species with relatively isolated adult populations of small size, which allows the collection of a high proportion of the breeding adults in a specific area, more accurate estimates of self-recruitment could be derived.

Here, we used parental assignment of recruiting juveniles as an alternative approach to estimating the level of self-recruitment and larval dispersal in brown rockfish (*Sebastes auriculatus*). We chose brown rockfish as a target species for several reasons: (1) adult brown rockfish have relatively small home ranges, and rarely move farther than 3 km (Matthews 1990, Stout et al. 2001), which minimizes influx of new and unsampled parents; (2) relatively small and insular populations of brown rockfish inhabit several artificial reefs in Puget Sound, which allows the collection of a large proportion of potential parents; (3) some of these artificial reefs have integrated and adjacent nursery habitat for the collection of recruiting juveniles; and (4) the feasibility of inducing trans-generational chemical marks in otoliths of larvae has been demonstrated recently in brown rockfish (Buckley et al. 2007), which provided an independent verification of genetic assignments.

Materials and methods

Sampling

The study site was an artificial reef at Point Heyer, on the eastern shoreline of Vashon Island in Puget Sound (47º25.2'N, 122º25.6'W, Buckley et al. 2007). The reef is relatively isolated from other rockfish habitat, and the next artificial reef is more than 7 km away. Adjacent to the reef is smaller boulder habitat suitable for juveniles and allowing the collection of settling recruits. During summer 2004, a total of 137 adult brown rockfish (>20 cm) were caught with hand nets by scuba divers, fin clipped, and released immediately. Thirty-one females were also injected with strontium chloride ($SrCl_2$) solution (see Buckley et al. 2007). Between spring 2004 and spring 2005, 209 recruits (<101 mm) were collected from the adjacent nursery habitats by divers who used hand nets. Fin clips of adults and juveniles were stored in 95% ethanol until analysis.

Molecular methods

DNA was extracted from each sample using DNeasy extraction kits (Qiagen), following the manufacturer's protocols. Thirty-five microsatellite loci from eight *Sebastes* species were PCR-amplified following the original protocols for each locus, though annealing temperature and number of cycles were adjusted as needed to optimize PCRs. Of the 35 loci screened, 13 loci from five species were selected for further analysis based on reliability of amplification and scoring (Table 1). All samples were amplified at all 13 loci using forward primers labeled with a fluorescent dye, 0.5 units Taq (GeneChoice), and reagents and conditions detailed in Table 1. Amplified PCR products were purified using ethanol precipitation and genotyped using a MegaBACE 1000 DNA Analysis System (Amersham Biosciences). Raw data were analyzed

Table 1. Source, amplification conditions, and repeat unit of microsatellite loci. Annealing temperatures and numbers of cycles in the PCR protocol are also presented. In loci where there are two annealing temperatures, the first was used for the first number of cycles, followed by the second number of cycles at the second temperature. Repeat unit size (Rp), focal species (the *Sebastes* species from which microsatellites were isolated), GenBank accession numbers, and reference are also shown.

Locus	dNTPs (μM)	$MgCl_2$ (mM)	Primer (μM)	DNA (μL)	Annealing temp. (°C)	Cycles	Rp	Focal species	GenBank accession	Reference
Sal1	80	1	0.3	5	47.5	29	4	*alutus*	AF153595	Miller et al. 2000
Sal3	80	1.5	0.3	5	53	25	5	*alutus*	AF153597	Miller et al. 2000
Sma2	200	1.5	0.5	3	53/56	7/18	2	*maliger*	AY654594	Wimberger et al. 1999
Sma4	200	1.5	0.3	3	55/58	7/18	3	*maliger*	AY654596	Wimberger et al. 1999
Sma10	200	1.5	0.3	3	57.5/60.5	7/18	2	*maliger*	AY654602	Wimberger et al. 1999
Sme5	200	1.5	0.15	3	58	34	4	*melanops*	AF142487	Seeb et al. (unpubl.)[a]
Sme8	200	1.5	0.15	3	54	34	4	*melanops*	AF142490	Seeb et al. (unpubl.)[a]
Spi4	100	1.5	0.5	5	59.3	30	4	*pinniger*	AY192599	Gomez-Uchida et al. 2003
Spi6	100	1.5	0.15	1.5	59.3	30	4	*pinniger*	AY192600	Gomez-Uchida et al. 2003
Sra6-52	200	1.5	0.5	3	54	36	2	*rastrelliger*	AF269057	Westerman et al. 2005
Sra7-25	200	1.5	0.09	3	66.5	36	2	*rastrelliger*	AF269056	Westerman et al. 2005
Sra15-8	200	1.5	0.3	3	54	36	4	*rastrelliger*	AF269059	Westerman et al. 2005
Sra16-5	100	1.5	0.15	3	64	36	4	*rastrelliger*	AF269061	Westerman et al. 2005

[a]L.W. Seeb et al., Alaska Department of Fish and Game.

with Genetic Profiler software (Amersham Biosciences), and automated allele assignments were manually reviewed for accuracy. DNA from 96 randomly picked samples was re-extracted and used in a blind trial to estimate genotyping error.

Data analyses and simulations

Genotype frequencies were tested for conformance to Hardy-Weinberg and linkage equilibrium by using the software package GENEPOP v3.4 (Raymond and Rousset 1995). Loci were also checked for evidence for mis-scoring due to large allele dropout, stuttering, and null alleles (Micro-Checker, van Oosterhout et al. 2004). Observed and expected heterozygosities, inbreeding coefficient (F_{IS}) values, and allelic diversities were estimated using FSTAT (Goudet 1995).

Parentage analysis was carried out based on exclusion, as well as by a method based on breeding likelihood (Sancristobal and Chevalet 1997). As the results of exclusion and likelihood were almost identical, only exclusion results are presented. Parents matching at a minimum of 11 out of 12 loci were considered in the assignment. Average exclusion probabilities (i.e., the average probability of excluding an unrelated individual as a parent) per locus and overall loci were calculated following the methods in Marshall et al. (1998).

To assess the power of the approach, simulations were carried out using the PopTools Add-In for Excel (Add-In for MS Excel, Greg Wood, CSIRO, Australia, available online at www.cse.csiro.au/poptools). First, allele frequencies estimated from all sampled fish were used to draw 137 random adults and 100 random juveniles and to estimate the number of matches that would be expected to occur by chance alone. This simulation was repeated after including 10% offspring of sampled parents to the sampled juveniles. Means and 95% confidence intervals were calculated from 1,000 permutations. Second, 10,000 random adults were drawn from the population, of which 137 were assumed to have been sampled. These 10,000 parents were used to produce 100 offspring—by chance, about 2.7% of these offspring would have at least one parent in the sample of 137 fish. Because of the large matrices involved in these simulations, means and 95% confidence limits of genotype matches were estimated from only 100 permutations. These simulations were used to estimate the distribution of the number of loci by matching between true parent-offspring pairs and between random matches. We also evaluated the difference in match between the most likely parent and the second most likely parent. In order to evaluate the significance of locus variability, we repeated the above simulations by drawing adult genotypes from allele frequencies of the four most polymorphic loci (Spi6, Sra16-5, Sal1, Sra7-25) three times. In all simulations, genotyping error was included by replacing a proportion of offspring alleles equal to the empirically estimated genotyping error with an allele randomly

drawn from the populations. Although this type of genotyping error may be somewhat unrealistic, distinction between different classes of errors is difficult and currently generally not implemented (Marshall et al. 1998, Duchesne et al. 2002). Furthermore, our mode of genotyping error is probably the most conservative in the present context, because replacing the true allele with a common allele is likely to increase the proportion of false matches.

An alternative approach to parental identification is the calculation of relatedness coefficients (Queller and Goodnight 1989). The program Kinship (Goodnight and Queller 1999) was used to simulate expected distributions of relatedness coefficients between unrelated individuals and parent offspring pairs. These distributions were compared with observed distributions of relatedness coefficients in the real data. Additionally, a log-likelihood test that compared the likelihood of unrelated vs. parent offspring relationships was carried out in Kinship—the number of tests significant at the 0.05 level was then compared within adults and recruits, and between these two groups.

Results

Locus variability and genotyping error

After repeating failed PCR amplifications, 99.2% of all genotypes were successfully determined. Variability was moderate; expected heterozygosity ranged between 0.6 and 0.9, and the mean allelic diversity was 13 alleles (Table 2). At most loci, there was no evidence for deviation of genotypic proportions from expected Hardy-Weinberg proportions—only Sra 15-8 and Sma 10 showed a significant deficiency of heterozygotes in both adults and recruits, and there was a significant excess of heterozygote adults at Sme 5. Correspondingly, Micro-Checker provided no significant evidence for mis-scoring due to stuttering or large allele drop out at most loci, with the exception of Sma 10, where there was significant evidence for mis-scoring due to stuttering. The genotyping error varied widely between loci, with no detectable error in 96 samples in seven of the thirteen loci, and an error of more than 7% at Sma 10. Because of the high genotyping error and the evidence for scoring problems, Sma 10 was excluded from subsequent analyses.

Out of the 66 possible tests for deviations from linkage equilibrium, eleven were significant at the 0.05 level in the adults, and five tests were significant in the recruits. There was no correspondence in apparent linkage between adults and recruits, except for the tests between Spi 4 and Spi 6. It is unlikely that loci other than Spi 4 and Spi 6 were indeed physically linked in a genome, a consideration that is important for the calculation of exclusion probabilities.

As expected from the relatively low variability estimates, exclusion probabilities (that is, average probabilities of excluding a randomly

Table 2. Vital statistics of loci surveyed in potential parents (A) and recruits (R), including heterozygosities (observed H_O and expected H_E), inbreeding coefficient (F_{IS}) and significant deviation from Hardy-Weinberg equilibrium, and allelic diversity (*NA* adjusted to a sample size of 135). An estimate of genotyping error based on a blind repeat screening of 96 random samples is also shown. Exclusion probabilities are based on allele frequencies from all fish. Bold F_{IS} values indicate significant deviations of genotype distributions from Hardy-Weinberg equilibrium with a $P < 0.05$; bold underline with a $P < 0.01$.

	A				R					
Locus	H_O	H_E	F_{IS}	*NA*	H_O	H_E	F_{IS}	*NA*	Exclusion probabilities	Genotyping error
Sal1	0.774	0.805	0.039	20.9	0.746	0.807	0.076	17.9	0.466	0.0
Sal3	0.737	0.750	0.017	7.0	0.737	0.733	−0.006	6.6	0.333	0.0
Sma2	0.547	0.617	0.112	3.0	0.612	0.615	0.005	3.0	0.193	0.0
Sma4	0.839	0.811	−0.036	11.0	0.823	0.807	−0.019	9.0	0.456	0.0
Sma10	0.725	0.783	**0.074**	9.9	0.707	0.773	**0.086**	12.3	0.400	7.4
Sme5	0.774	0.763	**−0.014**	13.0	0.789	0.765	−0.032	12.6	0.405	0.0
Sme8	0.672	0.699	0.039	5.0	0.703	0.707	0.005	4.6	0.286	0.0
Spi4	0.693	0.663	−0.046	19.9	0.615	0.654	0.060	20.8	0.269	2.1
Spi6	0.861	0.889	0.032	35.9	0.885	0.883	−0.003	37.5	0.662	2.1
Sra6-52	0.650	0.639	−0.017	6.0	0.699	0.655	−0.066	6.5	0.225	2.1
Sra7-25	0.830	0.855	0.029	15.0	0.813	0.820	0.008	16.2	0.504	4.2
Sra15-8	0.715	0.754	**0.051**	7.0	0.656	0.739	0.113	8.6	0.341	2.1
Sra16-5	0.905	0.923	0.019	23.9	0.919	0.907	**−0.013**	24.7	0.701	0.0
Average	0.748	0.765	0.023	13.7	0.746	0.759	0.016	13.9	0.403	1.5

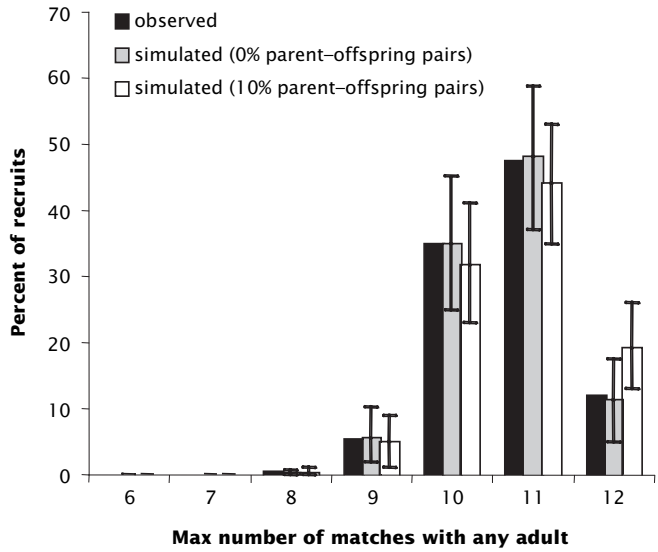


Figure 1. Frequency distribution of maximum matches between recruits and adults. The observed distribution (black) and simulated distributions with no parent-offspring pairs (gray) and 10% parent-offspring pairs (white) are shown. Error bars represent 95% confidence limit of 1,000 simulations. Note that the observed frequency of 12-locus matches falls below the lower 95% confidence limit of the 10% parent offspring simulation.

chosen individual from parentage) were also low (Table 2). Nevertheless, over all loci the exclusion probability was 99.88%.

Parental assignment

Of the 209 offspring, 25 matched at least one parent at all 12 loci, and 99 offspring matched at least one parent at 11 loci. Therefore, allowing for genotyping error at one locus, more than half of all offspring had at least one potential parent in the sample, despite the high average exclusion probability. Simulations showed that this distribution of matches is very close to that expected from chance matches among random genotypes, but that it is significantly lower than expected if 10% of juveniles are offspring of sampled adults (Fig. 1). These results indicated that true offspring of resident parents, if present, were relatively rare (<10% of juveniles).

The notion of rarity of true offspring was confirmed by relatedness indices. Both pairwise relatedness between adults and between adults and recruits closely followed the distribution of relatedness

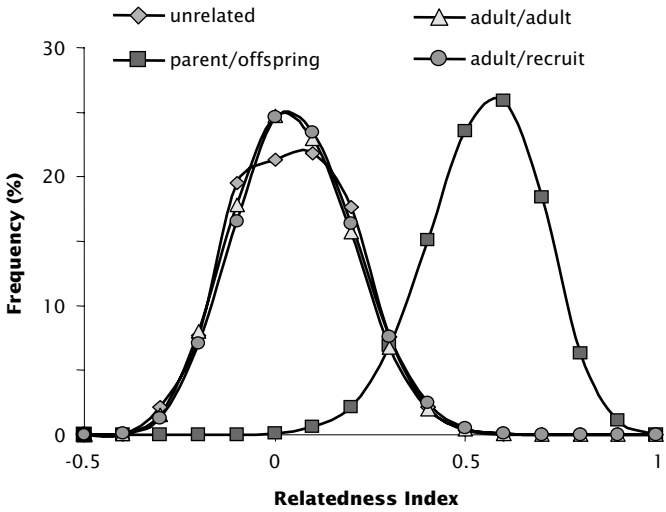


Figure 2. Frequency distribution of relatedness coefficients. Observed relatedness coefficients between adults and between adults and recruits are shown, as well as simulated relatedness between parent-offspring pairs and unrelated individuals. The distribution of observed relatedness follows closely that expected from unrelated individuals.

indices expected for unrelated fish (Fig. 2). However, there were some indications for relatedness from the number of log-likelihood tests that showed a significantly higher likelihood ($P < 0.05$) of first order relatedness as compared to the null hypothesis of no relatedness. Of the pairwise tests between adults, 5.2% were significant, while 6.0% were significant between adults and recruits. This slight excess of significant tests above the expected 5.0% may suggest a few, but not many, related individuals.

Simulations with 10,000 candidate parents, of which 137 parents were known, confirmed that about 10% of juveniles without a parent in the sample would have a random match at all 12 loci with one of the sampled adults (Fig. 3A). Although most juveniles with a sampled parent would also show such a match, they would not be obviously distinguishable from random matches. Furthermore, about 10% of the offspring with parents would match their true parent at only 11 loci because of genotyping error. It may be that a better distinguishing feature between true and random matches is the difference in the number of parents matching equally well. However, although the majority of offspring with parents in the sample have only their parent matching at

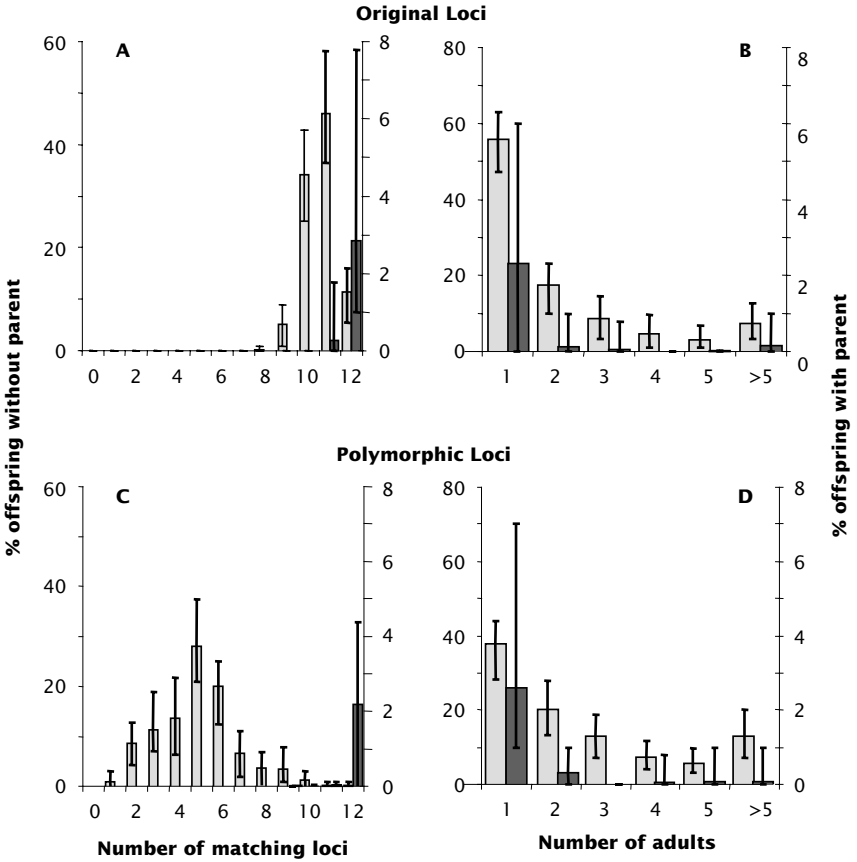


Figure 3. Results from simulations assuming a sample of 137 fish from a population of 10,000 candidate parents. Juveniles with parents in the sample are shown in dark gray and on the right hand scale, whereas juveniles with unsampled parents are shown in light gray and on the left hand scale. Error bars show confidence limits from 100 simulations. (A) Distribution of best matches between adults and juveniles using the original set of loci. (B) Distribution of the number of adults matching offspring at as many loci as the best matching candidate parent. (C) and (D): As in (A) and (B), but using the four most polymorphic loci three times.

all 12 loci, about 40% of random matches also have only one adult that matches best (Fig. 3B). Having a single matching parent is therefore no indication of a true parent-offspring relationship.

Equivalent simulations using the four most polymorphic loci taken three times demonstrated the value of a highly polymorphic data set for parental identification. Most offspring with no parent in the sample match any parent by chance at only five loci, and only 0.2% match at all 12 loci (Fig. 3C). In contrast, 96% of offspring with parent in the sample match that parent at all 12 loci—the other 4% being due to genotyping error. Interestingly, however, the number of potential parents matching at the same number as the maximum match was still not a good indicator for true parentage, as in almost 60% of random matches there was a single sampled parent matching best.

Discussion

The results of this study suggested that the molecular markers used here were not sufficiently variable to provide an unambiguous identification of offspring of resident rockfish. However, the data did indicate very limited self-recruitment, and in conjunction with $SrCl_2$ marking, led to the identification of a single offspring of an injected fish (Buckley et al. 2007). Furthermore, simulations showed that a more polymorphic marker set would have the power to identify offspring, despite the large number of potential candidate parents and the very small proportion of parents sampled.

Parental assignments and rates of self-recruitment

Our study identified 124 potential offspring of the rockfish sampled (matching at 11 or 12 loci to any candidate parent). However, simulations suggested that a very similar number of matching offspring would be expected by chance alone. Simulations that included 10% "true" parent offspring pairs produced significantly more matching pairs than observed, which suggested that the true value of self-recruitment is less than 10%. On the other hand, $SrCl_2$ marking clearly identified one offspring of an injected female (Buckley et al. 2007). Therefore, genetic and otolith results combined suggested that self-recruitment did occur, but at a rate of less than 10%, though any such conclusions are very preliminary due to the lack of accurate confidence estimates.

Low levels of self-recruitment may be expected, because of the long larval period of brown rockfish (2-2.5 months, Love et al. 2002) and the consequent potential of extensive larval dispersal. However, several lines of evidence also suggest considerable potential for larval retention and limited realized dispersal of brown rockfish. Puget Sound is an enclosed estuary that includes several basins. The artificial reef on Point Heyer is situated in the central basin, which is connected to

northern Puget Sound via Admirality Inlet (maximum depth 65 m) and to the southern basin via Tacoma Narrows (maximum depth 45 m) (Burns 1985). General circulation patterns are primarily caused by tidal exchange, and consist of outflow through Admiralty Inlet in the upper layer and inflow of marine waters at depth (Stout et al. 2001). In the southern part of the basin, currents generally flow north on the west side of Vashon Island, and south on the east side where Point Heyer is located (Ebbesmeyer et al. 1984). Such oceanographic patterns, bathymetric isolation, and tidal reversal of currents provide ample opportunity for larval retention via mechanisms such as vertical migration, habitat selection, and hydrographic retention (Joyeux 2001, Bilton et al. 2002). Nevertheless, on a very small scale, dispersal would probably be sufficient to explain the apparent low levels of self-recruitment on Point Heyer. Furthermore, the level of interannual variability in circulation patterns is currently understudied, though major circulation patterns, especially the depth of inflowing and outflowing currents, appear to be greatly influenced by decadal climate regimes (Ebbesmeyer et al. 1998). Recruitment estimates from additional years are therefore needed for more long term self-recruitment rates relevant to MPA design.

Expectations of self-recruitment also stem from indirect estimates of dispersal distances in brown rockfish and other *Sebastes* species. Isolation by distance patterns from microsatellite studies on the Pacific east coast indicated mean dispersal distances of less than 10 km in grass rockfish (*Sebastes rastrelliger*, Buonaccorsi et al. 2004), copper rockfish (*S. caurinus*, Buonaccorsi et al. 2002) and brown rockfish (*S. auriculatus*, Buonaccorsi et al. 2005). By assuming that the distribution of individual dispersal distances follows an exponential distribution (Botsford et al. 2001), about 10% of recruits would be expected to settle within 1 km of the point of release, that is, potentially on the same reef. These estimates correspond to our initial results, though more powerful markers are needed to confirm this notion.

An alternative explanation for the low self-recruitment rates estimated here may be a large variance in reproductive success among adults, resulting in a very limited number of adults actually producing recruits. Population genetic studies indicate that in many marine species the effective genetic population size (N_e) may be orders of magnitude smaller than the census population size (e.g., Turner et al. 2002, Hauser et al. 2002, Hoarau et al. 2005), which suggests that only one in several thousand fish is successful in reproducing. Maternal effects that lead to much higher larval survival in offspring of older females, in addition to the inherently higher fecundity of older and larger fish (Berkeley et al. 2004), may exacerbate these effects. If such few reproductively successful adults were not included in the adult sample, their offspring might not be identified, and self-recruitment rates would be underestimated. Indeed, most females sampled were smaller than 30

cm and inclusion of the few larger fish on the reef may increase the self-recruitment estimate considerably.

Variation in reproductive success may occur either among individuals within subpopulations (Hauser et al. 2002) or among subpopulations (Turner et al. 2002). Indeed, variation in productivity among subpopulations may decrease N_e by several orders of magnitude (Turner et al. 2002). Because self-recruitment was estimated as a proportion, it does not only depend on the productivity of the Point Heyer population, but also other populations in the vicinity, and may have been reduced by immigration from very productive populations. Such considerations emphasize the importance of interannual variability in recruitment.

Methodological considerations

Parentage analysis of marine species is not a trivial undertaking. "Biological" assumptions of common parentage methods are that the population is fairly small, that a large proportion of candidate parents have been sampled, that both parents are in the sample, and that the juvenile sample contains a large proportion of offspring of known parents. Violations of these assumptions result in a progressively restrictive range of analysis methods (Jones and Ardren 2003). The population size of brown rockfish in Puget Sound has been estimated as 100,000 individuals (Stout et al. 2001), all of which are potential parents of juveniles recruiting to the Point Heyer reef. However, the adult population of brown rockfish at Point Heyer is 200-250 fish (Buckley et al. 2007) and so about half of the adults were included in this study (N = 137). There is therefore a 25% chance that any true offspring of resident adults has both parents in the sample—a probability that is lower than in most other studies of parentage assignment (Jones and Ardren 2001). The proportion of offspring of these adults in the recruiting juveniles is unknown, and may range from 0% given the extensive larval period of 2 to 2.5 months (Love 2002) to 15-60% as was reported for reef fish (*Pomacentrus amboinensis*, Jones et al. 1999) on the Great Barrier reef. All these ecological features of many marine species, such as brown rockfish, complicate parental assignment, but certainly should not prevent it, given the appropriate set of marker loci and some way of verifying assignments.

There are also some assumptions regarding the markers in question. Most importantly, markers should have high variability, and so provide high exclusion probability for random genotypes. Our marker set was less variable than one would like for a parentage assignment study. Two reasons may account for this low variability: first, all loci were isolated from other rockfish species, and it is known that microsatellites are somewhat longer and more variable in the focal species (the species from which it was isolated) than in related species (Neff and Gross 2001). Second, brown rockfish in Puget Sound have lower genetic diversity

than their conspecifics on the Oregon and California coast (Buonaccorsi et al. 2005). The relatively low variability of microsatellites led to low exclusion probabilities (0.2-0.7, Table 2) and further reduced the power of parentage assignment.

Nevertheless, our simulations showed clearly that a more variable microsatellite data set would have high power in detecting true parent-offspring pairs in our samples. Using our suite of loci, about 10% of random pairs of individuals matched at all 12 loci, whereas a more variable set of microsatellites would reduce this percentage to 0.2%, while leaving the distribution of matches between true parent-offspring pairs unchanged. Similar increases in parentage assignment success with increasing diversity of marker loci were observed in other simulation studies (Bernatchez and Duchesne 2000). Interestingly, the distribution of numbers of candidate parents matching the offspring at the same number of loci as the maximum match found did not change noticeably with marker variability. This number of equally well matching parents is closely related to the concept of the difference in match between the most likely parent and the second most likely parent, a criterion often used in parental assignment studies (Marshall et al. 1998). These results suggest that with a small sample from a large number of candidate parents and genotyping error, such a criterion may be unsuitable.

Low genotyping error and low mutation rates are a further assumption of parental assignment. Some approaches allow the consideration of genotyping errors (e.g., Marshall et al. 1998), but in doing so reduce the power of assignment even further. Simulations that used a maximum likelihood approach (Marshall et al. 1998) showed that low marker variability, genotyping error, and a large proportion of unsampled parents together reduce the power sufficiently to prevent confident parental assignment (data not shown). In our study, the locus with the highest genotyping error (Sma 10) was removed from the analysis, and the remaining average genotyping error (1%) was within the average commonly observed in microsatellite studies (Hoffman and Amos 2005). Nevertheless, over the 12 loci, the genotyping error exceeded 12% per multilocus genotype, which resulted in false exclusion of parent offspring pairs. Furthermore, because of the rapidly increasing multilocus genotyping error, the addition of more loci does not always result in higher power of parental assignment, as the limited increase in information content with each additional locus is more than offset by an increase in overall error rate. It would therefore be best to use a limited number of loci with high variability and low genotyping error for parental assignment.

Implication for MPA design

One of the main assertions of MPAs is that protecting a spawning biomass of marine fishes will enhance progeny output, and that the patterns of larval dispersal from the MPAs will contribute to local and/or regional stocks. However, the dispersal of marine fish larvae is poorly documented and this basic assumption remains unverified. Although clearly only a "snapshot" in time, our results suggested that, at least on Point Heyer, recruitment of the 2004 year class occurred primarily from outside the resident population. However, concluding a low conservation priority from these data would be misleading, because data from additional years are needed to establish long-term temporal trends. Furthermore, the destination of Point Heyer offspring is currently unknown, and the population may be an important source of larvae for other reefs. Point Heyer may thus be an important component of the rockfish habitat in Puget Sound. Further surveys including other reefs are needed, optimally using a combination of otolith marking techniques (Buckley et al. 2007) and genetic methods. Our simulations clearly demonstrated the feasibility of the approach of identifying offspring of resident adults, which may be a powerful tool for estimating dispersal into and out of MPAs.

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Distribution and Population Genetic Structure of Sibling Rougheye Rockfish Species

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Abstract

Rougheye rockfish (*Sebastes aleutianus*) includes two genetically distinct species, type I and type II. We examined their spatial distributions, population genetic structures, and the effects of fish size, depth, and capture gear (trawl or longline) on their distributions from samples collected on the continental shelf and upper slope from the south end of the Queen Charlotte Islands to the western Aleutian Islands and the Bering Sea. Type I fish occurred throughout the Alaskan range, but type II fish were not abundant west of Kodiak Island. Their distributions overlapped in the northeastern Gulf of Alaska. Collections were pooled for genetic analysis into geographically defined groups. We examined allelic variation at seven microsatellite loci in 710 type I fish and 510 type II fish and restriction site variation in the ND3/ND4, 12S/16S, and ND5/ND6 mtDNA regions in 666 type I and 400 type II fish. Tests of homogeneity and adjacency tests that partitioned heterogeneity showed that both species have genetic structure that is consistent with a neighborhood model of dispersion. For both species, population divergence was apparent at the edges of the range, but divergence in the northeastern Gulf of Alaska was more pronounced in type II populations, which suggests structure on a finer scale than the management area

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boundaries. Analysis of the effect of fish size, depth, and capture gear (trawl or longline) on distributions of the species suggests that the species differ in habitat preference. In addition, numerous small type II fish were captured by trawl in relatively shallow water, but large numbers of small type I fish were not observed, which suggests that young fish have different habitat preferences.

Introduction

Recently, we observed variation both in the mtDNA and at microsatellite locus μ*Sma*6 that was strongly correlated in 633 rougheye rockfish sampled from North Pacific waters from Oregon to the western Aleutian Islands (Gharrett et al. 2005). Only six probable hybrids were detected. The two types of rougheye rockfish had overlapping geographic distributions, and both were captured in some longline and trawl hauls. There is overwhelming genetic evidence that the two types are distinct species, but no diagnostic morphometric or meristic features have yet been reported, although the species can be separated by discriminant analysis of morphological characters and they can be partially separated by coloration (Gharrett et al. 2006).

The discovery that the commercially valuable rougheye rockfish includes two distinct species further confuses an already complicated management situation. In 1991, the North Pacific Fishery Management Council (NPFMC) established three subgroups within the slope rockfish assemblage in an effort to protect the most sought-after rockfish species from overfishing. One of the subgroups combined rougheye and shortraker (*S. borealis*) rockfishes (Heifetz et al. 2000). In the 2005 fishery, rougheye rockfish were separated from shortraker rockfish for management purposes. Our discovery leaves the two types of rougheye rockfish lumped for management. In 2003, the rougheye rockfish exploitable biomass in the Gulf of Alaska was estimated at 40,280 t, from which managers defined an acceptable biological catch (ABC) of 1,007 t (Clausen et al. 2003). Geographical allocation of rougheye rockfish harvests is based on the distribution of biomass, with little or no emphasis on population structure or biological influences (Heifetz et al. 2000).

Although marine species have potential for high gene flow through larval transport, juvenile dispersal, and adult migratory behavior (Moser and Boehlert 1991, Stanley et al. 1994, Seeb 1998), the actual extent of dispersal from hatching to reproduction is unknown for many *Sebastes* species and may be more localized than suggested by speculation based on oceanic processes (e.g., Orlov 2001, Matala et al. 2004a,b). Consequently, heavy localized fishing effort, or "hot spots," could diminish the resource without recognition of the scale of productivity units to guide managers. Populations of slow growing marine species such as rougheye rockfish, which may have a restricted adult migratory

range and whose larvae are dispersed by planktonic transport, can be expected to recover slowly from local depletion (Mason 1998, Yoklavich 1998).

To examine and compare the distributions and population structures of type I and type II rockfish, we analyzed collections sampled along the continental shelf from the state of Oregon to the western Aleutian Islands and in the Bering Sea. We used a suite of seven microsatellite loci and restriction site variation in the mitochondrial ND3/ND4, ND5/ND6, and 12S/16S regions. We addressed four specific questions: (1) are population structures for types I and II rougheye rockfish detectable, (2) if divergence or structure exists, what is the geographic scale of their structures and how do the structures compare between species, (3) is the population structure compatible with current management, and (4) do their bathymetric distributions, sizes and the kind of gear with which they were sampled provide insight into habitat preferences?

Materials and methods

Sampling, species identification, and pooling samples for analysis

Between 1994 and 2003, rougheye rockfish dispersed among 126 collections were sampled throughout their total range, through combined fisheries agency efforts: (1) the continental shelf off Oregon, along the Alaska coast from southern Southeast Alaska to the western Aleutian Islands, in the Bering Sea, and from Surveyor Seamount by the National Marine Fisheries Service (NMFS); (2) the inside waters of Southeast Alaska, Prince William Sound, and Kachemak Bay by the Alaska Department of Fish and Game (ADFG); and (3) British Columbia by the Department of Fisheries and Oceans Canada (Fig. 1). Heart tissue was dissected from specimens and preserved (Gharrett et al. 2005).

Types I and II rougheye rockfish were distinguished by diagnostic mtDNA and microsatellite markers. Type I rougheye rockfish corresponds to *Sebastes aleutianus* unknown in Seeb (1986) and to *Sebastes* sp. cf. *aleutianus* in Hawkins et al. (2005). Type II rougheye rockfish correspond to *S. aleutianus* in both papers. Both rockfish types and their recent hybrids were distinguished using the program Structure version 2 (Pritchard et al. 2000), which sorts individuals in a mixture by minimizing the Hardy-Weinberg and gametic disequilibrium (Gharrett et al. 2005). For analysis, the 126 collections were pooled in two steps. In the first step, collections within 50 km of each other were pooled (Fig.1). At the second step, regional groups were defined. For convenience, the latter groups are referred to as populations in this paper. We defined 16 type I populations (including the Surveyor Seamount) and 10 type II populations (Fig. 1).

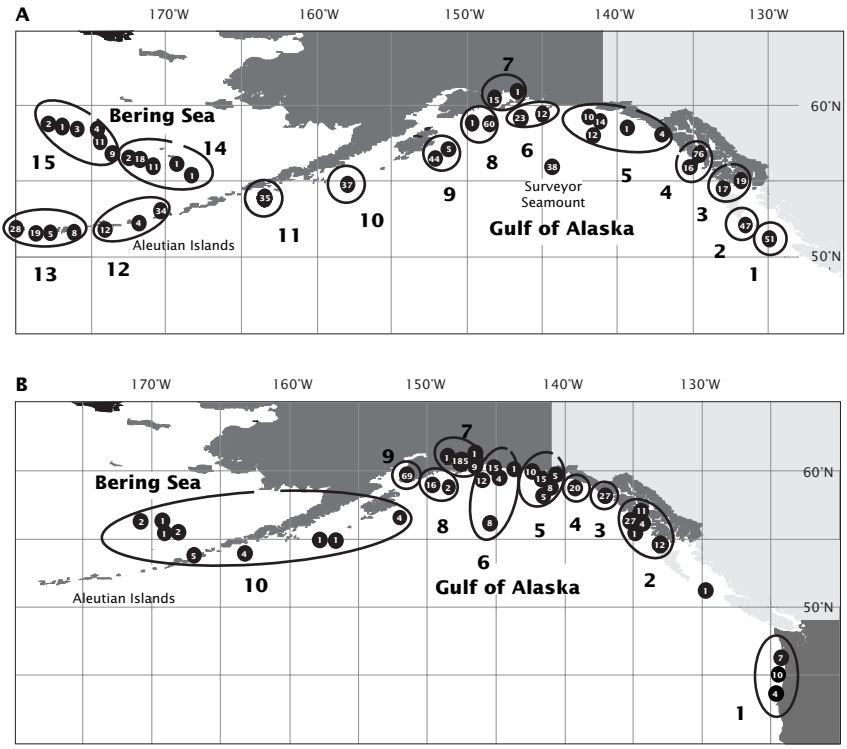


Figure 1. Locations of pools of collections and sample sizes, regional groups of pools defined as populations, and population labels (Arabic numerals) for: A. rougheye rockfish type I, and B. rougheye rockfish type II.

Microsatellite and mtDNA analysis

Microsatellite variation at eight variable loci: μ*Sma*3, μ*Sma*5, μ*Sma*6, μ*Sma*7, and μ*Sma*11 (Wimberger et al. 1999), and μ*Sr*7-2, μ*Sr*7-7, μ*Sr*7-25 (Westerman et al. 2005) was surveyed as described previously (Gharrett et al. 2005). The locus μ*Sma*6, which is diagnostic for differences between rougheye rockfish types I and II and has little intraspecific variation, was excluded from population analyses.

From our previous mtDNA restriction analyses (Gharrett et al. 2005), we identified the most abundant haplotype clusters in the mtDNA haplotype tree and completed our survey analyzing sites from restriction enzyme and region combinations that resolved those clusters: *Hin*f I in the 12S/16S region; *Bst*N I, *Dde* I, and *Hin*f I in the ND3/ND4 region; and *Bst*N I, *Mbo* I, and *Rsa* I in the ND5/ND6 region. It was unnecessary

to obtain data for all the site and enzyme combinations to identify the predominant haplotype clusters.

Data analysis

Microsatellite data

Allele frequencies at each locus in each population were estimated using GENEPOP version 3.2a (Raymond and Rousset 1995). Tests of Hardy-Weinberg equilibrium (HWE) were performed for all combinations of loci and populations with an exact test in GENEPOP (Raymond and Rousset 1995, settings: 100,000 dememorization steps and 1,000 batches of 1,000). Wright's (1978) inbreeding coefficient (F_{is}) and Nei's unbiased expected heterozygosity (H_e; Nei 1978) were estimated for each combination of locus and population (FSTAT version 2.9.1; Goudet 2000). The indices of inbreeding (F_{is}) show the direction of HWE departures; negative values of F_{is} indicate an excess of heterozygous types, whereas positive values indicate a deficit of heterozygotes. Probabilities of linkage disequilibrium at each pair of loci within each population were estimated using Arlequin 2.0 (Schneider et al. 1997). Simultaneous tests in these analyses were adjusted using a sequential Bonferroni correction with an α level of 0.05 (Rice 1989, Sankoh et al. 1997).

Log-likelihood ratio analysis (*G*-tests) was used to test for overall population heterogeneity (H_o: allele frequencies are homogeneous among populations). Monte Carlo simulations (Fortran program written by AJG) of the allele frequency data were used to estimate the probability distributions of the log-likelihood ratios (*G*-statistic). Probabilities were combined over loci using Fisher's method (Winer 1971).

Population substructure was also examined by tests that partition genetic variation based on allele identity (F_{ST} or θ; Weir and Cockerham 1984) using the FSTAT (Goudet 2000), GENEPOP (Raymond and Rousset 1995), and Arlequin 2.0 (Schneider et al. 1997) programs. Tests of isolation-by-distance (Mantel 1967) were conducted using GENEPOP (Raymond and Rousset 1995). We did not perform hierarchical analysis of molecular variation (AMOVA, Excoffier et al. 1992) because the divergences we detected among populations were very small and the isolation-by-distance test was not significant.

Collections (except from Surveyor Seamount) were distributed along the arc of the north Pacific Rim. Adjacent populations would be expected to be more similar than those separated by greater distance, whether or not allele frequencies among them form a geographic cline (which would be detected in isolation by distance tests). To obtain information about the geographic scale of genetic structure, the total genetic variation observed among populations was partitioned by grouping adjacent populations into homogeneous groups (Matala et al. 2004a,b)

mtDNA data

We used the minimum spanning tree for mtDNA haplotypes that was constructed previously (Gharrett et al. 2005) from our preliminary haplotypes surveys using the program NETW4.0.0.0 (Bandelt et al. 1995) as the foundation for adding new haplotypes. Correlation of haplotypes between populations (ϕ_{ST}) based on site was estimated using Arlequin 2.0 (Schneider et al. 1997) using differences between haplotypes.

Homogeneity of haplotype frequencies among populations was tested using the MONTE module (Roff and Bentzen 1989) in the program REAP (McElroy et al. 1990). One of the advantages of mtDNA haplotypes is that a genealogy can be inferred for them that presumably reflects their evolutionary relationships and provides a rational basis for pooling haplotypes to reduce the number of groups. Consequently, haplotypes pooled into the most abundant groupings (at least 10 individuals) were used to partition the mtDNA haplotype variation. Grouping homogeneous adjacent populations was conducted as described for microsatellites, but MONTE was used to estimate probabilities.

Distributions of types I and II rougheye rockfish

In a preliminary analysis of the geographic distributions of the two species, we noticed that individual trawl hauls and longline sets captured predominantly one species (type) or the other. Two collections of type II fish prompted us to evaluate the incidence of the two species in hauls and locations; one collection comprised five fish from an embayment on the north side of Unalaska Island in the Aleutian chain, which is west of the area in which they are abundant, and the other was a collection of 81 fish from Prince William Sound (Gharrett et al. 2005). Subsequently, we supplemented our data with samples from inside waters of Kachemak Bay, Prince William Sound, and Southeast Alaska; and we completed analysis of entire hauls from the northeastern GOA, which we had previously subsampled.

Analyses of the effects of depth of capture, gear used (trawl or longline), and fish size on the occurrence of type I and II rougheye rockfish are not straightforward because trawls and longlines are often applied in different situations. Longlines can be set in most habitats including rocky and steep seafloor. In addition, longlines are often set in deeper water than can be effectively fished by trawl. Habitats that can be trawled are flatter, smoother, and generally shallower. In addition, the combination of factors that describe the incidence of type I fish may differ in the western area where type II fish are rare and the eastern area where type II fish are common. Our longline samples were collected during routine surveys where depth was estimated only to stratum (100 m bands). Consequently, we asked the following set of questions in order to consider these obfuscating factors: (1) What are the effects of depth (or depth stratum), gear, and size and their interactions on the spe-

cies caught for the data set as a whole? (2) How do these factors affect capture of type I fish in eastern areas, where type II fish are abundant, and in western areas (west of Kodiak Island), where type II fish are not abundant? (3) How do depth, gear, and size and their interactions relate to the species caught in the eastern GOA where both species are common? (4) How do depth, gear, and size and their interactions relate to the species caught if only depths common to both gear types (200 m to 500 m) are analyzed? For question 4, both the entire range and common ranges were analyzed.

Because neither species was overtly targeted to obtain the collections analyzed here, their geographic distributions were compared by inspection of the locations and compositions of the catches. We used the general linear model (GLM) in SAS (Littell et al. 1991) to partition the variance and to analyze data on species, depth of capture, gear used, and the size of each fish.

Results

Type I rougheye rockfish

A total of 710 type I rougheye rockfish were analyzed for microsatellite variation. The number of alleles observed ranged from six at μ*Sma*5 to 53 at μ*Sr*7-2 (Appendix) and expected unbiased heterozygosities (H_e) for all fish ranged from 0.335 at μ*Sma*11 to 0.921 at μ*Sr*7-25. Bonferoni-corrected tests of Hardy-Weinberg equilibrium (HWE) frequencies showed significant excesses of homozygotes at μ*Sma*3 in five of the 16 populations, and two populations were significant at μ*Sr*7-25 and one population at μ*Sma*5. Because the frequency of null alleles might bias estimates of allele frequencies at μ*Sma*3, it was excluded from subsequent tests. The microsatellite allele frequency data (except μ*Sma*3) were also tested for linkage disequilibrium. After Bonferoni adjustment, none of the populations had pairs of alleles that exhibited gametic disequilibrium.

Partitioning the total variation into within- and among-population components yielded a very low F_{ST} (θ) of 0.0010, which indicates that little divergence exists among populations; however, the overall significance of the *G*-statistic-based homogeneity tests ($P < 0.01$) demonstrates that the value is significantly positive. A test of isolation by distance that correlated pairwise F_{ST} values between populations with geographic distances between populations was not significant ($P = 0.57$). The divergence observed was partitioned using homogeneity tests of adjacent populations and groups of adjacent populations (e.g., Matala et al. 2004ab). Surveyor Seamount was excluded from the analysis because it could not be placed in a linear array of populations. The analysis identified four areas that were distinct from adjacent populations: two in British Columbia (populations 1 and 2), one near Kodiak Island (population 9), and one near the end of the Aleutian chain (population 13) (Fig.

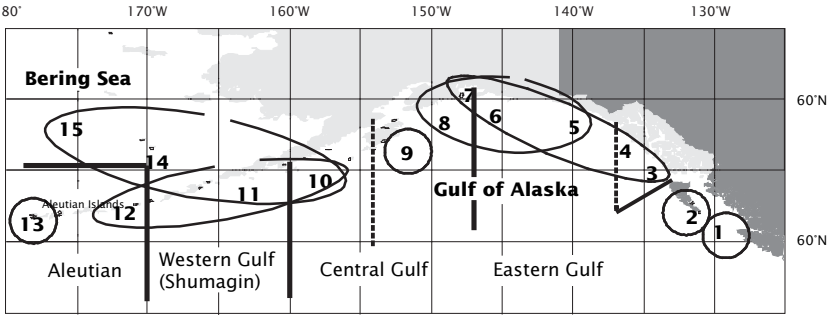


Figure 2. Homogeneous adjacent populations based on microsatellite variation at five loci for type I rougheye rockfish. Ellipses include populations that are homogeneous, and separate them from adjacent groups that produce heterogeneity ($P < 0.05$). Solid lines on the map distinguish regulatory area boundaries in the Gulf of Alaska and Aleutian Islands. For reference, the Chirikof (west) and Kodiak (east) International North Pacific Fisheries Commission (INPFC) statistical areas are shown in the Central GOA regulatory area (dashed line), and the Yakutat and Southeast INPFC areas of the Eastern GOA regulatory area are shown (dashed line).

2). The other populations made two sets of overlapping clusters, one along the northeastern Gulf of Alaska and the other along the central and eastern Aleutian Islands and Bering Sea.

In a parallel AMOVA analysis of mtDNA variation in 666 type I fish, the overall divergence was nearly significant ($P = 0.066$). Partitioning the divergence indicated structure near the ends of the Alaskan range sampled (results and data not shown).

Type II rougheye rockfish

A total of 510 type II rougheye rockfish were analyzed for microsatellite variation. The number of alleles observed within populations ranged from four at μ*Sma*7 to 47 at μ*Sr*7-25 (Appendix) and expected unbiased heterozygosities (H_e) for all fish ranged from 0.042 at μ*Sma*7 to 0.944 at μ*Sr*7-25. Tests of Hardy-Weinberg equilibrium (HWE) frequencies showed significant excesses of homozygotes at μ*Sma*3 in six of the 10 populations (Appendix). Fewer tests of HWE frequencies at other loci were significant: two populations were significant at μ*Sma*11 after adjusting for multiple testing. We excluded μ*Sma*3 and μ*Sma*11 from most subsequent analyses. The microsatellite allele frequency data (except μ*Sma*3 and μ*Sma*11) were also tested for linkage disequilibrium. Two locus pairs, μ*Sma*5 and μ*Sr*7-25 in population 4 and μ*Sma*5 and μ*Sr*7-7 in population

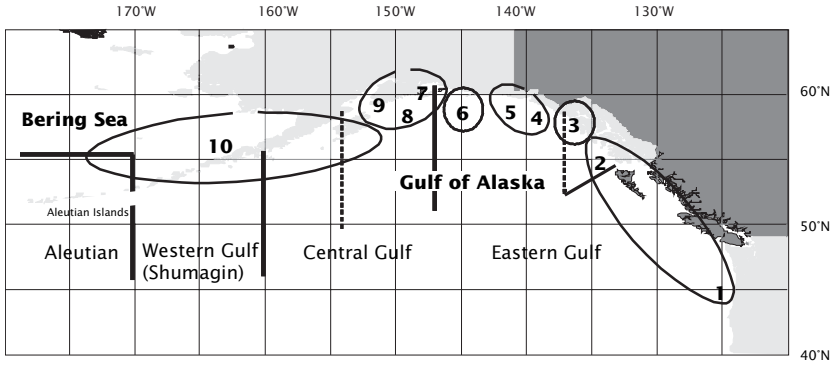


Figure 3. Homogeneous adjacent populations base on microsatellite variation at five loci for type II rougheye rockfish. Ellipses include populations that are homogeneous and separate them from adjacent groups that produce heterogeneity ($P < 0.05$). Solid lines on the map distinguish regulatory area boundaries in the Gulf of Alaska and Aleutian Islands. For reference, the Chirikof (west) and Kodiak (east) International North Pacific Fisheries Commission (INPFC) statistical areas are shown in the Central GOA regulatory area (dashed line), and the Yakutat and Southeast INPFC areas of the Eastern GOA regulatory area are shown (dashed line).

7, exhibited gametic disequilibrium after Bonferoni adjustment. Because no locus pair consistently indicated linkage disequilibrium, we used all five loci in subsequent analyses.

Partitioning the total variation into within- and among-population components yielded a very low F_{ST} (θ) of 0.0005, which indicated that very little divergence exists among the rougheye rockfish type II populations. However, a significant *G*-statistic-based test of homogeneity ($P < 0.01$) demonstrates that the value is significantly positive. A test of isolation by distance that correlated pairwise F_{ST} values between populations with geographic distances between populations was not significant ($P = 0.79$). Subsequent inclusion of μ*Sma*11 in the analyses increased both the θ and its significance.

The divergence observed was partitioned using homogeneity tests of adjacent populations and groups of adjacent populations (e.g., Matala et al. 2004a,b). The results identified six distinct non-overlapping groups of populations (Fig. 3). No significance structure ($P = 0.47$) was observed in analyses of mtDNA of 400 type II rougheye rockfish (data and analyses not shown).

Table 1. Significance of ANOVAs conducted on type I and II rougheye rockfish for G (gear), D (depth), S (size), and their interactions.

Analysis		G	D	D*G	S	S*G	D*S	D*S*G
Question 1	Both species: all areas, all depths	0.44	<0.0001	0.33	0.006	0.029	0.006	0.035
Question 2	Type I: western vs. eastern	0.52	0.16	0.64	0.94	0.21	0.60	0.98
Question 3	Both species eastern GOA, all depths	0.32	<0.0001	0.58	0.002	0.030	<0.0001	0.102
Question 4	Both species: eastern GOA, common depths	0.041	0.047	0.024	0.76	0.08	0.51	0.046

Distributions of types I and II rougheye rockfish

Comparison was made between type I fish collected west and east of 155ºW to see if presence of type II fish influenced their distribution (question 2). There were no apparent differences in fish size, depth, or gear between eastern and western type I fish (Table 1). The next two analyses compared type I and II rougheye rockfish (questions 1 and 3). Those analyses included all depths. One included all geographic areas and the other included only eastern (east of 155ºW) collections. There were no apparent differences in species contributions by gear, but there were significant differences in species composition related to the sizes of fish at capture and the average depths in which they were caught. These results are largely attributable to the relatively few type I fish that were caught in the shallow hauls and to the small average size of the type II fish.

In the last analysis (question 4), the very shallow and very deep catches were removed to provide similar depth ranges with which to assess the gear types. This subset of the data eliminated shallow trawls that captured many small type II fish as well as a few deep longline sets. The data set included depths from 200 to 500 m. The average sizes of fish in this depth range did not differ, but the average depths of capture and gear did. Also, the depth-by-gear interaction was significant, which indicates that the two types were caught using different gear and depth combinations, even within the limited depth range. There was also a weakly significant 3-way reaction between size, depth, and gear.

Although longline gear can be set where trawls can be made, the reverse is often not possible. Consequently, the significant effects of gear observed in the ANOVAs, suggests that the two rougheye rockfish species may favor different habitats. To further address that question,

Table 2. Distribution of type I rougheye rockfish in longline and trawl catches east of 155° that had a total of at least 10 fish.

Proportion of type I	Longline	Trawl
All type I	7	1
≥0.75	3	4
$0.25 < p < 0.75$	0	3
≤0.25	0	2
No type I	1	11

we examined the proportionate contribution of the two types to catches that included 10 or more fish. Twenty of 32 catches included only one species and nine others had at least 75% of one or the other species (Table 2). These observations also suggest that the species favor different habitats. In addition, the discovery of many small type II fish in shallow trawlable waters suggests partitioning at an early age.

Discussion

The purpose of this study was to examine the distributions and population genetic structures of types I and II rougheye rockfish to identify features that may improve their management and conservation. The type I rougheye rockfish is the predominant species west of Kodiak Island, but both species broadly overlap in the eastern Gulf of Alaska (Fig. 1). Sampling was insufficient to evaluate their relative abundances south of northern British Columbia or in the western Pacific Ocean.

Adjacency analysis of microsatellite variation resolved population structure in both species. Populations near the ends of the range sampled, appeared to be divergent from adjacent populations for both species, and both species exhibited divergence in the middle of the range, between northern British Columbia and Kodiak Island. The divergence among populations was stronger in the type II fish (Figs. 2 and 3), which suggests that type II rougheye rockfish have more limited dispersal. One of the purposes of partitioning the genetic variation using adjacency tests was to learn about the scale of the population structure and to compare it with the sizes of the management areas. The weaker divergence observed in type I fish suggests that the scale of the management areas is similar to the populations structure (Fig. 2). The scale of the structure of type II rougheye rockfish, however, is finer than that of the management areas (Fig. 3).

The apparent geographic structure observed for both rougheye rockfish species is consistent with the assumption of limited movement, and may conform to the neighborhood model of migration, in which population structure develops within the continuum of a species if the average movement of individuals between birth and reproduction is small compared to the species range (Malécot 1950). However, the interpretation of the observations of genetic structure is not unequivocal and the paucity of information about the biology and life history of rougheye rockfish provides no assistance in resolving the question. An alternative explanation for the observed heterogeneity among geographically based populations is that young rougheye rockfish return to their natal grounds to mate (e.g., Orlov 2001). A third explanation is that substantial divergence occurs among cohorts as a result of a sweepstakes-chance effect in which a few adult breeders successfully contribute offspring each season (Hedgecock 1994, Geiger et al. 1999). The heterogeneity we detect could result from differing age compositions in the samples rather than geographic isolation.

We also examined the effects of depth, gear, and fish size on the occurrence of types I and II rougheye rockfish. The results are not clear cut because longlines are often set in places that cannot be trawled, such as down steep grades or in areas strewn with large boulders. In addition, longlines are often fished in deeper water than trawls. We made efforts to account for the differences by analyzing subsets of data that were as comparable as possible. Several results from our analyses may help us draw conclusions about the distributions of these two species. The first is that type I rockfish appear to be distributed similarly with respect to size, depth, and sampling gear whether or not type II fish are present. That suggests that type I and type II rougheye rockfishes may not be competing for the same resources. Also, when no allowance was made for the differences in the gear type used, the occurrence of the species appeared to be affected by depth, size, and interactions between size and gear and size and depth. Some of these effects resulted because there were several large trawl hauls of small type II rougheye rockfish taken in shallow water. Clearly, young type II fish occupied those locations, but type I fish did not. We did not identify areas in which small type I fish were abundant. By limiting the data to depth strata at which both types of gear were commonly used (200 to 500 m), all of the effects involving size were removed, but the effects of depth remained and the effect of gear became significant as did the interaction between gear and depth (Table 1). The last result suggested that the two species do not occupy the same habitat. If that were true, one might expect to see gear selectivity. From a reexamination of the individual hauls, we observed that most hauls that captured at least 10 fish included only one or the other species. In addition, type I fish were more often caught by longline and type II fish by trawl (Table 2). These differences suggest that the two

species have different habitat preferences. Because the data used in this analysis were not from samples taken in parallel by the two gear types, the results of the analysis are not conclusive. However, they provide direction for subsequent investigation.

Many questions remain unanswered about rougheye rockfish. We need to learn about the geographic and ecological differences in their distributions, including basic biological information such as size at age of maturity and general life history descriptions. Information is also lacking on where larvae and juveniles are located in the water column, and to where juveniles disperse and ultimately settle out. These latter questions are important in identifying any environmental factors that influence production, and for addressing questions of how to manage these species most effectively. Morphological differences (Gharrett et al. 2006), the differences in geographic distribution, and the differences in gear and depth indicate that the species differ ecologically and probably have different habitat preferences.

The limited information available is not restricted to rougheye rockfish; there is relatively little known about any of the northern species of *Sebastes*, including the shortraker rockfish. Abundance assessments can be effective in helping to understand when conservation problems arise, but those data are largely ineffective in contributing to solutions of the problems. Because many rockfish species are long-lived and slow growing, it is crucial to learn about their life histories so that conservation problems can be remedied quickly, or even avoided.

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Appendix. Microsatellite allele (designated by size) frequencies for types I and II rougheye rockfish, sample size (n), unbiased expected heterozygosity (H_{exp}), and inbreeding coeficient (F_{is}).

Type I

m*Sma* 3	Population																
allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
144	0	0.011	0.014	0.011	0.012	0	0	0	0.010	0.014	0	0.010	0	0	0.033	0.013	0.008
146	0	0	0	0	0	0	0	0	0	0	0	0	0.017	0	0	0	0.001
148	0.010	0	0.014	0.033	0.012	0.014	0.063	0.041	0.020	0.027	0.059	0.040	0	0	0.017	0.039	0.023
150	0.539	0.500	0.403	0.462	0.439	0.4	0.188	0.426	0.449	0.473	0.515	0.410	0.433	0.485	0.500	0.368	0.447
152	0.127	0.074	0.111	0.076	0.073	0.171	0.219	0.098	0.122	0.135	0.118	0.110	0.150	0.076	0.083	0.053	0.107
154	0.196	0.202	0.208	0.114	0.232	0.229	0.125	0.213	0.102	0.149	0.118	0.120	0.217	0.197	0.117	0.250	0.173
156	0.069	0.128	0.139	0.190	0.134	0.129	0.156	0.123	0.133	0.149	0.118	0.180	0.108	0.121	0.133	0.132	0.136
158	0	0.011	0.028	0.005	0.012	0	0.063	0.033	0.041	0.014	0	0	0.008	0.015	0.050	0.013	0.015
160	0.010	0.032	0.028	0.033	0.012	0	0	0.025	0.031	0.027	0.015	0.040	0.008	0.015	0.033	0.079	0.025
162	0	0	0	0.022	0.012	0.014	0.031	0	0.010	0	0	0.050	0	0.015	0.033	0	0.011
164	0	0	0	0.005	0.012	0	0	0	0	0	0	0.010	0	0	0	0	0.002
166	0.049	0.043	0.056	0.033	0.037	0.043	0.063	0.041	0.051	0.014	0.044	0.030	0.058	0.030	0	0.026	0.039
168	0	0	0	0.011	0.012	0	0.063	0	0.031	0	0	0	0	0.045	0	0.013	0.008
170	0	0	0	0.005	0	0	0.031	0	0	0	0.015	0	0	0	0	0.013	0.003
n	51	47	36	92	41	35	16	61	49	37	34	50	60	33	30	38	710
F_{is}	0.282**	0.326**	0.280***	0.169*	0.074	0.241	0.444***	0.346***	0.056	0.178	-0.097	0.201	0.160	0.280**	0.400***	0.195*	
H_{exp}	0.654	0.692	0.768	0.732	0.737	0.75	0.888	0.749	0.756	0.722	0.698	0.774	0.733	0.713	0.718	0.783	0.7647

m*Sma* 5	Population																
allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
103	0	0	0.028	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
109	0.667	0.702	0.694	0.701	0.732	0.729	0.781	0.697	0.684	0.716	0.691	0.660	0.733	0.652	0.733	0.724	0.702
111	0.284	0.266	0.25	0.266	0.232	0.214	0.188	0.270	0.296	0.270	0.294	0.330	0.233	0.288	0.217	0.276	0.265
113	0.049	0.021	0.014	0.033	0.024	0.057	0.031	0.025	0.01	0.014	0.015	0.010	0.033	0.045	0.050	0	0.027
115	0	0.011	0.014	0	0	0	0	0.008	0.01	0	0	0	0	0.015	0	0	0.004
121	0	0	0	0	0.012	0	0	0	0	0	0	0	0	0	0	0	0.001
n	51	47	36	92	41	35	16	61	49	37	34	50	60	33	30	38	710
F_{is}	-0.028	-0.064	0.096	0.184*	0.061	-0.006	-0.207	0.153	-0.137	0.034	0.002	0	-0.016	0.088	0.048	0.026	
H_{exp}	0.477	0.44	0.461	0.439	0.415	0.426	0.365	0.444	0.449	0.42	0.442	0.46	0.41	0.498	0.42	0.405	0.4361

m*Sma* 7	Population																
allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
110	0.490	0.489	0.389	0.408	0.390	0.457	0.406	0.434	0.459	0.278	0.441	0.380	0.383	0.394	0.483	0.395	0.418
112	0.010	0	0	0	0	0	0	0	0.031	0	0.015	0	0	0.015	0	0	0.004
116	0.480	0.489	0.569	0.582	0.585	0.514	0.594	0.533	0.480	0.681	0.515	0.550	0.608	0.561	0.467	0.566	0.549
118	0.010	0.021	0.042	0.005	0.024	0.014	0	0.033	0.020	0.042	0.029	0.050	0	0.03	0.033	0.039	0.023
120	0	0	0	0.005	0	0.014	0	0	0	0	0	0.020	0.008	0	0.017	0	0.004
122	0	0	0	0	0	0	0	0	0.010	0	0	0	0	0	0	0	0.001
124	0.010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
n	51	47	36	92	41	35	16	61	49	36	34	50	60	33	30	38	709
F_{is}	0.008	0.030	-0.050	-0.070	0.238	0.091	0.125	-0.050	0.022	0.104	0.251	0.174	0.042	-0.130	0.164	0.056	
H_{exp}	0.534	0.526	0.53	0.498	0.511	0.534	0.498	0.531	0.563	0.464	0.547	0.556	0.487	0.538	0.557	0.53	0.5239

Type II

m*Sma* 3	Population										
allele	1	2	3	4	5	6	7	8	9	10	Total
142	0	0	0	0	0	0	0	0	0.014	0	0.002
146	0.024	0.055	0.019	0.025	0.105	0.141	0.051	0.028	0.094	0	0.062
148	0.214	0.236	0.130	0.150	0.105	0.205	0.211	0.278	0.217	0.167	0.199
150	0.619	0.391	0.519	0.375	0.500	0.41	0.470	0.417	0.428	0.357	0.452
152	0.095	0.136	0.185	0.35	0.174	0.179	0.157	0.083	0.152	0.143	0.161
154	0	0.073	0.037	0.05	0.047	0.051	0.041	0.083	0.036	0.190	0.051
156	0.024	0.082	0.111	0	0.047	0.013	0.043	0.056	0.022	0.024	0.043
158	0	0.018	0	0.025	0	0	0.018	0.056	0.007	0.071	0.016
160	0.024	0	0	0	0	0	0.003	0	0.007	0.048	0.005
162	0	0.009	0	0.025	0.023	0	0.008	0	0.007	0	0.008
166	0	0	0	0	0	0	0	0	0.014	0	0.002
n	21	55	27	20	43	39	197	18	69	21	510
F_{is}	0.258	0.384***	0.018	0.457***	0.406***	0.452***	0.353***	0.264	0.415***	-0.013	
H_{exp}	0.574	0.764	0.679	0.728	0.701	0.744	0.706	0.75	0.741	0.799	0.722

m*Sma* 5	Population										
allele	1	2	3	4	5	6	7	8	9	10	Total
94	0	0	0	0	0	0	0.003	0	0	0	0.001
99	0	0	0	0	0	0	0.005	0	0	0	0.002
103	0	0.036	0.037	0.05	0.035	0.026	0.015	0.028	0.022	0.024	0.024
107	0	0	0	0.025	0	0.026	0	0	0	0	0.003
109	0.833	0.809	0.741	0.825	0.895	0.846	0.800	0.778	0.804	0.786	0.811
111	0.143	0.155	0.167	0.100	0.047	0.090	0.141	0.111	0.152	0.190	0.133
113	0.024	0	0.056	0	0.023	0.013	0.033	0.083	0.022	0	0.026
115	0	0	0	0	0	0	0.003	0	0	0	0.001
n	21	55	27	20	43	39	195	18	69	21	508
F_{is}	-0.148	-0.127	0.047	0.046	-0.065	-0.108	0.155	-0.157	-0.094	-0.216	
H_{exp}	0.292	0.323	0.427	0.314	0.197	0.278	0.34	0.386	0.331	0.354	0.324

m*Sma* 7	Population										
allele	1	2	3	4	5	6	7	8	9	10	Total
110	1	0.991	1	0.975	0.988	0.962	0.975	0.944	0.993	0.929	0.978
112	0	0	0	0.025	0	0.013	0.025	0.056	0.007	0.071	0.018
114	0	0	0	0	0	0.026	0	0	0	0	0.002
116	0	0.009	0	0	0.012	0	0	0	0	0	0.002
n	21	55	27	20	43	39	197	18	69	21	510
F_{is}	--	--	--	--	--	-0.108	-0.023	-0.030	--	0.655	
H_{exp}	0	0.018	0	0.05	0.023	0.076	0.05	0.108	0.014	0.136	0.042

Appendix. (Continued.)

mSma 11 allele	Population 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
155	0	0	0	0	0	0	0	0	0	0	0	0.010	0	0	0	0	0.001
161	0.010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
165	0	0	0	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0.001
167	0	0	0	0	0	0	0	0.008	0.010	0	0	0	0	0	0	0	0.001
171	0.010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
173	0	0	0	0	0	0	0	0.008	0.010	0	0	0	0	0	0	0	0.001
175	0	0	0.014	0	0.012	0	0	0	0.020	0	0	0	0.008	0	0.017	0	0.004
179	0	0.011	0	0	0	0.014	0	0	0.061	0.027	0	0	0.025	0	0.033	0.013	0.011
181	0.784	0.915	0.792	0.766	0.841	0.786	0.781	0.754	0.745	0.892	0.809	0.830	0.792	0.833	0.733	0.763	0.799
183	0.186	0.074	0.194	0.217	0.146	0.171	0.188	0.213	0.133	0.068	0.162	0.130	0.150	0.167	0.217	0.211	0.166
185	0.010	0	0	0.011	0	0.014	0.031	0.008	0.010	0.014	0.029	0.02	0.008	0	0	0.013	0.010
187	0	0	0	0.005	0	0	0	0.008	0	0	0	0	0.017	0	0	0	0.003
195	0	0	0	0	0	0	0	0	0.010	0	0	0	0	0	0	0	0.001
201	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0.001
n	51	47	36	92	41	35	16	61	49	37	34	50	60	33	30	38	710
F_{is}	-0.055	-0.071	-0.063	0.113	-0.161	-0.120	-0.207	-0.012	-0.148	-0.073	-0.185	0.192	-0.183	0.034	0.050	-0.116*	
H_{exp}	0.353	0.159	0.34	0.367	0.274	0.358	0.365	0.389	0.427	0.202	0.324	0.297	0.353	0.282	0.421	0.378	0.3346

mSma 11 allele	Population 1	2	3	4	5	6	7	8	9	10	Total
157	0	0	0	0	0	0.026	0	0	0	0	0.002
161	0	0	0	0	0	0.026	0	0	0	0	0.002
165	0	0	0	0	0	0	0.003	0	0	0	0.001
167	0	0	0.056	0	0	0	0.003	0	0	0.024	0.005
171	0	0	0	0	0	0	0.003	0	0	0	0.001
173	0	0	0	0.025	0	0	0	0	0	0	0.001
175	0	0	0.037	0	0	0	0	0	0	0.024	0.003
177	0	0	0.019	0	0	0	0.010	0	0	0	0.005
179	0.071	0.045	0.074	0.075	0.058	0.039	0.089	0.028	0.065	0.119	0.072
181	0.119	0.236	0.130	0.125	0.174	0.171	0.157	0.167	0.152	0.19	0.165
183	0.024	0.009	0	0	0.023	0.013	0.063	0	0.014	0	0.031
185	0.738	0.464	0.481	0.500	0.535	0.408	0.398	0.583	0.457	0.476	0.458
187	0.024	0.064	0.037	0	0.070	0.079	0.104	0.111	0.152	0.095	0.090
189	0.024	0.136	0.167	0.250	0.047	0.118	0.096	0.111	0.087	0.071	0.103
191	0	0.009	0	0	0.023	0.026	0.020	0	0.029	0	0.017
193	0	0.018	0	0	0.023	0	0.005	0	0	0	0.006
195	0	0	0	0	0.012	0	0.010	0	0	0	0.005
197	0	0	0	0	0	0	0.005	0	0	0	0.002
199	0	0.018	0	0.025	0.012	0.026	0.018	0	0	0	0.013
201	0	0	0	0	0	0.026	0.008	0	0.007	0	0.006
203	0	0	0	0	0.023	0	0.005	0	0.014	0	0.006
205	0	0	0	0	0	0.013	0.003	0	0.007	0	0.003
209	0	0	0	0	0	0	0	0	0.007	0	0.001
213	0	0	0	0	0	0.026	0	0	0	0	0.002
239	0	0	0	0	0	0	0	0	0.007	0	0.001
n	21	55	27	20	43	38	197	18	69	21	509
F_{is}	-0.072	0.182	0.494***	0.123	0.110	0.235**	0.089	0.021	0.057	-0.053	
H_{exp}	0.445	0.71	0.725	0.682	0.679	0.788	0.785	0.624	0.737	0.725	0.738

mSr7 7 allele	Population 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
184	0.020	0.043	0.069	0.033	0	0	0.063	0	0	0.014	0.029	0	0.025	0.030	0.050	0.013	0.022
190	0.020	0.011	0.014	0.027	0.012	0.029	0	0.016	0.070	0	0.015	0.040	0.017	0.045	0	0	0.022
194	0	0	0	0	0	0	0	0.008	0	0	0	0	0	0	0	0	0.001
196	0	0	0	0	0	0	0.031	0.016	0	0.014	0	0.010	0.008	0.015	0	0	0.005
198	0.069	0.064	0.153	0.114	0.073	0.057	0.031	0.016	0.050	0.122	0.118	0.100	0.067	0.061	0.067	0.118	0.081
200	0.353	0.234	0.167	0.217	0.183	0.314	0.281	0.336	0.290	0.297	0.265	0.170	0.192	0.258	0.267	0.184	0.248
202	0.127	0.160	0.181	0.120	0.110	0.1	0.156	0.131	0.100	0.108	0.103	0.110	0.150	0.152	0.1	0.105	0.125
204	0.039	0.011	0.028	0.038	0.024	0.029	0	0.025	0.050	0.027	0.029	0.030	0.017	0.015	0	0.053	0.028
206	0.029	0.064	0	0.011	0.049	0.071	0.063	0.016	0.020	0.014	0	0.030	0.033	0.045	0.017	0.026	0.028
208	0.010	0.011	0	0.005	0	0	0.094	0.008	0	0.041	0.015	0.010	0.017	0	0.017	0	0.011
210	0	0.043	0.042	0.027	0.037	0.029	0	0.016	0	0.041	0.029	0.030	0.067	0.015	0	0.053	0.028
212	0.147	0.106	0.167	0.185	0.134	0.171	0.063	0.254	0.140	0.135	0.132	0.160	0.225	0.136	0.167	0.158	0.165
214	0.029	0.043	0.042	0.060	0.207	0.086	0.063	0.041	0.070	0.068	0.059	0.090	0.058	0.076	0.067	0.066	0.068
216	0.059	0.074	0.069	0.038	0.098	0.014	0.094	0.049	0.050	0.068	0.074	0.110	0.050	0.045	0.1	0.079	0.063
218	0.029	0.128	0.042	0.071	0.061	0.029	0.031	0.033	0.050	0.027	0.059	0.050	0.033	0.045	0.1	0.092	0.056
220	0.059	0.011	0.028	0.016	0	0.029	0	0.008	0.050	0.014	0.044	0.030	0	0.030	0.017	0.026	0.023
222	0.010	0	0	0.011	0.012	0.014	0.031	0.008	0.010	0	0.015	0	0.017	0.015	0.017	0.026	0.011
224	0	0	0	0.005	0	0.014	0	0.008	0.020	0.014	0	0.020	0.017	0	0	0	0.007
226	0	0	0	0.005	0	0.014	0	0	0	0	0	0.010	0.008	0	0.017	0	0.004
228	0	0	0	0.005	0	0	0	0.008	0	0	0.015	0	0	0.015	0	0	0.003
230	0	0	0	0.011	0	0	0	0	0.020	0	0	0	0	0	0	0	0.003
n	51	47	36	92	41	35	16	61	49	37	34	50	60	33	30	38	710
F_{is}	-0.113	0.011	-0.069	-0.024	0.003	0.097*	-0.059	-0.122	0.064	0.030	-0.101	-0.018	-0.044	-0.028	0.046	-0.023	
H_{exp}	0.829	0.882	0.884	0.881	0.881	0.854	0.888	0.804	0.872	0.864	0.883	0.904	0.878	0.885	0.873	0.901	0.8738

mSr7 2 allele	Population 1	2	3	4	5	6	7	8	9	10	Total
133	0	0	0	0	0	0	0	0	0.007	0	0.001
135	0	0.009	0	0	0	0	0.005	0	0	0	0.003
139	0	0	0	0	0	0	0.003	0	0.014	0	0.003
141	0	0	0	0	0	0.013	0	0	0	0	0.001
147	0	0	0.019	0	0	0.026	0.005	0	0.007	0.024	0.007
149	0.310	0.336	0.389	0.350	0.221	0.372	0.379	0.278	0.333	0.381	0.347
151	0.190	0.127	0.037	0.150	0.209	0.077	0.087	0.139	0.138	0.071	0.113
153	0.286	0.245	0.259	0.100	0.116	0.295	0.267	0.278	0.268	0.262	0.248
155	0.071	0.073	0.093	0.150	0.221	0.103	0.110	0.139	0.109	0.214	0.119
157	0.024	0.091	0.093	0.100	0.093	0.038	0.054	0.056	0.058	0.024	0.062
159	0.024	0.009	0.019	0.025	0.012	0	0.028	0.028	0	0	0.017
161	0	0.018	0	0.050	0.035	0	0.013	0	0	0	0.012
163	0	0.036	0.037	0	0.023	0.026	0.021	0	0.014	0	0.020
165	0.048	0.009	0	0.075	0.023	0.038	0.005	0.028	0.022	0	0.017
167	0.024	0.018	0.037	0	0.023	0.013	0.013	0	0	0.024	0.014
169	0.024	0	0	0	0	0	0.005	0.028	0.022	0	0.007
171	0	0	0.019	0	0	0	0.003	0.028	0	0	0.003
173	0	0	0	0	0.012	0	0	0	0	0	0.001
175	0	0	0	0	0	0	0.003	0	0	0	0.001
177	0	0	0	0	0.012	0	0	0	0	0	0.001
181	0	0.009	0	0	0	0	0	0	0	0	0.001
189	0	0	0	0	0	0	0	0	0.007	0	0.001
193	0	0.009	0	0	0	0	0	0	0	0	0.001
195	0	0.009	0	0	0	0	0	0	0	0	0.001
n	21	55	27	20	43	39	195	18	69	21	508
F_{is}	0.165	0.002	-0.103	-0.032	0.091	0.060	0.065	-0.012	-0.089	-0.014	
H_{exp}	0.796	0.802	0.774	0.825	0.843	0.764	0.763	0.824	0.787	0.752	0.786

Appendix. (Continued.)

Type I mS*r7* 2	Population																
allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
137	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
139	0.010	0	0	0	0.012	0	0	0	0	0	0	0	0	0	0	0	0.001
141	0.010	0	0	0	0	0	0.031	0.008	0	0.014	0	0	0	0	0	0	0.003
143	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.013	0.001
145	0	0	0	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0.001
147	0	0	0.028	0	0	0	0.031	0	0	0.014	0	0	0.008	0	0	0	0.004
151	0	0.011	0	0.005	0.012	0.014	0	0	0	0	0.015	0.010	0	0	0	0	0.004
153	0.020	0.022	0.014	0.011	0.037	0.014	0	0.067	0.051	0	0.074	0.050	0.050	0.045	0.017	0.066	0.035
155	0.029	0.033	0.028	0.049	0.012	0.057	0.031	0.033	0.020	0.027	0.015	0.020	0.025	0.030	0.050	0.039	0.032
156	0	0.011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
157	0.069	0.043	0.028	0.060	0.061	0.043	0	0.017	0.010	0.041	0.029	0.020	0.025	0.030	0.033	0.013	0.035
159	0.039	0.011	0.028	0.016	0.012	0.057	0.094	0.017	0	0.014	0.015	0.020	0.017	0.045	0.017	0.013	0.022
160	0	0	0	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0.001
161	0.216	0.196	0.139	0.120	0.171	0.229	0.125	0.133	0.173	0.149	0.147	0.110	0.217	0.106	0.200	0.158	0.161
163	0.078	0.120	0.042	0.076	0.049	0.029	0.125	0.067	0.133	0.122	0.103	0.110	0.067	0.167	0.067	0.066	0.086
165	0.176	0.120	0.153	0.158	0.122	0.086	0.125	0.133	0.092	0.135	0.132	0.110	0.025	0.182	0.200	0.105	0.126
166	0	0	0	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0.001
167	0.118	0.141	0.167	0.130	0.183	0.186	0.125	0.208	0.214	0.135	0.147	0.220	0.225	0.152	0.200	0.197	0.173
169	0.029	0.054	0.028	0.033	0.049	0.043	0.125	0.067	0.041	0.068	0.059	0.040	0.050	0	0.033	0.066	0.046
171	0.020	0.033	0.042	0.049	0.024	0.014	0.031	0.025	0.041	0.054	0.029	0	0.017	0.106	0.017	0.053	0.034
173	0.020	0.011	0.014	0.022	0.037	0	0.031	0	0.031	0	0.015	0.030	0.058	0.045	0	0.053	0.023
175	0.010	0.022	0.014	0.022	0.012	0.029	0.031	0	0	0.041	0.015	0	0.008	0	0	0.013	0.013
177	0	0	0	0.022	0.012	0.014	0	0.008	0.020	0.014	0	0.010	0.017	0	0.017	0.013	0.011
179	0	0.022	0	0.022	0	0.014	0	0	0	0	0	0.010	0.017	0	0.017	0	0.008
181	0.029	0	0.014	0.022	0.024	0.029	0	0	0.010	0.027	0.015	0.040	0.008	0	0.017	0.026	0.017
183	0.020	0.022	0.028	0.022	0.012	0	0	0.017	0.020	0.014	0.029	0.020	0.050	0.015	0.017	0.013	0.020
185	0.010	0	0.014	0.005	0	0.029	0	0.017	0.010	0	0	0.010	0	0	0.017	0	0.007
187	0	0	0	0	0	0	0	0	0.020	0	0	0.010	0	0	0	0	0.002
189	0	0	0	0	0	0	0	0	0	0	0	0	0.025	0	0	0	0.002
191	0.020	0	0.042	0.016	0.012	0	0	0.025	0.010	0	0.015	0.030	0.008	0.015	0	0.026	0.015
193	0.010	0.011	0.028	0.011	0.012	0	0	0.008	0.010	0	0	0.040	0	0	0	0	0.009
195	0.010	0	0.014	0.022	0.037	0	0.031	0.025	0.020	0	0	0.030	0	0	0.017	0	0.013
197	0	0.011	0.028	0	0.012	0	0	0.008	0	0.027	0.015	0.010	0	0	0.033	0	0.008
199	0.010	0.011	0	0.016	0.012	0.014	0.031	0.033	0	0.014	0.015	0	0.008	0.015	0	0	0.011
201	0	0.022	0	0.011	0	0	0	0.017	0.010	0	0.015	0	0.008	0	0	0	0.006
203	0	0.011	0	0.005	0	0.014	0	0.008	0.010	0	0.044	0.020	0.008	0	0	0	0.008
205	0	0	0.014	0.016	0.012	0	0	0	0	0	0	0	0.017	0.015	0	0	0.006
207	0	0.011	0	0.005	0	0	0	0.008	0	0.014	0	0	0.008	0	0.017	0.013	0.005
209	0	0	0.014	0.005	0	0.014	0	0	0.010	0.014	0	0.010	0.008	0	0	0	0.005
211	0	0	0	0.005	0	0.014	0	0.008	0.010	0.027	0	0	0.008	0.015	0	0	0.006
213	0	0	0	0.005	0	0	0	0.008	0	0	0.015	0	0	0	0	0	0.002
215	0.010	0	0	0	0.024	0	0	0.008	0	0	0	0.010	0	0	0	0.026	0.005
217	0	0	0	0.011	0.012	0.014	0	0.008	0	0.014	0	0.010	0	0	0.017	0	0.006
219	0	0.011	0	0.005	0.012	0	0	0.008	0	0.014	0	0	0.008	0	0	0.013	0.005
221	0.020	0.011	0.014	0.005	0	0	0.031	0	0	0	0	0	0	0	0	0	0.004
223	0.010	0.011	0.014	0	0	0	0	0	0	0	0.029	0	0	0.015	0	0.013	0.005
225	0	0.011	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0.001
227	0	0.011	0	0	0	0	0	0	0.010	0	0	0	0.008	0	0	0	0.002
229	0	0	0.014	0	0.012	0	0	0	0.010	0	0	0	0	0	0	0	0.002
231	0.010	0	0.014	0.005	0	0	0	0	0	0.014	0.015	0	0	0	0	0	0.004
233	0	0	0	0.005	0	0	0	0	0.010	0	0	0	0	0	0	0	0.001
237	0	0	0	0	0	0	0	0.008	0	0	0	0	0	0	0	0	0.001
257	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
n	51	46	36	92	41	35	16	60	49	37	34	50	60	33	30	38	708
F_{is}	0.151	0.023	-0.018	0.040	-0.038	0.147*	-0.074	0.121*	-0.070	0.005	0.015	-0.076	0.121	-0.047	0.094	-0.009	
$H_{o\times0}$	0.899	0.912	0.928	0.929	0.917	0.903	0.934	0.909	0.897	0.923	0.925	0.912	0.89	0.898	0.881	0.913	0.912

Type II mS*r7* 7	Population										
allele	1	2	3	4	5	6	7	8	9	10	Total
196	0.024	0.009	0	0	0.035	0.013	0.003	0	0.022	0	0.010
198	0	0.009	0.037	0.025	0.023	0.026	0.014	0	0	0	0.013
200	0.024	0.027	0	0.025	0.012	0.026	0.016	0.056	0.022	0	0.019
202	0.048	0.018	0	0	0.035	0	0.024	0.083	0.022	0.048	0.024
204	0.024	0.009	0.074	0.025	0.058	0	0.019	0	0.007	0.024	0.021
206	0.024	0.100	0.130	0.100	0.081	0.077	0.1	0.083	0.101	0.071	0.093
208	0.167	0.182	0.204	0.200	0.174	0.179	0.173	0.139	0.188	0.071	0.174
210	0.048	0.155	0.148	0.125	0.128	0.103	0.124	0.194	0.130	0.119	0.128
212	0.190	0.218	0.241	0.300	0.244	0.269	0.241	0.250	0.203	0.333	0.240
214	0.190	0.127	0.037	0.050	0.081	0.103	0.07	0.083	0.123	0.119	0.092
216	0.071	0.091	0.019	0.075	0.035	0.064	0.095	0.028	0.065	0.048	0.072
218	0.095	0.018	0.019	0.075	0.058	0.051	0.046	0.028	0.043	0.071	0.046
220	0	0	0.037	0	0.012	0.026	0.035	0.028	0.036	0.048	0.026
222	0.024	0.018	0.019	0	0.012	0.013	0.011	0	0.014	0	0.012
224	0.024	0	0.019	0	0.012	0.038	0.011	0	0.022	0.024	0.014
226	0.024	0	0.019	0	0	0	0.011	0	0	0.024	0.007
228	0	0.009	0	0	0	0.013	0.003	0	0	0	0.003
230	0	0	0	0	0	0	0.003	0.028	0	0	0.002
232	0.024	0	0	0	0	0	0.003	0	0	0	0.002
234	0	0.009	0	0	0	0	0	0	0	0	0.001
n	21	55	27	20	43	39	185	18	69	21	498
F_{is}	0.046	0.078	0.061	0.120	0.021	-0.063	-0.006	-0.013	-0.007	0.114	
$H_{o\times0}$	0.898	0.867	0.867	0.85	0.879	0.869	0.870	0.878	0.878	0.857	0.870

Appendix. (Continued.)

Type I mSr7 25	Population																
allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	SM	Total
168	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0.001
172	0	0	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0.001
174	0.02	0.043	0	0	0.024	0.014	0	0.016	0	0	0	0	0.025	0.045	0	0.026	0.013
176	0.02	0	0	0.016	0.012	0	0	0.008	0	0	0.015	0	0.008	0.015	0.033	0	0.008
178	0	0	0.014	0.022	0.024	0	0.031	0.008	0.01	0	0.015	0.01	0	0	0.017	0	0.009
180	0.01	0	0.014	0	0	0	0	0	0.02	0.014	0.015	0.01	0.008	0.015	0	0.013	0.007
182	0.02	0.011	0.042	0	0	0.014	0	0.016	0.01	0	0	0.02	0.025	0.015	0.017	0	0.012
184	0	0.033	0	0.016	0.012	0.014	0	0.025	0	0.014	0.015	0	0.017	0.045	0	0	0.013
186	0.029	0.022	0.014	0.022	0.012	0	0.031	0.033	0.02	0	0.015	0.01	0.017	0.045	0.05	0	0.020
188	0.118	0.076	0.042	0.076	0.061	0.157	0.031	0.057	0.092	0.122	0.044	0.05	0.05	0.197	0.10	0.079	0.083
190	0.176	0.185	0.125	0.141	0.22	0.186	0.156	0.172	0.224	0.095	0.147	0.17	0.167	0.091	0.117	0.224	0.164
192	0.186	0.13	0.153	0.152	0.085	0.129	0.063	0.139	0.133	0.095	0.162	0.13	0.142	0.061	0.117	0.079	0.129
194	0.059	0.087	0.083	0.065	0.146	0.10	0.094	0.148	0.071	0.095	0.059	0.08	0.117	0.076	0.167	0.079	0.094
196	0.069	0.011	0.083	0.06	0.012	0.071	0.063	0.025	0.071	0.041	0.118	0.13	0.042	0.045	0.067	0.066	0.059
198	0.059	0.065	0.069	0.087	0.073	0.071	0.063	0.049	0.061	0.081	0.044	0.06	0.067	0.03	0.05	0.079	0.065
200	0.049	0.043	0.069	0.071	0.098	0.043	0.031	0.049	0.02	0.108	0.015	0.05	0.075	0.03	0	0.053	0.054
202	0.01	0.054	0.028	0.027	0	0.057	0.063	0.016	0.02	0.014	0.044	0.04	0.033	0.061	0.05	0.039	0.032
204	0.049	0.065	0.014	0.038	0.012	0.014	0.094	0.033	0.031	0.041	0.059	0.04	0.05	0.03	0.017	0.066	0.039
206	0.02	0.022	0.042	0.049	0.061	0.029	0.063	0.041	0.051	0.068	0.044	0.05	0.042	0.061	0.017	0.026	0.042
208	0.02	0.098	0.042	0.049	0.049	0.086	0.063	0.049	0.041	0.081	0.059	0.05	0.017	0.061	0.067	0.092	0.054
210	0.029	0.011	0.056	0.016	0.024	0	0.063	0.041	0.051	0.027	0.088	0.02	0.017	0.015	0.017	0.039	0.030
212	0.02	0.011	0.042	0.022	0.024	0	0.063	0.016	0.02	0.041	0.015	0.01	0.042	0.015	0.017	0.013	0.022
214	0	0.011	0	0	0	0.014	0	0.025	0.01	0.054	0	0.02	0.008	0.015	0.017	0.013	0.011
216	0.02	0.011	0.028	0.005	0.012	0	0	0.008	0.02	0.014	0	0.02	0	0.015	0.017	0	0.011
218	0.01	0.011	0.014	0.022	0.024	0	0	0.008	0	0	0.029	0	0	0.015	0	0	0.009
220	0	0	0.014	0.022	0	0	0	0.008	0.01	0	0	0.01	0.033	0	0	0	0.008
222	0	0	0	0.016	0.012	0	0	0	0	0	0	0.01	0	0	0.033	0.013	0.006
224	0	0	0.014	0	0	0	0.031	0	0	0	0	0	0	0	0	0	0.001
226	0	0	0	0	0	0	0	0.008	0.01	0	0	0	0	0	0	0	0.001
228	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.017	0	0.001
232	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
n	51	46	36	92	41	35	16	61	49	37	34	50	60	33	30	38	709
F_{is}	0.159***	0.029	0.021	0.120**	0.058	0.083	-0.053	0.035	0.057	0.103*	0.045	0.023	0.078	0.060	0.141**	-0.069	
H_{exp}	0.908	0.918	0.936	0.925	0.906	0.903	0.952	0.917	0.908	0.932	0.924	0.921	0.921	0.934	0.93	0.912	0.9206

Type II mSr7 25	Population										
allele	1	2	3	4	5	6	7	8	9	10	Total
164	0	0	0	0	0	0	0.003	0	0	0	0.001
166	0	0	0.019	0	0	0	0	0	0	0	0.001
168	0	0.018	0.019	0	0.012	0.014	0.015	0	0	0	0.011
170	0	0	0	0	0.012	0.014	0.003	0	0	0	0.003
172	0	0.027	0	0	0.012	0	0.005	0.056	0.014	0	0.010
174	0.024	0.018	0.019	0.050	0.012	0.081	0.046	0	0.022	0.048	0.036
176	0.190	0.164	0.093	0.150	0.093	0.189	0.144	0.194	0.138	0.167	0.146
178	0.143	0.091	0.148	0.125	0.163	0.095	0.103	0.056	0.051	0.095	0.102
180	0.071	0.027	0.019	0.050	0.023	0	0.023	0.111	0.036	0.071	0.032
182	0.048	0.082	0.074	0.025	0.116	0.081	0.059	0.083	0.087	0	0.069
184	0.048	0.045	0.074	0.100	0.047	0.068	0.044	0	0.058	0.095	0.052
186	0.024	0.055	0.019	0.025	0.035	0.054	0.041	0	0.043	0.024	0.039
188	0.048	0.009	0.037	0.025	0	0.014	0.026	0.056	0.043	0	0.025
190	0.024	0.073	0.037	0.025	0.035	0.068	0.036	0.028	0.029	0.048	0.041
192	0	0.018	0	0.100	0.035	0.027	0.028	0.028	0.036	0	0.028
194	0.071	0.055	0.056	0.025	0.023	0.041	0.049	0.083	0.065	0.024	0.049
196	0.024	0.045	0	0	0.035	0	0.056	0.028	0.043	0.024	0.039
198	0.024	0.009	0.074	0	0.023	0.041	0.028	0.028	0.022	0.024	0.027
200	0.024	0.018	0.037	0	0.058	0.027	0.038	0	0.065	0.048	0.038
202	0.024	0.036	0.037	0.025	0.058	0.027	0.036	0	0.051	0.048	0.038
204	0.024	0.045	0.037	0.025	0.023	0	0.008	0	0.007	0.048	0.017
206	0	0.009	0.019	0.075	0.012	0.014	0.023	0.056	0.014	0.048	0.022
208	0.024	0.018	0.019	0	0.012	0.014	0.021	0	0.007	0.024	0.016
210	0	0	0.037	0	0.012	0	0.005	0.056	0.007	0	0.008
212	0.024	0.018	0	0	0.023	0.041	0.015	0	0.029	0	0.018
214	0	0.018	0.019	0.025	0.023	0.027	0.015	0	0.029	0	0.018
216	0.024	0.009	0.037	0	0.012	0.014	0.013	0.028	0	0.048	0.014
218	0.024	0	0	0.050	0	0	0.018	0.028	0.007	0.024	0.013
220	0.048	0.018	0	0	0.012	0.014	0.021	0	0.029	0	0.018
222	0.024	0.027	0	0	0.023	0.014	0.023	0	0	0	0.016
224	0	0	0	0	0.012	0	0.003	0	0	0.048	0.004
226	0	0	0.019	0.050	0.012	0.014	0.010	0.056	0.007	0	0.012
228	0	0.009	0	0	0.012	0	0.005	0.028	0.007	0.024	0.007
230	0	0.018	0.019	0	0.012	0	0.003	0	0.007	0	0.006
232	0	0.009	0	0.025	0	0.014	0.005	0	0	0	0.005
234	0	0	0	0	0	0	0.005	0	0	0	0.002
236	0	0	0	0	0.012	0	0.003	0	0	0	0.002
238	0	0	0	0	0	0	0.005	0	0.022	0	0.005
240	0.024	0.009	0	0	0	0	0.003	0	0	0	0.003
242	0	0	0	0	0	0	0.003	0	0	0	0.001
244	0	0	0.037	0	0	0	0	0	0.007	0	0.003
246	0	0	0	0	0	0	0.003	0	0	0	0.001
248	0	0	0	0	0	0	0	0	0	0.024	0.001
250	0	0	0	0	0	0	0.003	0	0	0	0.001
256	0	0	0	0.025	0	0	0.003	0	0.007	0	0.003
262	0	0	0	0	0	0	0.003	0	0.007	0	0.002
268	0	0	0	0	0	0	0.003	0	0	0	0.001
n	21	55	27	20	43	37	195	18	69	21	506
F_{is}	0.037	-0.023	-0.050	-0.061	0.014	0.103*	0.019	-0.007	-0.023	-0.004	
H_{exp}	0.939	0.942	0.953	0.944	0.943	0.933	0.946	0.938	0.949	0.949	0.944

A Simulation Approach of Population Differentiation and Individual Assignment to Assess the Relevance of Spatial Genetic Data among Rockfishes

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Abstract

We combine temporal estimates of variance effective population size (N_e) and spatial genetic structure analyses from darkblotched rockfish (*Sebastes crameri*) to analyze the theoretical relationship between F_{ST} and population assignment (PA) of individuals to their site of origin under different migration scenarios. Although F_{ST} is the most common parameter to measure spatial genetic differentiation, its statistical significance can appear "inflated" by employing markers with numerous alleles (e.g., microsatellite DNA). PA can also assess the data's strength for population discrimination by minimizing departures from Hardy-Weinberg and linkage (gametic) equilibria if genetic structure exists. Our results suggest that it is unrealistic to obtain informative PAs (>1/k, k = number of populations) when $F_{ST} < 0.007$, even though all simulations showed statistically significant F_{ST} values. This limit was proposed as threshold value to classify northeastern Pacific rockfishes using published and unpublished genetic information, and thus assessing which species are more or less likely to lose spatially unique genetic diversity if local populations are extirpated.

Introduction

Information on the spatial genetic structure of marine organisms has been incorporated into management and conservation practices for

several decades (Carvalho and Hauser 1995). For instance, genetic differentiation among samples in space has been commonly understood as evidence for discrete stocks, thus granting them status of separate management units. The rationale behind this decision-making process is to avoid overexploitation of local (sub) populations, which might ultimately lead to loss of spatially unique genetic diversity. However, Waples (1998) exposed numerous potential flaws in interpreting marine genetic data for conservation initiatives. One important conclusion from that review is the importance of identifying when statistical and biological differences are in agreement. Current molecular tools containing a high number of alleles (e.g., microsatellites) have more intrinsic statistical power for hypothesis testing than less variable markers (Hedrick 1999, Kalinowski 2002); they are therefore more likely to show significant results, but do they reflect evolutionary processes that are relevant for management?

Genetic differentiation (GD) is commonly reported in the literature as F_{ST}, a parameter that varies theoretically between 0 and 1, although average values for marine and anadromous fish populations within species do not usually exceed 0.1 (Waples 1998). Sampling among populations with large F_{ST} results in: (*i*) genotype frequencies that depart from Hardy-Weinberg equilibrium (HWE) expectations, and (*ii*) linkage (gametic) disequilibrium (LD) among physically unlinked loci (Hedrick 2000). Minimizing these two phenomena facilitates successful population assignment (PA) of individuals to their most likely source population by clustering methods (Pritchard et al. 2000). PA methods therefore represent another direct measure of the genetic data's strength to discriminate populations. However, they and their implications for management are rarely considered when analyzing marine genetic data.

A typical example of clear-cut management based on genetic data is found among salmon populations; a statistically significant $F_{ST} = 0.07$ among chinook salmon (*Oncorhynchus tshawytscha*) fall, winter, and spring life-history types from California's Central Valley (Banks et al. 2000) ensures PA = 99% of individuals into their natal sources (Banks and Jacobson 2004). In comparison, darkblotched rockfish (*Sebastes crameri*), a typical marine example, shows $F_{ST} = 0.002$ that is also statistically significant, but clustering results in extremely low PA owing to negligible values of LD and deviations from HWE (Gomez-Uchida and Banks 2005). This finding further extends Waples' (1998) question of how much GD is biologically significant, in this case from a management and conservation standpoint.

Increasing numbers of endangered and overfished northeastern Pacific rockfishes (genus *Sebastes*) offer particular management challenges (Parker et al. 2000, Berkeley et al. 2004); varying levels of genetic differentiation across species complicates classification of which species face greater or lesser conservation risks if discrete management units

are not implemented. In this paper, our goal was to identify a range of F_{ST} values for which levels of PA were "informative." Because the number of source populations (k) defines the minimum level (random) of individual assignment, we considered informative if PA > $1/k$. To accomplish this, we analyzed a series of theoretical F_{ST} vs. PA values under different migration/gene flow scenarios, which were compared to published and unpublished estimates of genetic differentiation within the *Sebastes* complex.

Material and methods

The input model for our simulations was based on spatial genetic structure analyses (Gomez-Uchida and Banks 2005) and estimates of variance effective population size ($N_e \approx 10{,}000$) for darkblotched rockfish *Sebastes crameri* in the northeastern Pacific (Gomez-Uchida and Banks 2006). Genetic drift and rates of inbreeding depend on N_e rather than census sizes (N) (Wright 1931). We assumed ideal conditions where $N_e = N$, and specified 24 populations with random mating—each containing 500 ($10{,}000/24 \approx 500$) diploid individuals and equal number of males and females—distributed in one-dimension stepping-stone model of migration using Easypop (Balloux 2001). First, we chose 24 populations based on the number of samples that maximized estimates of GD for *S. crameri* after pooling small-size samples (Gomez-Uchida and Banks 2005). Second, the stepping-stone migration model (SSMM) was based on isolation-by-distance (IBD) patterns found in *S. crameri* (Gomez-Uchida and Banks 2005). Decay of gene flow with increasing geographic distance is characteristic of SSMM (Slatkin 1993).

To generate a series of theoretical F_{ST} values, we ran ten simulations within eight migration or gene flow scenarios: 5%, 10%, 15%, 20%, 25%, 50%, 75%, and 95% of individuals to adjacent demes. We chose the K-allele mutation (KAM) model (Crow and Kimura 1970) for seven unlinked loci with different mutation schemes to account for the observed differences among loci found in Gomez-Uchida and Banks (2005). Mutation rates were estimated from the total number of alleles scored for each locus (Gomez-Uchida and Banks 2005) and using Ewens' (1972) relationship between the expected number of neutral alleles in a sample of $n = 250$, and $\theta = 4N_e$, where μ = mutation rate (Table 8.3, Nei 1987). We then used a linear regression ($R^2 = 0.98$) to estimate θ from the observed number of alleles for each locus, and thus derive μ using N_e from Gomez-Uchida and Banks 2006. We calculated the following mutation rates: $\mu_1 = 0.000036$; $\mu_2 = 0.000042$; $\mu_3 = 0.000062$; $\mu_4 = 0.00013$; $\mu_5 = 0.00015$; $\mu_6 = 0.00015$, and $\mu_7 = 0.000010$. Populations drifted for 10,000 generations with the option of minimal variability (i.e., all individuals start with the same allele); this setting provided a distribution of allele frequencies that best resembled those found in Gomez-Uchida and Banks (2005).

Population genotypes from each simulation were analyzed using FSTAT (Goudet 1995) for several overall genetic statistics: (*i*) level of genetic differentiation using F_{ST} (Weir and Cockerham 1984), (*ii*) number of locus pairs in LD, and (*iii*) departures from HWE using F_{IT} (Weir and Cockerham 1984). Given that each simulation is an independent event, we report average values and standard deviations that were plotted against all migration scenarios. Statistics from Gomez-Uchida and Banks (2005) were included as a reference in the plots. Significant probabilities ($P < 0.05$) associated with F_{ST}s were calculated through randomizations (Goudet 1995).

To estimate PA, we relied on a Bayesian estimator that probabilistically assigns individuals to hypothetical clusters so as to minimize departures from HWE and to minimize LD within each cluster (Pritchard et al. 2000). We then selected three populations from each simulation covering the entire linear theoretical distribution—two from the extremes and one from the middle. Likewise, genotypes from three sampling locations off the West Coast in Gomez-Uchida and Banks (2005)—Washington (W4), central Oregon (O10) and northern California (C5)—were included for comparison. Here, we used Whichloci (Banks et al. 2003) to enlarge sample sizes to match those of theoretical populations. We then utilized the software Structure version 2 (Pritchard et al. 2000) to determine membership coefficients for each individual into three independent clusters. The average individual membership coefficient into each cluster provides a measure of PA. Software settings included: burnin length = 15,000 repetitions; Markov Chain Monte Carlo run = 50,000 iterations; ancestry model = admixture; and allele frequency model = correlated (Falush et al. 2003). All runs assumed k (number of populations) = 3.

We finally plotted the relationship between F_{ST} and average PA among clusters for each migration scenario. To draw our conclusions, we took into account that PA had to be higher than 0.33 ($k = 3$) to be considered informative. These values were compared to published and unpublished genetic statistics (mainly F_{ST}) from 11 other congeneric species studies that used microsatellite markers.

Results

Genetic statistics

The magnitudes of F_{ST}, F_{IT}, and LD decreased as levels of migration increased (Fig.1). The highest values were obtained with 5% of migration and the lowest with 75% or 95% of migration. Results from these high levels of gene flow best resembled actual darkblotched rockfish data. All F_{ST} values were statistically significant throughout all simulations.

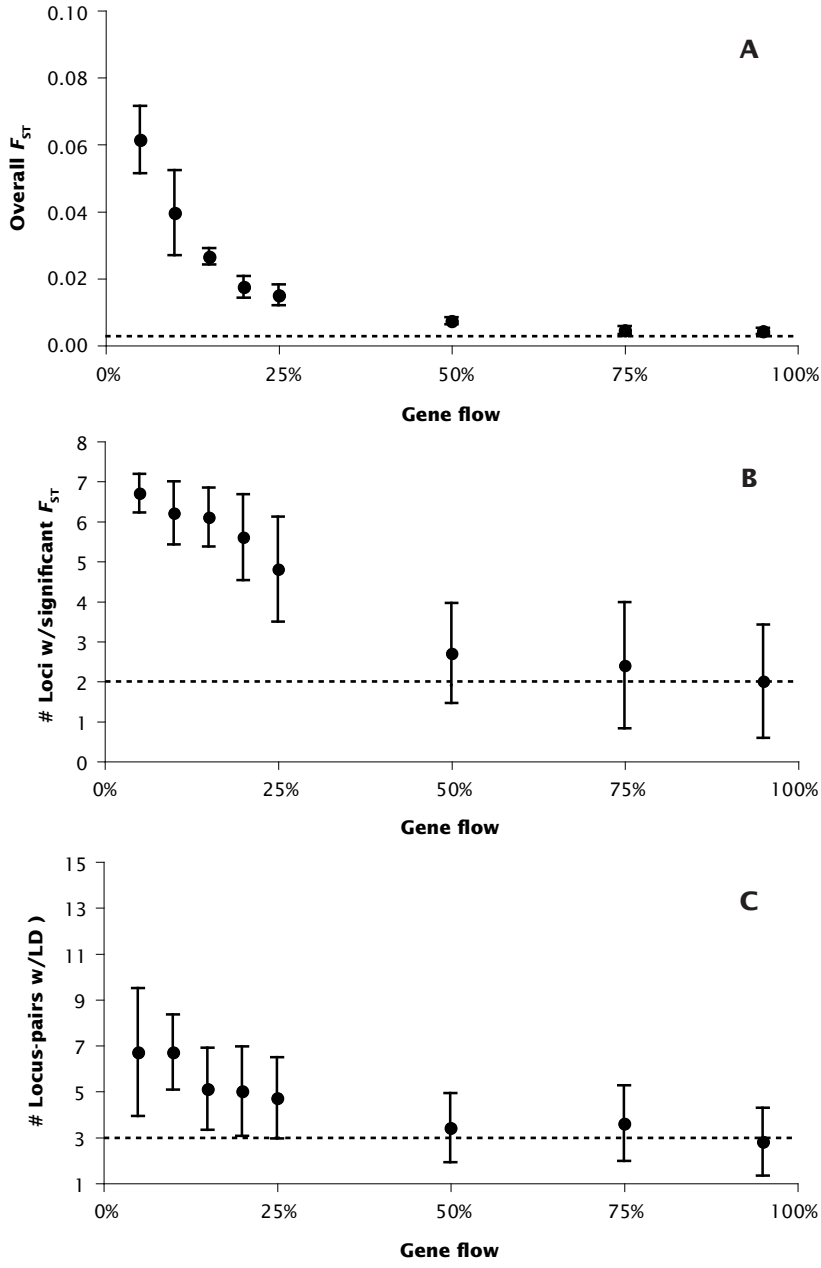


Figure 1. Plots of genetic statistics such as (A) overall F_{ST}, (B) departures from Hardy-Weinberg equilibrium (F_{IT}), and (C) linkage (gametic) disequilibrium (LD) as a function of varying levels of gene flow among theoretical populations of *Sebastes crameri*. Actual genetic statistics for *S. crameri* (Gomez-Uchida and Banks 2005) are represented with a dashed line for comparison (# = number).

Table 1. Population assignment (PA) of three theoretical populations—top, middle, and bottom—from the linear stepping-stone distribution, and three reference samples of *Sebastes crameri* taken off Washington (W4), Oregon (O10), and California (C5) (Gomez-Uchida and Banks 2005) to three clusters.

Migration scenario	Top			Middle			Bottom		
5%	1	2	3	1	2	3	1	2	3
	0.96	0.02	0.02	0.05	0.91	0.04	0.02	0.02	0.96
10%	1	2	3	1	2	3	1	2	3
	0.90	0.02	0.08	0.07	0.84	0.09	0.08	0.02	0.90
15%	1	2	3	1	2	3	1	2	3
	0.84	0.13	0.03	0.16	0.72	0.12	0.12	0.04	0.84
20%	1	2	3	1	2	3	1	2	3
	0.78	0.15	0.07	0.21	0.61	0.18	0.20	0.06	0.74
25%	1	2	3	1	2	3	1	2	3
	0.72	0.07	0.21	0.19	0.61	0.20	0.20	0.08	0.72
50%	1	2	3	1	2	3	1	2	3
	0.60	0.26	0.14	0.23	0.51	0.26	0.17	0.60	0.23
75%	1	2	3	1	2	3	1	2	3
	0.31	0.35	0.34	0.33	0.33	0.34	0.35	0.32	0.33
95%	1	2	3	1	2	3	1	2	3
	0.34	0.32	0.34	0.33	0.34	0.33	0.33	0.34	0.32
Reference samples	W4			O10			C5		
	1	2	3	1	2	3	1	2	3
	0.31	0.36	0.35	0.32	0.32	0.36	0.33	0.34	0.32

PA was obtained from average individual membership coefficients of each population or sample into each cluster using the software Structure version 2 (Pritchard et al. 2000). Migration scenarios indicate percentage of individuals exchanged to adjacent theoretical populations. Reference samples were enlarged to a size of $n = 500$ using Whichloci (Banks et al. 2003) to match theoretical population sizes.

PA and F_{ST}

The value of PA diminished rapidly as migration increased (Table 1). For the lowest level of migration (5%), PA of individuals to clusters was the highest (>95%) and cluster separation was clear with a few misclassified individuals (Fig. 2a). When gene flow was between 10% and 50%, PA varied between 90% and 51%, respectively (Table 1); here, between 10% and 49% of individuals were generally misclassified (Figs. 2b-2f). Informative PA was not attainable for simulations with 75% and 95% of gene flow (Table 1) showing poor cluster separation (Fig. 2g and 2h). The estimate of PA of darkblotched rockfish data from Gomez-Uchida

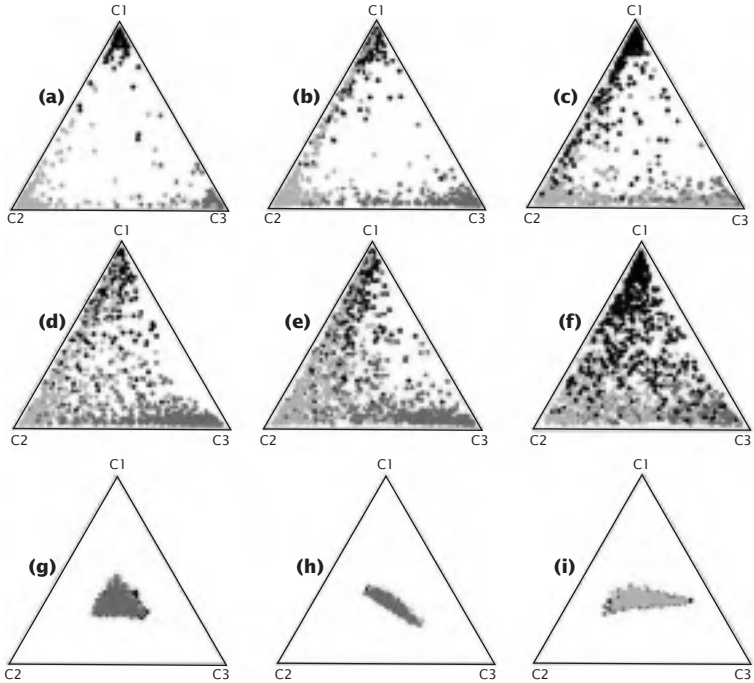


Figure 2. Diagram of population assignment (Pritchard et al. 2000) of three theoretical populations of *Sebastes crameri* (black, light gray, and dark gray) to three clusters (triangle's vertices) in simulations with (a) 5%, (b) 10%, (c) 15%, (d) 20%, (e) 25%, (f) 50%, (g) 75%, and (h) 95% of stepping-stone migration. Description of the theoretical populations is found in Table 1. Diagram (i) was obtained using three reference samples off Washington (W4), Oregon (O10), and California (C5)(Gomez-Uchida and Banks 2005) after enlarging sample sizes using Whichloci (Banks et al. 2003) to match theoretical population sizes (500 individuals).

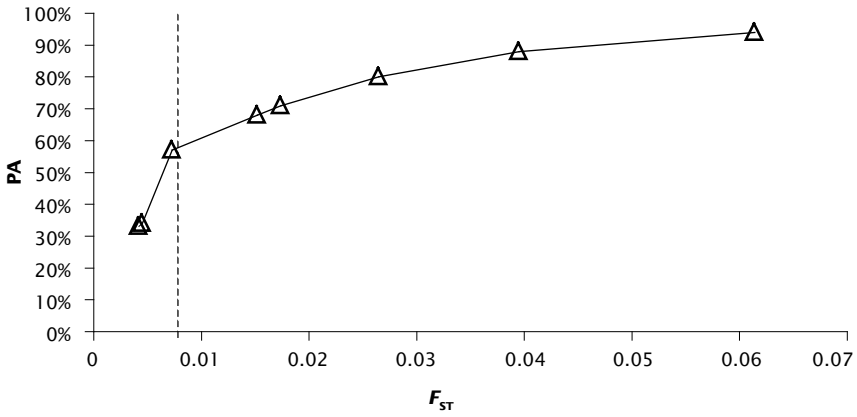


Figure 3. Plot of population assignment (PA) of individuals to their population of origin using model-based clustering (Pritchard et al. 2000) vs. F_{ST} (genetic distance) from theoretical populations of *Sebastes crameri*. The vertical dotted line indicates our criterion (F_{ST} = 0.007) to roughly separate informative and uninformative levels of genetic differentiation.

and Banks (2005) was similar to that obtained for the last two migration scenarios (Table 1, Fig. 2f).

From the relationship between PA and F_{ST}, we found that when $F_{ST} <$ 0.007, PA declined rapidly to uninformative levels (Fig. 3); the opposite trend was found when $F_{ST} >$ 0.007.

Discussion

We have demonstrated empirically through simulations that informative PA decreases rapidly when $F_{ST} <$ 0.007; likewise, PA increases steadily when $F_{ST} >$ 0.007. Adopting this criterion, it is possible to classify rockfishes according to their F_{ST} values from published and unpublished studies using microsatellites. For instance, bocaccio *S. paucispinis* (F_{ST} = −0.001; Matala et al. 2004a), grass rockfish *S. rastrelliger* (F_{ST} = 0.001; Buonaccorsi et al. 2004), shortraker rockfish *S. borealis* (F_{ST} = 0.001; Matala et al. 2004b), canary rockfish *S. pinniger* (F_{ST} = 0.001; Gomez-Uchida and Banks 2006), and darkblotched rockfish *S. crameri* (F_{ST} = 0.002; Gomez-Uchida and Banks 2005) are located to the left of the reference, where spatially explicit management would be less critical; Pacific ocean perch *S. alutus* (F_{ST} = 0.015; Withler et al. 2001), black rockfish *S. melanops* (F_{ST} = 0.018; Miller et al. 2005), copper rockfish *S. caurinus* (F_{ST} = 0.036; Buonaccorsi et al. 2002), and brown rockfish *S. auriculatus*

(F_{ST} = 0.056; Buonaccorsi et al. 2005), on the other hand, are positioned toward the right of this reference, where spatially explicit management would be more critical. While spatial management of cryptic species of vermillion rockfish *S. miniatus* (F_{ST} = 0.097; J.R. Hyde, Scripps Institution of Oceanography) and rougheye rockfish *S. aleutianus* (F_{ST} = 0.301; Gharrett et al. 2005) is not an issue; they represent extreme examples of GD found in the complex. Failure to recognize their separate taxonomic status and geographic locations of putative hybridization zones might result in extirpation of local and unique genetic diversity.

We have reached these conclusions by assuming that our simulations based on parameters for *S. crameri* could be extrapolated to other representatives of the rockfish complex. Many rockfishes have shown IBD patterns (e.g., Withler et al. 2001; Buonaccorsi et al. 2002, 2004, 2005), suggesting that SSMM might have general application. However, other input parameters such as N_e, number of populations and their biological attributes, number of selectively neutral loci, and sample sizes clearly limit the impact of our results. These caveats are discussed in detail in the following paragraphs.

First, different estimates of N_e will generate a different set of mutation rates and will affect the amount of genetic drift in the population; bottlenecks, range expansions or selective sweeps described for particular species can therefore affect the outcome of our simulations. For instance, Buonaccorsi et al. (2004, 2005) have provided genetic evidence for bottlenecks in copper and brown rockfish populations from Puget Sound; our conclusions might then be appropriate to only the coastal segment of the geographic distribution of the aforementioned species. In addition, no other N_e estimates are available for rockfishes to our knowledge, which emphasize the increasing need for demographic genetics studies in rockfish conservation.

Second, we assumed a fixed number of populations and ideal conditions within each one; this is necessary in order to reproduce the evolutionary process under specific settings. Ideal conditions are normally violated in real populations. For example, our results possess restricted value for species out of migration-drift-equilibrium, which might suggest a recent colonization event (e.g., Slatkin 1993). In non-equilibrium species, an estimate of population differentiation based on F_{ST} will be biased (Waples 1998). In these cases, the absolute allelic divergence rather than the proportion of variation among populations can be a better predictor (A.J. Gharrett, University of Alaska Fairbanks, pers. comm.).

Third, Cornuet et al. (1999) described in a similar study that using Pritchard et al.'s (2000) Bayesian approach it is possible to attain 100% of PA using 10 microsatellite loci and 30-50 individuals per population when F_{ST} is approximately 0.1. Genetic studies in the genus *Sebastes* have commonly utilized between 5 and 12 microsatellite loci, so our

choice of 7 microsatellite loci falls within this range. Incorporating more loci none-the-less increases both the chance of successful PA (Cornuet et al. 1999) and the precision of F_{ST} estimates (Kalinowski 2002). In addition, these loci were assumed to be selectively neutral, and therefore provide limited insight into adaptive evolutionary processes of rockfish populations. In general, wide latitudinal ranges characterize the geographic distribution of rockfishes; many of them are found between the coasts of Alaska and California (Love et al. 2002), which may offer ample opportunities of local adaptation given contrasting oceanographic conditions.

Fourth, how sample sizes might affect our analyses was overlooked in the present study and deserves further consideration in subsequent simulation experiments. In simple terms, the higher the F_{ST}, the smaller the required sample sizes to obtain precise estimates (Kalinowski 2005). Because we analyzed all population genotypes, the sampling bias would then be more pronounced within high gene flow scenarios ($F_{ST} < 0.007$).

In conclusion, traditional (F_{ST}) and novel (PA) measures of population discrimination hold great promise to elucidate basic questions in conservation genetics, such as defining the empirical boundaries of the "population" concept (Waples and Gaggiotti 2006). Similarly, the goal of our study was to present a critical look at the management value of significant GD among populations within congeneric *Sebastes* species. Differences in their genetic structure should warrant different conservation strategies. Despite the analytical restrictions previously discussed, our criterion sought to identify which species are more likely to lose spatially unique genetic diversity represented by particular genotypes (which ultimately ensure informative PA) if local populations are extirpated.

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Preliminary Identification of Pelagic Juvenile Rockfishes Collected in the Gulf of Alaska

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Abstract

Many pelagic juvenile rockfish (*Sebastes*) were collected in juvenile salmonid surveys in the Gulf of Alaska (GOA) from 1998 to 2002. Often, species identification of rockfish is difficult or impossible at this stage of development (20 to 40 mm), and the juveniles of only a few species indigenous to Alaska waters have been described. These collections are samples of the first large aggregations observed in GOA waters and provided an opportunity to document the occurrence of several species of rockfish. Using mtDNA markers developed to identify rockfish species, we were able to identify unequivocally four species (*Sebastes alutus*, *S. aleutianus*, *S. borealis*, *S. reedi*) from subsamples of the collections. Other individuals were assigned to groups of two or three species. Using morphological data alone, we identified *S. borealis*, *S. crameri*, and *S. reedi*. The other species were initially indistinguishable by their mor-

phology from *S. alutus*. The combined genetic and morphological data successfully resolved the other species as *S. entomelas* and probably *S. ciliatus/variabilis*, although *S. polyspinis* cannot be ruled out. In addition to documenting the presence of these species in the GOA, the results provide useful information for identifying pelagic juvenile rockfishes in surveys targeting this early life history stage.

Introduction

Little is known about the ecology of pelagic juvenile rockfishes in the Gulf of Alaska (GOA); most species have not even been described at this stage of development (see Kendall 1991). However, sampling for juvenile rockfishes off central California has provided an index of year-class strength for several species (Adams 1995). The challenge is that it is presently difficult or impossible to identify the larvae and juveniles of many rockfish species from their morphology. Consequently, it is not possible to trace the early life history of many species.

Under the Auke Bay Laboratory's Ocean Carrying Capacity (OCC) Program, we conducted a number of surveys to study the distribution of young salmonids. Along several transects spaced around the northern GOA, many young-of-the-year (YOY) rockfish were also collected. These specimens offered an unparalleled opportunity to learn about the seasonal distributions of the species sampled. Recently we developed methods to identify rockfishes, including larvae and juveniles, using mitochondrial DNA (mtDNA) markers (Gharrett et al. 2001, Li et al. 2006a). With these markers we can identify most of the species found in the GOA and along the North American Pacific coast. The few species that we cannot unequivocally identify form small groupings of two or three species.

It would be convenient in the field to be able to identify juvenile rockfishes visually. The challenge is that it is first necessary to know what the species are before morphological characteristics can be relied on to distinguish species. The mtDNA markers can assist in evaluating morphological characteristics useful for species identification by determining the species, independent of visual examination (Li et al. 2006b).

One objective of the present study was to apply morphological criteria to identify fish, and then to compare and combine results with the genetic information. A second objective was to obtain preliminary information about the diversity of species in the hauls. The fish sampled from several of the collections were chosen to represent as many of the species and morphologies present in the hauls as possible. If the predominant species were commercially important, subsequent studies of their genetic structure could provide useful management information.

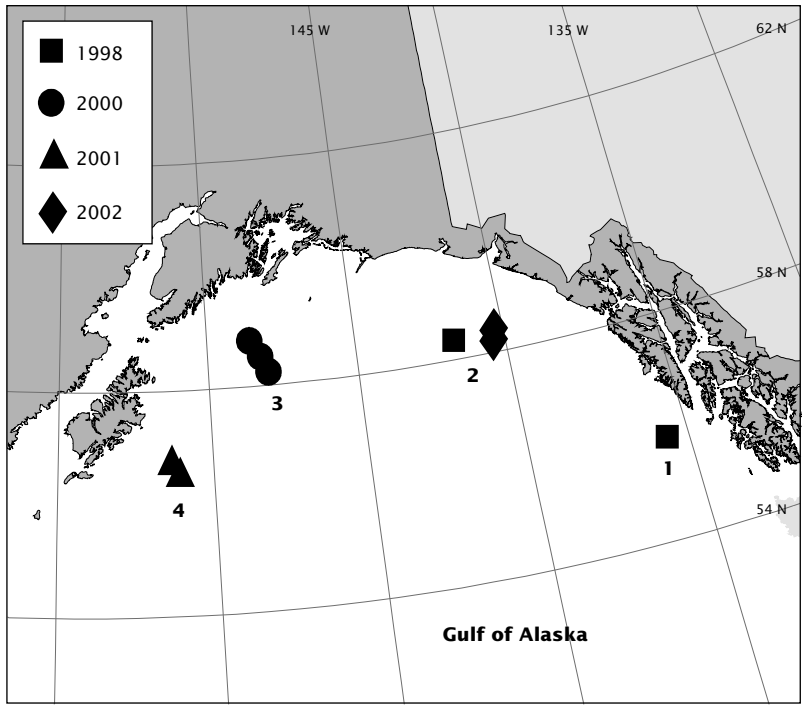


Figure 1. Sites at which juvenile rockfish analyzed in this paper were collected in 1998-2002. Details of collections are in Table 1. Site 1 is off Cape Ommaney, site 2 is off Ocean Cape, site 3 is along the Seward Line, and site 4 is off Cape Chiniak.

Materials and methods

Samples

Juvenile rockfishes were collected in the GOA by NOAA personnel during the 1998, 2000, 2001, and 2002 OCC/Global Ocean Ecosystem Dynamics (GLOBEC) salmonid research surveys onboard the contracted fishing vessel *Great Pacific*, a 38 m stern ramp trawler (see Farley et al. 2001 for details). Samples were collected using a midwater rope trawl towed at or near the surface during daylight hours. After collection, rockfishes from each tow were frozen as a group at –70ºC. Later, the fish were transferred to –70ºC freezers at the Auke Bay Laboratory where they were partially thawed to facilitate the removal of 55 individuals from the masses of frozen fish collected in all four years. Two or three hauls were sampled from each year (Fig. 1; Table 1). The fish were briefly examined to note obvious qualitative differences in morphology. A small fillet was

Table 1. Location, mtDNA haplotype, and species identification of juvenile rockfish based on genetic and morphological analysis.

Fish no.	Location[a]	Initial category[b]	MtDNA haplotype[c]	Genetic identification	First morphological exam	Final identification
1	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
2	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
3	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
4	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
5	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
6	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
7	Cape Chiniak 59	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
8	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
9	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
10	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
11	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
12	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
13	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
14	Cape Chiniak 58	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
15	Seward Line 1	1	FA____	*S. ciliatus*/ *variabilis*, *polyspinis*, or *crameri*	*S. alutus* group	*S. ciliatus*/ *variabilis* or *polyspinis*
16	Seward Line 1	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
17	Seward Line 1	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
18	Seward Line 1	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
19	Seward Line 1	1	FA____	*S. ciliatus*/ *variabilis*, *polyspinis*, or *crameri*	*S. alutus* group	*S. ciliatus*/ *variabilis* or *polyspinis*
20	Seward Line 1	1	KF__E_	*S. aleutianus*	*S. alutus* group	*S. aleutianus*
21	Seward Line 1	2	FA____	*S. ciliatus*/ *variabilis*, *polyspinis*, or *crameri*	*S. crameri*	*S. crameri*
22	Seward Line 5	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
23	Seward Line 5	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
24	Seward Line 5	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
25	Seward Line 5	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
26	Seward Line 5	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*

Table 1. (Continued.)

Fish no.	Location[a]	Initial category[b]	MtDNA haplotype[c]	Genetic identification	First morphological exam	Final identification
27	Seward Line 3	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
28	Seward Line 3	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
29	Seward Line 3	3	FF_D__	*S. borealis*	*S. borealis*	*S. borealis*
30	Seward Line 3	3	FF_D__	*S. borealis*	*S. borealis*	*S. borealis*
31	Seward Line 3	4	rAD__F	*S. reedi*[d]	*S. reedi*	*S. reedi*
32	Seward Line 3	4	rAD__F	*S. reedi*[d]	*S. reedi*	*S. reedi*
33	Cape Ommaney	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
34	Cape Ommaney	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
35	Cape Ommaney	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
36	Cape Ommaney	6	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
37	Cape Ommaney	5	EFCI__	*S. mystinus* or *entomelas*	*S. alutus* group	*S. entomelas*
38	Cape Ommaney	5	EFCI__	*S. mystinus* or *entomelas*	*S. alutus* group	*S. entomelas*
39	Cape Ommaney	5	EFCI__	*S. mystinus* or *entomelas*	*S. alutus* group	*S. entomelas*
40	Ocean Cape 88	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
41	Ocean Cape 88	4	rAD__F	*S. reedi*[d]	*S. reedi*	*S. reedi*
42	Ocean Cape 88	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
43	Ocean Cape 88	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
44	Ocean Cape 88	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
45	Ocean Cape 88	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
46	Ocean Cape 88	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
47	Ocean Cape 9	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
48	Ocean Cape 9	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
49	Ocean Cape 9	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
50	Ocean Cape 9	2	FAD__F	*S. ciliatus/ variabilis*, *polyspinis*, or *crameri*	*S. crameri*	*S. crameri*
51	Ocean Cape 8	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
52	Ocean Cape 8	2	FA____	*S. ciliatus/ variabilis*, *polyspinis*, or *crameri*	*S. crameri*	*S. crameri*

Table 1. (Continued.)

Fish no.	Location[a]	Initial category[b]	MtDNA haplotype[c]	Genetic identification	First morphological exam	Final identification
53	Ocean Cape 8	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
54	Ocean Cape 8	1	BB____	*S. alutus*	*S. alutus* group	*S. alutus*
55	Ocean Cape 8	2	FA____	*S. ciliatus/ variabilis*, *polyspinis*, or *crameri*	*S. crameri*	*S. crameri*

[a]Cape Chiniak 59 = Aug 1, 2001, 56.4N, 151.2W
Cape Chiniak 58 = Aug 1, 2001, 56.3N, 151.0W
Seward Line 1 = Aug 11, 2000, 58.1N, 147.6W
Seward Line 5 = Aug 12, 2000, 58.5N, 148.3W
Seward Line 3 = Aug 11, 2000, 58.3N, 148.1W
Cape Ommaney = July 26, 1998, 55.8N, 135.7W
Ocean Cape 88 = July 29, 1998, 58.3N, 141.7W
Ocean Cape 9 = July 18, 2002, 58.2N, 140.4W
Ocean Cape 8 = July 18, 2002, 58.3N, 140.3W

[b]1 = Silver sided, blackish head.
2 = Large with about 4 brown vertical bands across back.
3 = White, deep body.
4 = Some vertical brown banding.
5 = Large, reddish tinge, narrow body.
6 = Larger with faint vertical banding.

[c]Haplotypes given in order for these enzymes: *Mbo* I, *Bst*N I, *Bst*U I, *Dde* I, *Hinf* I, and *Rsa* I. Underlined spaces indicate enzymes that were not used. See Li et al. 2006a for restriction fragment patterns observed in this study.

[d]After *S. reedi* added to reference set.

removed for genetic analysis from the right side of the fish, taking care not to damage the head, left side, or fins. Fillets were placed in a DNA preservative solution (Seutin et al. 1991). The sampled fish were then refrozen, and later were thawed, fixed in 10% formalin for a week, and then preserved in 70% ethanol for morphological examination.

Genetic analysis

Total cellular DNA was isolated using DNeasy® Tissue Kits (Qiagen, Valencia, California). The ND3/ND4 target region was PCR-amplified from total genomic DNA using primers and methods described in Gharrett et al. (2001). Subsamples of the PCR-amplified mtDNA regions were subjected to restriction endonuclease digestion in order to detect species-specific restriction site fragments using conditions recommended by the manufacturers. Restriction fragments were separated by electrophoresis through 1.5% agarose (a mixture composed of one part Ultra Pure® agarose [BRL Gibco, Grand, New York] and two parts Synergel® [Diversified Biotech Inc., Boston]) in 0.5x TBE buffer (TBE is

90 mM Tris-boric acid, and 2 mM EDTA, pH 8.3). The DNA in the gel was stained with ethidium bromide and digitally photographed on an ultraviolet light transilluminator. One kilobase and 100 base pair ladders were used as references to estimate restriction fragment sizes. Fragment sizes were estimated from digital images using ProRFLP 2.38 (DNA ProScan Inc., Nashville, Tennessee). The restriction sites were positioned using the restriction site maps we constructed for 71 *Sebastes* species (Gharrett et al. 2001, Li et al. 2006a). New haplotypes were analyzed by electrophoresis through 12% polyacrylamide (29:1 acrylamide:bisacrylamide) in 1x TBE and stained with SYBR Green 1 Nucleic Acid Stain® (Molecular Probes, Eugene, Oregon) to estimate accurately the sizes of small (about 25 base pairs) restriction fragments. We also confirmed species identifications based on the key by including known reference samples on gels.

Morphological descriptions

Morphological characters of the YOY fish were examined to confirm the utility of using previously reported species-determining characters, to characterize the juvenile life history stage of previously undescribed species, and to look for useful identifying characters. The results of the genetic analysis of the 55 juvenile rockfish were not communicated until a thorough preliminary morphological analysis had been conducted. The initial morphological examination consisted of grouping the fish based on pigmentation, meristics, and body shape. Observations made on each specimen included standard length and body depth (measured at the deepest point, usually at the insertion of the pelvic fins), details of the pigment patterns, and head spine patterns, appearance, and strength. The fish were x-rayed at the University of Washington's Fish Collection using a standard soft x-ray machine. It was not possible to count fin rays accurately on these x-rays, so the fish were x-rayed again using a digital x-ray machine at the Alaska Fisheries Science Center in Seattle. Although vertebrae were countable, it was still difficult to count the fin rays on some of the images, so representatives of each group were lightly stained with Alizarin red to make the fin elements and head spines easier to see.

Once all the observations were made, the fish were grouped into similar appearing morphs and these were compared with published descriptions of *Sebastes* juveniles that occur in the GOA. Probable values for the meristics (vertebrae, dorsal, anal, and pectoral fin rays) of each species of *Sebastes* occurring in the Gulf of Alaska (Orr et al. 2000) were generated based on data in Chen (1986) and compared with the values observed in the juveniles. Based on these observations, a "best guess" was made for the identity of each specimen. Subsequently, the information from the genetics analysis was compared with the results

from the morphological study, and specimens that did not concur with the genetic analysis were re-examined.

Results

Preliminary visual examinations

A cursory visual examination revealed six general categories of fishes in the samples taken (Table 1). After identifications of species had been made using combined genetic and morphological criteria, only one species occurred in more than one category. That discrepancy was a Pacific ocean perch (*Sebastes alutus*) juvenile (specimen 36), which was larger than the other *S. alutus*. One species, rougheye rockfish (*S. aleutianus*), and one species group, dusky rockfish (*S. ciliatus/variabilis*; this work was done before the description of S. *variabilis* [Orr and Blackburn 2004]) and northern rockfish (*S. polyspinis*), were indistinguishable from *S. alutus* in this cursory visual examination.

Genetic analysis

Although we made an effort to broadly sample the species in our collections, *S. alutus* was the predominant species in the subsample of 55 YOY rockfishes, accounting for 40 of the specimens (Table 1). The mtDNA markers in *S. alutus* are distinct from all other rockfishes we have examined. We also observed two shortraker rockfish (*S. borealis*, specimens 29 and 30) and one *S. aleutianus* (specimen 20); both species have unequivocal mtDNA markers. The possible species identification of specimens 37, 38, and 39 was reduced to either the blue rockfish (*S. mystinus*) or the widow rockfish (*S. entomelas*). We reduced the number of possible species for the remaining nine fish to *S. ciliatus/variabilis*, *S. polyspinis*, or the darkblotched rockfish (*S. crameri*). Specimens 31, 32, and 41, which made up one of the visually determined preliminary categories, had an *Mbo* I fragment pattern not observed in the initial set of species included in our reference baseline. Because the *Bst*U I, *Bst*N I, and *Rsa* I fragment patterns were the same as for the genetically indistinguishable *S. ciliatus/variabilis–S. polyspinis–S. crameri* group, we initially presumed the new pattern represented intraspecific variation. However, the morphological examination suggested that these three fish were the yellowmouth rockfish (*S. reedi*). A subsequent examination of known adult specimens of *S. reedi*, in addition to comparison with the key developed by Li et al. (2006a), revealed the new *Mbo* I fragment patterns as well as the patterns observed in digests by the other enzymes. The identity of the species of the other six *S. ciliatus/variabilis–S. polyspinis–S. crameri* specimens (15, 19, 21, 50, 52, and 55) cannot be determined with the mtDNA markers we currently use.

Morphological descriptions

The removal of fillets from the right side of the fish for genetic analysis did not affect our ability to perform thorough morphological analyses. Both spinous and soft fin rays were counted in the dorsal and anal fins, and the soft fin rays were counted in pectoral fins. Counts of trunk and caudal vertebrae were made from x-rays, but much of the published comparative data included only total vertebral counts (Table 2). At this stage of development, it is likely that the fin rays and vertebral number reflect the numbers observed in adults. Head spines may be obscured with further development in some species. Accounts of individual species given below will focus on distinguishing characteristics and pigmentation patterns.

Sebastes borealis: Both morphological and genetic methods indicate that specimens 29 and 30 are *S. borealis*. Morphologically these specimens are similar to *S. borealis* larvae that were previously collected in the Bering Sea and Gulf of Alaska and identified morphologically and genetically (A.W. Kendall Jr. and A.J. Gharrett, unpubl.). The larval form was unknown previously. The pelagic juvenile specimens in this study are considerably larger than the larvae previously seen, all of which were less than 15 mm long, but differ little from them morphologically and are quite distinct from other known larvae and juveniles of *Sebastes* species. The pelagic juvenile stage of *S. borealis* is known only from an illustration of a 53 mm specimen (Laroche 1987) which is considerably further developed than the specimens observed here. Pigmentation consists of a saddle of fine spots on the spinous dorsal fin and onto the body at the paired fins. The paired fins are heavily pigmented, the head is pigmented, and there is pigment on the body along the dorsal fin. A midlateral caudal peduncle line of pigment exists on specimen 29. There is no pigment on the anal or caudal fins.

Sebastes crameri: Specimens 21, 50, 52, and 55 were identified genetically as *S. ciliatus/variabilis*, *S. polyspinis*, or *S. crameri*. Morphologically the numbers of dorsal rays, anal rays, and vertebrae resemble *S. crameri*, but not the other two species (Table 2). Also, the pigment pattern of these specimens is similar to that on an illustrated pelagic juvenile of *S. crameri* (Matarese et al. 1989). These specimens are pigmented with a bar through the eye, a bar on the opercle (at the origin of the spinous dorsal fin), a double band at the spinous dorsal fin (inverted "W" shape), a band from the rayed dorsal fin through the anal fin, and a caudal peduncle band. The paired fins are heavily pigmented.

Sebastes ciliatus/variabilis –S. polyspinis: The initial morphological examination placed specimens 15 and 19 in “category 1.” All specimens in “category 1” except for these two fish, along with specimen 20 (*S. aleutianus*), were identified genetically as *S. alutus*. Genetic examination indicated that specimens 15 and 19 were *S. ciliatus/variabilis*, *S. polyspinis*, or *S. crameri*, and reduced the number of species to choose

Table 2. Morphometric and dominant or modal meristic values in identified juvenile rockfishes collected in the Gulf of Alaska, and adult characteristics of these species (based on Chen 1986 and Orr et al. 2000). Meristics of adults are proportions of fishes with dominant value of character seen in juveniles.

				Dorsal		Anal		Pectoral	Vertebrae			Head spines[a]							
Specimen numbers	Species	Size (mm SL)	Body depth (% SL)	Spines	Rays	Spines	Rays	Rays	Trunk	Caudal	Total	Nasal	Preocular	Supraocular	Postocular	Tympanic	Coronal	Parietal	Nuchal
29, 30	*S. borealis*	28.0, 31.0	29, 32	XIII	12	III	8	19	11	16	27	x	x	---	x	a	x	b	x
20	*S. aleutianus*	29.5	24	XIII?	14	III	7	18	11	16	27	x	x	x	x	x	---	x	c
31, 32, 41	*S. reedi*	38.6-40.4	27-29	XIII	14	III	7	19	11	15	26	x	x	x	x	x	---	x	d
21, 50, 52, 55	*S. crameri*	32.0-43.5	33-36	XIII	13	III	7	18	11	15	26	x	x	x	x	x	---	x	x
15, 19	*S. ciliatus/ variabilis*	29.5, 29.6	24, 25	XIII	15	III	8	18	11-12	16-17	28	x	x	x	x	x	---	e	x
37, 38, 39	*S. entomelas*	57.0-59.0	24-26	XIII	15	III	8	18	11	15	26	x	x	x	x	x	---	x	---
All others	*S. alutus*	27.0-49.5	19-27	XIII	15	III	8	18	11	16	27	x	x	f	x	x	---	x	f
Adult characteristics																			
	S. borealis			1	0.6	1	0.1	0.7	NA	NA	1	x	x	x	x	x	f	x	x
	S. aleutianus			0.97	0.7	1	0.9	0.9	NA	NA	1	x	x	x	x	x	x	x	x
	S. reedi			1	0.8	1	1	0.8	NA	NA	1	x	x	x	x	x	---	x	---
	S. crameri			0.95	0.5	1	1	0	NA	NA	1	x	x	x	x	x	---	x	f
	S. ciliatus/ variabilis			1	0.8	1	0.9	0.9	NA	NA	1	f	---	---	---	---	---	f	---
	S. entomelas			1	0.8	1	0.9	1	NA	NA	0.6	x	x	f	f	f	---	f	---
	S. alutus			0.95	0.7	1	0.8	0.9	NA	NA	1	x	x	f	x	x	---	x	---

[a]a = bifid?; b = ridge heavy, serrate; c = malformed; d = weaker than *S. alutus*; e = serrate; f = on some; x = spine present; "---" = spine absent.
NA = not available; SL = standard length.

among using morphology. Further morphological examination of these two specimens indicated that the most likely identification is *S. ciliatus/variabilis*, although *S. polyspinis* cannot be ruled out. At a larger size the distinctive dorsal spine count (14) of *S. polyspinis* separates it from other species of *Sebastes* in the GOA. Previously the pelagic juvenile stage of *S. ciliatus/variabilis* was known only from an illustration of a 44 mm specimen (Laroche 1987), which is further developed than the specimens observed here. The pigment and body shape is very similar to that of *S. alutus* at this size, and the meristics overlap with those of *S. alutus*, but *S. ciliatus/variabilis* generally have 28 vertebrae, whereas *S. alutus* generally have 27 (Table 2). These specimens have relatively uniform body pigmentation with a darker caudal peduncle blotch, and midlaterally the pigment is dense. Because adult *S. ciliatus/variabilis* consistently have only nasal spines, the other head spines observed on the two pelagic juvenile specimens indicate that these structures are lost during further development.

Sebastes reedi: Although they possessed a previously unobserved *Mbo* I haplotype, specimens 31, 32, and 41 were presumed to be *S. ciliatus/variabilis*, *S. polyspinis*, or *S. crameri* in the initial genetic analysis because *S. reedi* was not part of the initial reference data. Morphologically, however, the meristics of these specimens (Table 2) fit *S. reedi* better than the species suggested genetically. Also, the pigmentation of these specimens is similar to that on an illustration of a *S. reedi* pelagic juvenile (Matarese et al. 1989). Body pigment consists of fine spots over the dorsal three-quarters of body and head. The myosepta and lateral line have spots. The distal halves of paired fins are heavily pigmented. Bars are on the dorsal part of the body and on the dorsal fins: anterior, medial, and posterior of the spinous dorsal fin, at the rayed dorsal fin, and on the caudal peduncle (extends below the lateral line). There is a line of pigment at the base of the caudal fin. A spot is centered on the third anal spine.

Sebastes aleutianus: Based on initial morphological examination, specimen 20 was included in the category that was genetically identified as *S. alutus*. Genetic examination indicated that this specimen was *S. aleutianus*, and further morphological examination concurred. Although the head was slightly damaged, and accurate determination of head and dorsal spines was not possible, the meristics of this specimen (Table 2) agreed well with those of known *S. aleutianus*. This specimen has uniform body pigment that is darker under the dorsal fins and on the caudal peduncle. It has spots in the midlateral septum and a line of spots at the base of the caudal fin rays; otherwise, the fins are unpigmented. Other than a 57 mm specimen, pelagic juveniles have not been previously identified (Matarese et al. 1989).

Sebastes entomelas: Based on initial morphological examination, specimens 37, 38, and 39 were included in the group that was identified

genetically as *S. alutus*. Genetic examination indicated that these were either *S. mystinus* or *S. entomelas*, and reduced the number of species to choose among by using morphology. The largest specimens in this group had the distinctive Sebastosomus blotch of pigment on the posterior part of the spinous dorsal fin. The dorsal and anal ray counts and illustrations (Matarese et al. 1989) are more consistent with *S. entomelas*. There is slight barring on specimen 37; otherwise the body pigment is uniform. Geographic distribution of these two species also supports identification of *S. entomelas*; *S. mystinus* has a northern limit of distribution near the collection site, whereas *S. entomelas* has a distribution nearly centered at the collection site.

Sebastes alutus: Forty of the 55 specimens were identified from genetic analysis as *S. alutus*. Previously the pelagic juvenile stage of *S. alutus* was known only from an illustration of a 57 mm specimen (Matarese et al. 1989). Morphologically there is considerable variation among these specimens, including both meristic counts (Table 2) and the uniformity of body pigment. On some individuals there is no pattern of body pigmentation; on others there are blotches on the caudal peduncle and midlaterally near the insertion of the anal fin. Some have only the caudal peduncle blotch. On still others, there is faint, predominantly dorsal barring on the body under both the spinous and rayed dorsal fin and on the caudal peduncle. Head and body pigment consists of fine spots, except on the ventral fourth of the body. Spots are concentrated in myosepta and along the lateral line; the opercle has a blotch of pigment. The fins are not pigmented; however, a line of pigment on the hypurals extends slightly onto the caudal rays.

Discussion

Comparison of the initial genetic and morphological analyses resulted in agreement on 42 of the 55 specimens. Re-evaluation of the results led to a change in some of the morphological species determinations, removed some of the ambiguity from the genetic results, and pointed out more variation in the morphology of juvenile *S. alutus* than was expected. Genetic results confirmed that the morphological analysis correctly identified *S. borealis*, *S. crameri*, and *S. reedi*. Genetic analysis unequivocally identified four of the species observed (*S. alutus*, *S. aleutianus*, *S. borealis*, and after further analysis, *S. reedi*) and reduced the remaining possibilities to a group that included *S. entomelas* and *S. mystinus* and another group that included *S. ciliatus/variabilis*, *S. polyspinis*, and *S. crameri*. In combination, genetics and morphology identified all the specimens to species or one species group, *S. ciliatus/variabilis –S. polyspinis*. After reviewing the genetic identifications, pigment and meristic characters were used to identify *S. entomelas* and *S. ciliatus/variabilis –S. polyspinis*. Morphologically, *S. aleutianus*, *S. entomelas*, and

S. ciliatus/variabilis –S. polyspinis were readily confused with *S. alutus*; however, the mtDNA markers for *S. alutus* are quite distinctive. The variability in morphology of *S. alutus*, especially in the uniformity of body pigment, contributes to the uncertainty in identifying this and other species of juvenile rockfishes and must be considered when developing a morphological key to juvenile *Sebastes*.

These results document the occurrence of juvenile rockfish in the northern GOA during July and August. Because these subsamples of the collections were intended to determine which species were present, they do not reflect abundances. In addition, not every collection was subsampled, so the species observed are not necessarily inclusive. Future analysis of these collections will provide information about spatial and temporal distribution in the GOA during summer months. This and future work based on larger numbers of specimens, should help to better define morphological characters that can be used to identify the GOA rockfishes at this life stage.

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Evaluation of Rockfish (*Sebastes* spp.) Population Declines from Microsatellite Data

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Abstract

Rockfish (genus *Sebastes*) have been a heavily targeted fishery on the west coast of North America for several decades. Eighteen species of rockfish were tested for evidence of reduced population size using microsatellite data from recently published literature. Long-term effective population size was calculated from expected heterozygosity, and indicated species with lowest effective sizes were *S. borealis* (1,299 SE ± 67.9), *S. ruberrimus* (1,339; point estimate), and *S. paucispinis* (1,369; SE ± 36.9). However, effective size values varied greatly depending on mutation rate (slow, medium, and fast rates) and mutation model (stepwise versus infinite allele) chosen. Values of *M* ratio (number of alleles/range of alleles) were calculated to provide an additional parameter to evaluate reduced population size. Bocaccio rockfish (*S. paucispinis*) had consistent *M* ratios and N_e suggestive of significant reductions in population size at all sites, while three other species (*S. caurinus*, *S. maliger*, and *S. borealis*) had evidence for reduced population size at individual sites. This study confirms that some species and populations of rockfish are declining and have reduced genetic diversity. Species of greatest concern correspond to those that have been most heavily targeted for commercial and recreational harvest (i.e., *S. paucispinis*), but life history also appears to influence susceptibility to decline.

Introduction

Of the approximately 70 species of rockfish (genus *Sebastes*) in the northeastern Pacific Ocean (Chen 1971), few were historically thought to

have limited abundance and/or geographic structure (Love et al. 2002). Two long-held assumptions regarding marine fishes, inexhaustible abundance and high gene flow among populations (panmixia), have been eroded in recent years due to the collapse of major fisheries (e.g., cod and haddock; Hutchings 2000) and evidence to support restricted gene flow in many marine species (e.g., Ruzzante et al. 1998, Buonaccorsi et al. 2002). The combination of reduced population size with low gene flow presents a potential problem for maintaining genetic diversity and long-term sustainability in natural populations. While this problem has long been recognized in relatively isolated freshwater populations (e.g., Meffe and Vrijenhoek 1988), only recently have studies provided evidence for limited gene flow and low effective population sizes in marine species (e.g., Hauser et al. 2002).

Rockfishes have unusual combinations of reproductive and life history characteristics such as complex courtship behavior (Gingras et al. 1998), internal fertilization, viviparity, pelagic larvae, long generation/life times, and defense of demersal territories (Larson 1980). Despite a pelagic juvenile stage that promotes dispersal, evidence to support genetic structure has been observed in multiple species of rockfish including *S. borealis* (Matala et al. 2004b), *S. caurinus* (Buonaccorsi et al. 2002), and *S. thompsoni* (Sekino et al. 2001). Complex life history traits and limited gene flow in some species of rockfish suggest that these traits may contribute to limited recovery following reductions in population size.

Rockfishes have been a heavily targeted fishery on the west cost of North America for several decades and at least seven commercial species of rockfish have been harvested below 25% of their 1970 biomass (reviewed in Love et al. 2002). Several species have experienced sharp declines in harvest in recent years (e.g., *S. paucispinis*; Ralston et al. 1996). These declines in harvest are accompanied by a decrease in length during that time (Love et al. 1998), which is evidence that rockfish have been overharvested. Until recent years, very few regulations regarding commercial or recreational harvest of rockfish have been in place (Love et al. 2002). Marine protected areas are now enforced in some coastal areas with the intent of conserving groundfish species including rockfish.

In this study, I reviewed rockfish genetics literature in order to estimate effective population sizes and calculate parameters related to recent reductions in population size. Estimates of expected heterozygosity and allele diversity within populations were the primary data gathered from literature searches. Microsatellite data reported from 18 species of rockfish was obtained from recent literature and analyzed to test the null hypothesis that species and populations of *Sebastes* were immense with no evidence to support recent population declines.

Materials and methods

Literature searches found 12 studies that have used microsatellite DNA to evaluate rockfish populations (Appendix A). These studies provided data for 18 species of *Sebastes*, and many of the studies contained sample collections from multiple sites. In total, 91 collections of *Sebastes* were evaluated and recorded for this review (Appendix A). Expected heterozygosity (H_E), number of observed alleles per locus, and range of alleles per locus were recorded from each of the 12 studies as available. Species analyzed included those with a range of 3-13 microsatellite loci and sample sizes of 19 to 700. For several species, data were available from at least two independent studies.

Two population parameters related to abundance were estimated from available data, long-term effective population size (N_e) and recent reductions in population size (e.g., bottlenecks) using the "*M*" ratio. Long-term effective population size (N_e) was calculated as described by Nei (1987) with both the stepwise mutation model (SMM): $N_e = [(1 / 1 - H_E)^2 - 1] / (8\ \mu)$ and infinite allele model (IAM): $N_e = H_E / [4\mu\ (1 - H_E)]$. Where H_E is expected heterozygosity and μ is mutation rate. Nei's (1987) method uses the relationship of heterozygosity, mutation rate, and N_e to calculate long-term estimates of N_e. Here we provide point estimates of long-term N_e using the Nei (1987) method, and correlate expected heterozygosity to our estimates. Further, we evaluate fast (1.0×10^{-3}), medium (5.0×10^{-4}), and slow (1.0×10^{-4}) mutation rates for two models of mutation (SMM and IAM) and their affect on estimates of N_e.

Tests for reduced population size and recent bottleneck events were calculated with Garza and Williamson's (2001) *M* ratio of allele number to allele size range that uses the stepwise mutation model. Published literature suggests a cut-off value of 0.68 to indicate reduced effective population size ($M < 0.68$ = probable bottleneck; Garza and Williamson 2001, Shrimpton and Heath 2003). Of the 12 studies included, two (Yamanaka et al. 2000, Roques et al. 2001) did not provide information regarding allele number and range of alleles, so *M* ratio was not calculated for collections in these studies.

Ratios of *M* were plotted against N_e to examine the concordance between the two parameters. Concordance between the two estimates was evaluated in light of conservation of intraspecific genetic diversity. Estimates of N_e (Nei 1987) were a direct reflection of population heterozygosity, and were assumed to be lower than historic effective size in populations with low *M* ratios.

Results

Since expected heterozygosity and mutation rate directly influence estimates of long-term effective population size (Nei 1987), factors that

could bias estimates of N_e among the 12 studies were evaluated. There was no evidence to suggest correlation between the number of loci and the expected heterozygosity or *M* ratio (Fig. 1) would bias estimates of N_e as the result of varying number of loci among studies. However, the wide range of heterozygosities among studies with equal numbers of loci (Fig. 1) and comparisons among studies of the same species (Table 1), suggest that some suites of loci were inherently more polymorphic and had larger numbers of alleles and higher heterozygosities.

Rates of mutation and the mutation model had a significant influence on estimates of N_e. Slow, medium, and fast mutation rates provided the highest, intermediate, and lowest N_e estimates, respectively (Fig. 2; Appendix A). Further, comparisons of mutation models show that N_e estimates from the SMM are 1.4 to 5.1 fold greater than estimates from IAM (Fig. 2). While mutations in microsatellites may not follow a strict SMM, N_e estimates with this model provide conservative values (higher than most likely results). Point estimates of N_e for each species will be reported henceforth using the intermediate mutation rate (5.0×10^{-4}) and the SMM since these are likely the most appropriate parameters for species and marker type in this analysis (Shriver et al. 1993, Di Rienzo et al. 1994, DeWoody and Avise 2000). Estimates of N_e among species collections ranged from 552 for *S. entomelas* to 20,792 for *S. mentella*. When N_e was averaged over collection sites for each species, N_e ranged from 1,299 in *S. borealis* to 15,987 for *S. mentella*. Species with the lowest average N_e included *S. borealis* (1,299 SE ± 67.9), *S. ruberrimus* (1,339; single estimate), and *S. paucispinis* (1,369; SE ± 36.9). The complete table of 18 species with N_e estimates for multiple mutation rates and calculated *M* ratios are listed in Appendix A.

Ratios of *M* were calculated from studies that reported allele number and allele range (10 of 12 the studies reviewed). In two cases, Buonaccorsi et al. (2002, 2004), *M* ratios were calculated and reported in the original papers. The range in *M* ratios calculated for each species collection was from 0.61 in *S. paucispinis* to 0.99 for *S. alutus* (Appendix A). When *M* was averaged over collection sites for each species, the range was from 0.64 in *S. paucispinis* to 0.90 in *S. thompsoni*. Only *S. paucispinis* showed consistently significant *M* ratios across sample sites. The only other species that had a significant *M* ratio below the value of 0.68 was *S. caurinus* with $M = 0.66$ in the Gulf Islands, Canada site. Ratios of *M* for *S. caurinus* at two other sites were low (0.70 and 0.72), but multiple sites also had much higher *M* ratios (0.83 to 0.88). Low *M* ratios were also observed in a handful of other collections: two *S. rastrelliger* collections (Hardy Creek $M = 0.69$ and San Diego $M = 0.71$), one *S. borealis* collection (south of Prince William sound $M = 0.72$), *S. carnatus* (Big Creek $M = 0.71$), *S. chrysomelas* (Big Creek $M = 0.69$). Small sample size ($n < 20$) reduced *M* ratios because fewer alleles were observed in those collections with smaller, less representative, samples. However, *M* ratio

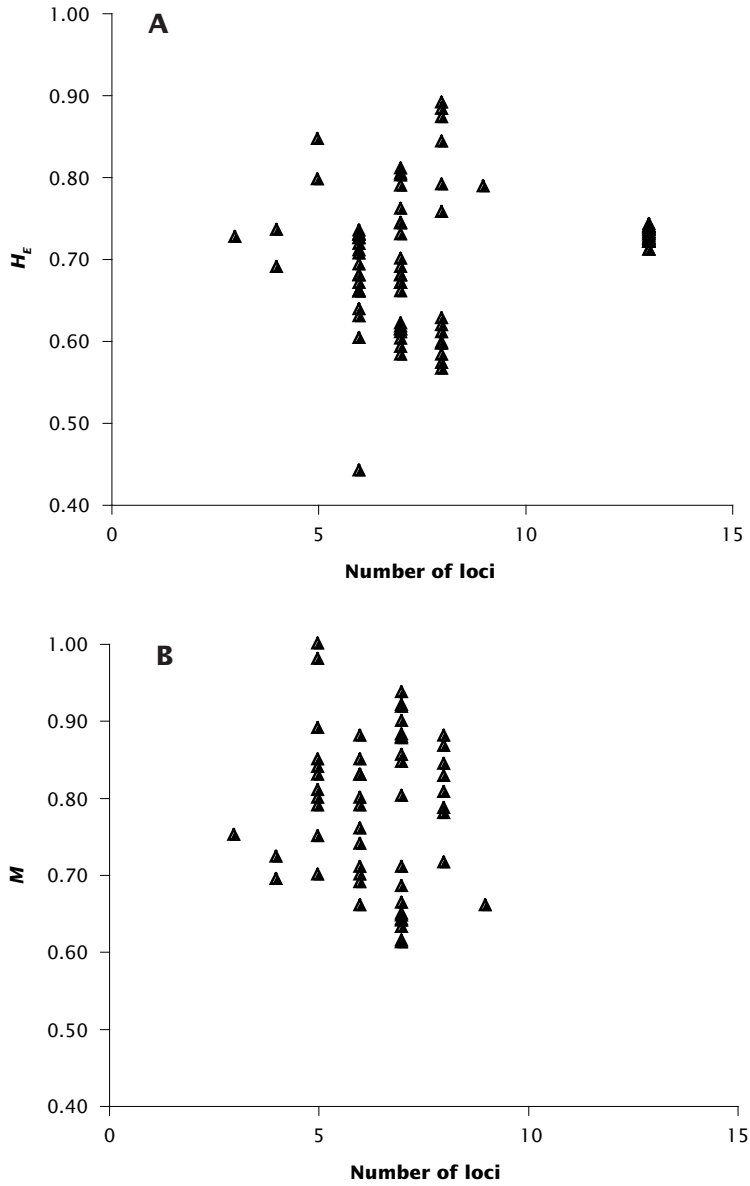


Figure 1. Average (a) expected heterozygosity (H_E), and (b) *M* ratio, as a function of number of loci for 91 collections of rockfish. Data presented were assembled from literature reviews of 12 rockfish studies. Of the 12 studies included, two (Yamanaka et al. 2000, Roques et al. 2001) did not provide information regarding allele number and range of alleles, so *M* ratio was not calculated for collections in these studies.

Table 1. Comparisons of effective population size (N_e) and heterozygosity (H_E) for the same species of *Sebastes* rockfish from multiple studies.

				$N_e(\mu = 1.0 \times 10^{-4})$		$N_e(\mu = 5.0 \times 10^{-4})$		$N_e(\mu = 1.0 \times 10^{-3})$	
Species	Reference	# loci	H_E	IAM	SMM	IAM	SMM	IAM	SMM
S. rastrelliger	Buonaccorsi et al. 2004	6	0.719	6,427	14,722	1,285	2,944	643	1,472
	Westerman et al. 2004	6	0.730	6,759	15,897	1,352	3,179	676	1,590
S. paucispinis	Matala et al. 2004a	7	0.607	3,859	6,846	772	1,369	386	685
	Westerman et al. 2004	5	0.846	13,734	51,457	2,747	10,291	1,373	5,146
S. mentella	Roques et al. 2001	8	0.873	17,478	79,934	3,496	15,987	1,748	7,993
	Miller et al. 2000	3	0.727	6,646	15,481	1,329	3,096	665	1,548
S. ruberrimus	Yamanaka et al. 2000	13	0.729	6,738	15,835	1,348	3,167	674	1,584
	Miller et al. 2000	6	0.603	3,803	6,694	761	1,339	380	669
S. caurinus	Buonaccorsi et al. 2002	6	0.668	5,079	10,301	1,016	2,060	508	1,030
	Westerman et al. 2004	6	0.660	4,853	9,563	971	1,913	485	956
	Miller et al. 2000	4	0.735	6,934	16,550	1,387	3,310	693	1,655
S. maliger	Westerman et al. 2004	6	0.660	4,853	9,563	971	1,913	485	956
	Miller et al. 2000	4	0.690	5,565	11,757	1,113	2,351	556	1,176

SMM = stepwise mutation model, IAM = infinite allele model, and μ = mutation rate.

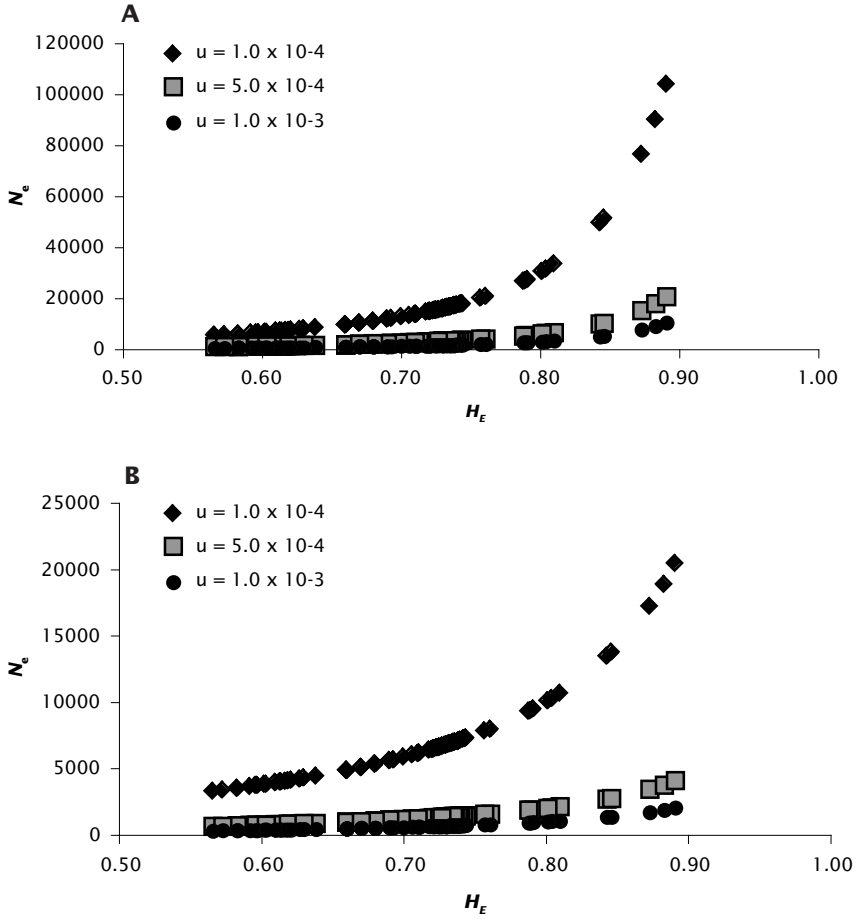


Figure 2. Effective population size (N_e) of 91 rockfish collections as a function of expected heterozygosity (H_E) for three different mutation rates (slow, medium, fast) for each of two mutation models (a) stepwise mutation model (SMM); and (b) infinite allele model (IAM).

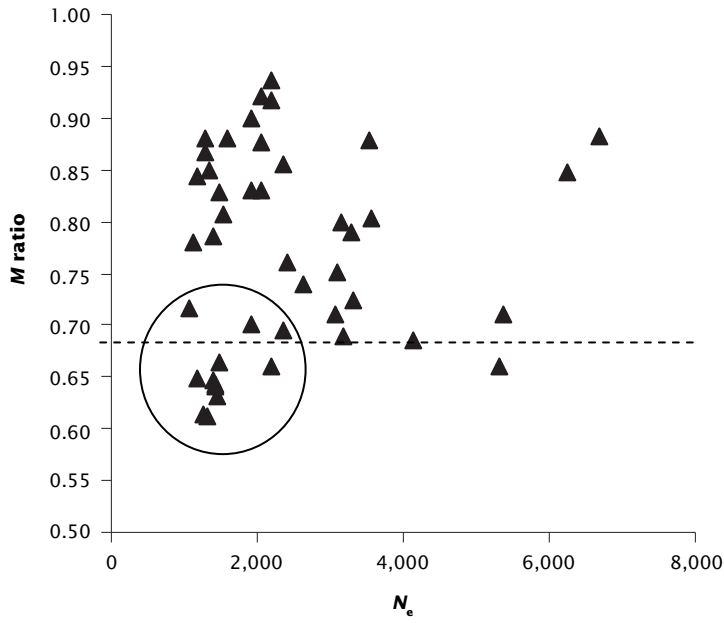


Figure 3. Plots of *M* ratio and effective population size (N_e) for 91 collections of rockfish. Collections of concern for conservation (both low *M* ratio and small N_e) are circled. The dashed horizontal line indicates an approximate *M* value cut-off (0.68) for populations with reduced population size.

appeared to be more reflective of biological processes than of sample size as there was no consistent trend in the relationship of sample size and M ratio. Relatively small sample sizes ($n = 20$) produced *M* ratios as high as 0.88 in *S. chrysomelas* and *S. thompsoni*. Large sample sizes ($n > 90$) tended to give high *M* ratios (> 0.88), but not in all cases as one collection of *S. ruberrimus* with $n = 700$ had an *M* ratio of 0.85. When the *M* ratio was graphed in conjunction with N_e (Fig. 3), 12 collections had both a combination of low effective population size and small *M* ratio.

Discussion

Although N_e was relatively low in some collections, estimates were highly variable depending on H_E values that are partially dependent upon polymorphism and ascertainment of loci. Given this, low N_e estimates in this study should not be interpreted solely without additional estimates of population size and growth. In an ideal situation, the same

suite of loci would be genotyped for all species but this is unrealistic because primer sites are rarely conserved for all rockfish species (e.g., Wimberger et al. 1999, Miller et al. 2000). Since gene flow is expected to occur among populations of the same species over multiple generations, estimates of long-term N_e in this study reflect the diversity of the species. In agreement with this, many of the N_e estimates in Appendix A from single studies of multiple populations of a single species, were similar across populations.

Ratios of *M* were unlikely to be biased by polymorphism of loci, but small sample sizes (< 25) may not adequately represent rare alleles and will decrease *M* ratio (Garza and Williamson 2001). However, only six of the 91 collections had sample sizes less than 25. The combination of small N_e and low *M* ratios provided a method to infer species that had likely experienced reductions in population size. Those collections circled in Fig. 3 are of specific concern for conservation. The 12 collections include the following: *S. borealis* (south of Prince William Sound site), *S. caurinus* (Puget Sound and Gulf Island sites), *S. maliger* (Miller et al. 2000), and *S. paucispinis* (all eight sites).

Of the four species with concordant results to support reduced population sizes, three (*S. caurinus*, *S. maliger*, and *S. paucispinis*) have been heavily targeted in commercial and recreational fisheries (Love et al. 2002). Other species included in this study have been overharvested (e.g., *S. alutus*; Withler et al. 2001); however, genetic data did not show evidence to support reduction in population size. In the case of *S. alutus*, extensive sample sizes (144 to 640) likely increased values of *M* relative to other collections with much smaller sample sizes (median sample size among studies was 53). Other species in this study that may be overharvested, yet did not have genetic evidence, may be due to delayed signals associated with long generation time and species that only recently have been targeted in fisheries. This suggests that species with long generation times may not show significant genetic evidence of reduced population size until well after a population crash has occurred. This implies that proactive management may be necessary.

The fourth species (*S. borealis*) with concordant evidence indicating reduced population size, has been shown to exhibit significant population structure with limited gene flow across a wide geographic range in regions with relatively high abundance (Matala et al. 2004b). Specific populations with limited gene flow and decreasing size are at high risk for loss of genetic diversity resulting in slow recovery or even local extirpation. Slow recovery is expected in rockfish species that are long lived with limited gene flow, suggesting that the rare life history characteristics of *Sebastes* need to be taken into consideration for appropriate fisheries management.

Of greatest conservation priority are species that have consistent evidence for reduced abundance across their geographic range, such as

observed here in *S. paucispinis*. Significant reduced population size at all eight *S. paucispinis* collection sites is particularly disturbing because of gene flow demonstrated in this species (Matala et al. 2004a). No populations with high diversity have been observed that could act as sources for other depleted populations. This is consistent with the supposition that *S. paucispinis* of the northeastern Pacific have been severely overharvested (total current biomass is 1.8-2.3% of 1969 level; Love et al. 2002) to the extent of extreme loss of genetic diversity. At one time, overexploitation of vast marine species was unfathomable, but several fishery collapses and recent studies (e.g., New Zealand snapper; Hauser et al. 2002) have shown contrary conclusions. Several rockfish species are over-exploited and many more are potentially headed towards collapse as harvest shifts to new species as others are removed. Inevitably, all rockfish species may be at risk under the current harvest regime as even dwarf species (e.g., *S. hopkinsi*) are now targeted in lieu of depleted larger species (Love et al. 2002).

In order for rockfish species to be maintained at stable levels, widespread over-exploitation must be avoided. This requires conservative approaches to regulating commercial and recreational harvest and dramatically reducing bycatch. Bycatch of deep dwelling species of rockfish results in rupture of their gas bladders and no chance for live release. Time has shown that only short-lived, pelagic marine species (i.e., herring) can be harvested on a regular basis without overharvest, and even those fisheries need to be highly regulated to avoid collapse. Inability to conserve genetic diversity will lead to inability for species to adapt to changing environmental conditions, possibly followed by local extirpation or extinction. Loss of keystone species has dramatic effects to food webs and entire ecosystems. For the long-term health of marine fish and ecosystems, harvest of marine species must be carefully regulated.

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Appendix A. Rockfish (*Sebastes*) species collections reviewed from the literature and calculated values of N_e and *M* ratio for each collection.

Species	Collection	*n*	# loci	*M* ratio	Reference	H_E	$N_e(\mu = 1.0 \times 10^{-4})$ IAM	$N_e(\mu = 1.0 \times 10^{-4})$ SMM	$N_e(\mu = 5.0 \times 10^{-4})$ IAM	$N_e(\mu = 5.0 \times 10^{-4})$ SMM[a]	$N_e(\mu = 1.0 \times 10^{-3})$ IAM	$N_e(\mu = 1.0 \times 10^{-3})$ SMM
S. rastrelliger	Brookings	78	6	0.79	Buonaccorsi et al. 2004[c]	0.734	6,898	16,416	1,380	3,283	690	1,642
	Hardy Creek	58	6	0.69		0.730	6,759	15,897	1,352	3,179	676	1,590
	Fort Bragg	46	6	0.80		0.729	6,725	15,770	1,345	3,154	673	1,577
	Big Creek	56	6	0.76		0.693	5,643	12,013	1,129	2,403	564	1,201
	Vandenberg	49	6	0.74		0.706	6,003	13,212	1,201	2,642	600	1,321
	Los Angeles	43	6	na		0.718	6,365	14,469	1,273	2,894	637	1,447
	San Diego	51	6	0.71		0.725	6,591	15,279	1,318	3,056	659	1,528
S. paucispinis	Queen Charlotte Island	50	7	0.61	Matala et al. 2004a	0.592	3,627	6,259	725	1,252	363	626
	Vancouver Island	50	7	0.65		0.610	3,910	6,968	782	1,394	391	697
	Monterey Bay	67	7	0.61		0.602	3,781	6,641	756	1,328	378	664
	North Point Conception	35	7	0.64		0.614	3,977	7,139	795	1,428	398	714
	Tanner Banks	30	7	0.65		0.583	3,495	5,938	699	1,188	350	594
	Santa Barbara Channel	55	7	0.64		0.613	3,960	7,096	792	1,419	396	710
	Santa Monica Bay	41	7	0.63		0.617	4,027	7,271	805	1,454	403	727
	Punta Colnett	58	7	0.66		0.621	4,096	7,452	819	1,490	410	745
S. borealis	South of Baranof Island	42	8	0.87	Matala et al. 2004b	0.597	3,708	6,458	742	1,292	371	646
	NW of Chichagof Island	55	8	0.79		0.610	3,910	6,968	782	1,394	391	697
	NW of Yakutat	74	8	0.84		0.583	3,495	5,938	699	1,188	350	594
	S. of Prince William Sound	38	8	0.72		0.566	3,260	5,386	652	1,077	326	539
	S. of Seward	48	8	0.81		0.627	4,202	7,734	840	1,547	420	773

Appendix A. (Continued.)

Species	Collection	n	# loci	M ratio	Reference	H_E	$N_e(\mu = 1.0 \times 10^{-4})$ IAM	$N_e(\mu = 1.0 \times 10^{-4})$ SMM	$N_e(\mu = 5.0 \times 10^{-4})$ IAM	$N_e(\mu = 5.0 \times 10^{-4})$ SMM[a]	$N_e(\mu = 1.0 \times 10^{-3})$ IAM	$N_e(\mu = 1.0 \times 10^{-3})$ SMM
	S. of Kodiak Island	47	8	0.83		0.619	4,062	7,361	812	1,472	406	736
	Shumagin Islands	38	8	0.78		0.573	3,355	5,606	671	1,121	335	561
	W. Aleutian Islands	186	8	0.88		0.596	3,688	6,409	738	1,282	369	641
S. carnatus	Big Creek	19	7	0.71	Narum et al. 2004	0.789	9,348	26,827	1,870	5,365	935	2,683
	Fort Bragg	33	7	0.85		0.804	10,255	31,289	2,051	6,258	1,026	3,129
	San Miguel Island	59	7	0.88		0.810	10,658	33,376	2,132	6,675	1,066	3,338
S. chrysomelas	Big Creek	19	7	0.69	Narum et al. 2004	0.761	7,960	20,633	1,592	4,127	796	2,063
	Fort Bragg	20	7	0.88		0.743	7,228	17,675	1,446	3,535	723	1,768
	San Miguel Island	52	7	0.80		0.744	7,266	17,823	1,453	3,565	727	1,782
S. fasciatus	Gulf of Maine	30	8	na	Roques et al. 2001	0.791	9,462	27,367	1,892	5,473	946	2,737
	Nova Scotia	35	8	na		0.757	7,788	19,919	1,558	3,984	779	1,992
S. mentella	Grand Banks	44	8	na	Roques et al. 2001	0.843	13,424	49,462	2,685	9,892	1,342	4,946
	Grand Banks	47	8	na		0.873	17,185	76,250	3,437	15,250	1,719	7,625
	Labrador	52	8	na		0.883	18,868	90,064	3,774	18,013	1,887	9,006
	Labrador	52	8	na		0.891	20,436	103,960	4,087	20,792	2,044	10,396
S. thompsoni	Aomori	45	7	0.94	Sekino et al. 2001	0.680	5,313	10,957	1,063	2,191	531	1,096
	Akita	37	7	0.90		0.660	4,853	9,563	971	1,913	485	956
	Yamagata	96	7	0.92		0.670	5,076	10,228	1,015	2,046	508	1,023
	Niigata	50	7	0.92		0.680	5,313	10,957	1,063	2,191	531	1,096
	Kyoto	53	7	0.86		0.690	5,565	11,757	1,113	2,351	556	1,176
	Shimane	20	7	0.88		0.670	5,076	10,228	1,015	2,046	508	1,023

Appendix A. (Continued.)

Species	Collection	*n*	# loci	*M* ratio	Reference	H_E	$N_e(\mu = 1.0 \times 10^{-4})$ IAM	$N_e(\mu = 1.0 \times 10^{-4})$ SMM	$N_e(\mu = 5.0 \times 10^{-4})$ IAM	$N_e(\mu = 5.0 \times 10^{-4})$ SMM[a]	$N_e(\mu = 1.0 \times 10^{-3})$ IAM	$N_e(\mu = 1.0 \times 10^{-3})$ SMM
S. ruberrimus	Bowie Smt. (D), July 1998	90	13	na	Yamanaka et al. 2000	0.739	7,079	17,100	1,416	3,420	708	1,710
	Bowie Smt. (D), July 1999	170	13	na		0.730	6,759	15,897	1,352	3,179	676	1,590
	Bowie Smt. (D), Aug. 1999	90	13	na		0.711	6,151	13,716	1,230	2,743	615	1,372
	Bowie Smt. (D), Sept. 1999	90	13	na		0.742	7,190	17,529	1,438	3,506	719	1,753
	Bowie Smt. (B), July 1998	95	13	na		0.732	6,828	16,154	1,366	3,231	683	1,615
	Bowie Smt. (B), July 1999	110	13	na		0.733	6,863	16,284	1,373	3,257	686	1,628
	Bowie Smt. (B), Aug. 1999	90	13	na		0.724	6,558	15,159	1,312	3,032	656	1,516
	Bowie Smt. (B), Sept. 1999	110	13	na		0.725	6,591	15,279	1,318	3,056	659	1,528
	Barber Point (D), May 1999	100	13	na		0.738	7,042	16,960	1,408	3,392	704	1,696
	Barber Point (D), Sept. 1999	65	13	na		0.721	6,461	14,808	1,292	2,962	646	1,481
	Barber Point (B), May 1999	175	13	na		0.727	6,658	15,522	1,332	3,104	666	1,552
	Barber Point (B), Sept. 1999	65	13	na		0.725	6,591	15,279	1,318	3,056	659	1,528
	Sitka, Dec. 1999	90	13	na		0.721	6,461	14,808	1,292	2,962	646	1,481
	Tasu, May 1998	80	13	na		0.740	7,115	17,241	1,423	3,448	712	1,724

Appendix A. (Continued.)

Species	Collection	n	# loci	M ratio	Reference	H_E	$N_e(\mu = 1.0 \times 10^{-4})$ IAM	$N_e(\mu = 1.0 \times 10^{-4})$ SMM	$N_e(\mu = 5.0 \times 10^{-4})$ IAM	$N_e(\mu = 5.0 \times 10^{-4})$ SMM[a]	$N_e(\mu = 1.0 \times 10^{-3})$ IAM	$N_e(\mu = 1.0 \times 10^{-3})$ SMM
S. ruberrimus	Tasu, Jan. 2000	180	13	na	Yamanaka et al. 2000	0.738	7,042	16,960	1,408	3,392	704	1,696
	Cape St. James, May 1998	85	13	na		0.732	6,828	16,154	1,366	3,231	683	1,615
	Cape St. James, Jan. 1999	80	13	na		0.711	6,151	13,716	1,230	2,743	615	1,372
	Cape St. James, Oct. 1999	130	13	na		0.723	6,525	15,041	1,305	3,008	653	1,504
	Cape St. James, Feb. 2000	65	13	na		0.736	6,970	16,685	1,394	3,337	697	1,669
	Triangle Island, May 1998	80	13	na		0.720	6,429	14,694	1,286	2,939	643	1,469
	Triangle Island, Jan. 2000	145	13	na		0.738	7,042	16,960	1,408	3,392	704	1,696
	Topknot, May 1998	85	13	na		0.735	6,934	16,550	1,387	3,310	693	1,655
	Topknot, Mar. 2000	135	13	na		0.721	6,461	14,808	1,292	2,962	646	1,481
	Brooks Bay, Oct. 1998	70	13	na		0.736	6,970	16,685	1,394	3,337	697	1,669
	Esperanza, Sept. 1999	45	13	na		0.730	6,759	15,897	1,352	3,179	676	1,590
S. rastrelliger	Fort Bragg	46	6	na	Westerman et al. 2004[d]	0.730	6,759	15,897	1,352	3,179	676	1,590
S. atrovirens	Fort Bragg	21	6	0.79		0.680	5,313	10,957	1,063	2,191	531	1,096
S. carnatus	Fort Bragg	94	7	0.80		0.801	10,090	30,451	2,018	6,090	1,009	3,045
S. chrysomelas	Fort Bragg	74	7	0.81		0.730	6,759	15,897	1,352	3,179	676	1,590
S. caurinus	Fort Bragg	49	6	0.83		0.660	4,853	9,563	971	1,913	485	956
S. auriculatus	Fort Bragg	73	6	0.75		0.725	6,591	15,279	1,318	3,056	659	1,528
S. dallii	Fort Bragg	30	7	0.84		0.700	5,833	12,639	1,167	2,528	583	1,264

Appendix A. (Continued.)

Species	Collection	*n*	# loci	*M* ratio	Reference	H_E	$N_e(\mu = 1.0 \times 10^{-4})$ IAM	$N_e(\mu = 1.0 \times 10^{-4})$ SMM	$N_e(\mu = 5.0 \times 10^{-4})$ IAM	$N_e(\mu = 5.0 \times 10^{-4})$ SMM[a]	$N_e(\mu = 1.0 \times 10^{-3})$ IAM	$N_e(\mu = 1.0 \times 10^{-3})$ SMM
S. nebulosus	Fort Bragg	38	6	0.70		0.638	4,412	8,306	882	1,661	441	831
S. maliger	Fort Bragg	39	6	0.85		0.660	4,853	9,563	971	1,913	485	956
S. entomelas	Fort Bragg	74	6	na		0.442	1,978	2,760	396	552	198	276
S. paucispinis	Fort Bragg	96	5	na		0.846	13,734	51,457	2,747	10,291	1,373	5,146
S. maliger	British Columbia	32	4	0.69	Miller et al. 2000	0.690	5,565	11,757	1,113	2,351	556	1,176
S. caurinus	British Columbia	32	4	0.72		0.735	6,934	16,550	1,387	3,310	693	1,655
S. ruberrimus	British Columbia	700	6	0.85		0.603	3,803	6,694	761	1,339	380	669
S. mentella	British Columbia	40	3	0.75		0.727	6,646	15,481	1,329	3,096	665	1,548
S. pinniger	Oregon coast	59	9	0.66	Gomez-Uchida et al. 2003	0.788	9,292	26,562	1,858	5,312	929	2,656
S. caurinus	Queen Charlotte Island	38	6	0.88	Buonaccorsi et al. 2002[c]	0.630	4,257	7,881	851	1,576	426	788
	Canadian gulf islands	39	6	0.66		0.680	5,313	10,957	1,063	2,191	531	1,096
	Puget Sound	36	6	0.70		0.660	4,853	9,563	971	1,913	485	956
	Crescent City	49	6	0.83		0.660	4,853	9,563	971	1,913	485	956
	Big Creek	22	6	na		0.710	6,121	13,613	1,224	2,723	612	1,361
	San Miguel Island	53	6	0.83		0.670	5,076	10,228	1,015	2,046	508	1,023
S. alutus	Vancouver Island	144	5	0.89	Withler et al. 2001	0.797[b]	9,815	29,083	1,963	5,817	982	2,908
	E. Queen Charlotte Island	543	5	0.98		0.797[b]	9,815	29,083	1,963	5,817	982	2,908
	W. Queen Charlotte Island	640	5	1.00		0.797[b]	9,815	29,083	1,963	5,817	982	2,908

na = data not available for calculation.
[a]Mutation model and rate chosen for N_e estimates reported in the text.
[b]H_E only reported for overall populations.
[c]*M* ratio calculated and reported in original paper.
[d]Only five loci used to calculate *M* ratio.

Are the Subgenera of *Sebastes* Monophyletic?

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Abstract

We examined genetic relationships among *Sebastes* rockfishes to evaluate the subgeneric relationships within *Sebastes*. We analyzed restriction site variation (12S and 16S rRNA and NADH dehydrogenase-3 and -4 genes) by using parsimony and distance analyses. Seventy-one *Sebastes* species representing 16 subgenera were included. Thirteen subgenera were represented by more than one species, and three subgenera were monotypic. We also evaluated three currently unassigned species. The only monophyletic subgenus was *Sebastomus*, although some consistent groups were formed by species from different subgenera. The northeastern Pacific species of *Pteropodus* clustered with one northeastern Pacific species of the subgenus *Mebarus* (*S. atrovirens*) and two northeastern Pacific species of the subgenus *Auctospina* (*S. auriculatus* and *S. dalli*) forming a monophyletic group distinct from northwestern Pacific

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Pteropodus species. The subgenera *Acutomentum* and *Allosebastes* were polyphyletic, although subsets of each were monophyletic. *Sebastes polyspinis* and *S. reedi*, which have not yet been assigned to subgenera, are closely related to two other northern species, *S. crameri* (subgenus *Eosebastes*) and the *S. ciliatus/variabilis* complex (subgenus *Sebastosomus*), which differed from other species assigned to their subgenera. These and other molecular studies show promise in determining the phylogenetic relationships among *Sebastes* species.

Introduction

The genus *Sebastes* is a species-rich and ecologically diverse group. Currently about 100 species are recognized; members of this genus are currently assigned to 21 subgenera, including six that are monotypic (Kendall 2000). Historically, morphological, meristic, and morphometric characters have been used for species identification and subgeneric determination. Abundant variation in many characters has provided means to separate most morphologically similar species. However, some characters that are subjective and possibly adaptive, are inappropriate for cladistic analysis (Li et al. 2006a). Consequently, the current subgeneric groupings need to be reevaluated using alternative methods that consider characters more suitable for cladistic analysis. Molecular methods have been used to test the validity of some subgenera of *Sebastes*. Comparison of sequences of a mitochondrial cytochrome *b* gene led to the conclusion that the subgenus *Sebastomus* as defined by Chen (1971) was monophyletic (Rocha-Olivares et al. 1999). All members of a monophyletic group descend from a common ancestor, i.e., they are part of the same genetic lineage. Relationships among species of another subgenus, *Pteropodus*, have also been evaluated (Kai et al. 2003, Li et al. 2006a). Our analysis of restriction site variation in the NADH-dehydrogenase subunit -3 and -4 genes (ND3/ND4 region) and the 12S and 16S rRNA genes (12S/16S region) of the mitochondrial DNA (mtDNA) showed that the northeastern Pacific members of *Pteropodus*, along with three northeastern Pacific species from two other subgenera, form a monophyletic group (Li et al. 2006a). However, the northwestern Pacific members of *Pteropodus* were distinct from the northeastern Pacific *Pteropodus* species and need to be evaluated further and reassigned (Li et al. 2006a).

In this paper, we extended our evaluation of *Sebastes* subgenera validity to 71 species and 16 subgenera. We used the subgeneric assignments summarized in Kendall (2000), except for *S. gilli*, which is unassigned (A.W. Kendall, pers. comm.). In addition, we examined the extent to which intraspecific variation interferes with phylogenetic determination by surveying variation in large samples of individuals from five of

the 71 species. Restriction site variation was used to generate maximum parsimony and neighbor-joining trees, and to estimate the extent of nucleotide divergences within and among subgenera.

Materials and methods

Species studied

Seventy-one species from 16 *Sebastes* subgenera were examined (Table 1). *Sebastolobus alascanus* and *Helicolenus hilgendorfi* were included as outgroup species. The northeastern Pacific *Sebastes* species and *Sebastolobus alascanus* were captured in the Gulf of Alaska and along the coast of California. The northwestern Pacific *Sebastes* species and *H. hilgendorfi* were collected along the coasts of Japan. Generally, five individuals were used to represent each species. In several instances, fewer individuals were used because of limited availability. Many additional individuals of *S. alutus*, *S. aleutianus*, *S. borealis*, *S. caurinus*, and the *S. carnatus/S. chrysomelas* complex were included to evaluate the influence of intraspecific variation on the analysis.

DNA amplification

A sample of heart tissue of each specimen was preserved in either 95% ethanol or a DNA preservation solution (Seutin et al. 1991). Total genomic DNA was extracted using Puregene™ DNA isolation kits (Gentra Systems Inc., Minneapolis). The mitochondrial ND3/ND4 and 12S/16S regions were amplified by polymerase chain reaction (Gharrett et al. 2001, Li et al. 2006b).

Restriction site analysis

A restriction site map was developed for both the ND3/ND4 and 12S/16S regions for endonucleases: *Bst*N I, *Bst*U I, *Cfo* I, *Dde* I, *Hin*d II, *Hin*f I, *Mbo* I, *Msp* I, *Rsa* I, and *Sty* I. All restriction sites were mapped from fragment sizes observed in double digests (Li et al. 2006b).

We attempted to find species-specific variation to separate *S. emphaeus*, *S. variegatus*, *S. wilsoni*, and *S. zacentrus* by identifying restriction site differences in published cytochrome *b* sequences (Rocha-Olivares et al. 1999). Although we expected to observe species-specific restriction digest patterns, the digests failed to delineate the species, probably because the nucleotide differences to which restriction enzymes were applied are the result of intraspecific variation shared by the four species. We also examined variation in the NADH-dehydrogenase subunit-5 and -6 genes for these four species. Although additional intraspecific variation was observed, there was little useful interspecific variation.

Table 1. Names, abbreviation, subgenus assignments, and range of species included.

Common name	Species[a]	Abbr.	Subgenus	Range
Rougheye rockfish	*aleutianus*	*ale*	*Zalopyr*	NE-NW Pacific
Pacific ocean perch	*alutus*	*alu*	*Acutomentum*	NE-NW Pacific
Kelp rockfish	*atrovirens*	*atr*	*Mebarus*	NE Pacific
Brown rockfish	*auriculatus*	*ari*	*Auctospina*	NE Pacific
Aurora rockfish	*aurora*	*aro*	*Eosebastes*	NE Pacific
Redbanded rockfish	*babcocki*	*bab*	*Rosicola*	NE Pacific
Shortraker rockfish	*borealis*	*bor*	*Zalopyr*	NE-NW Pacific
Silvergray rockfish	*brevispinis*	*bre*	*Acutomentum*	NE Pacific
False jacopever	*capensis*	*cap*	*Sebastomus*	NE Pacific/ S. Hemisphere
Gopher rockfish	*carnatus*	*car*	*Pteropodus*	NE Pacific
Copper rockfish	*caurinus*	*cau*	*Pteropodus*	NE Pacific
Greenspotted rockfish	*chlorosticus*	*dhl*	*Sebastomus*	NE Pacific
Black-and-yellow rockfish	*chrysomelas*	*chr*	*Pteropodus*	NE Pacific
Dusky rockfish	*ciliatus/ variabilis*	*cil*	*Sebastosomus*	NE Pacific
Starry rockfish	*constellatus*	*con*	*Sebastomus*	NE Pacific
Darkblotched rockfish	*crameri*	*cra*	*Eosebastes*	NE Pacific
Calico rockfish	*dalli*	*dal*	*Auctospina*	NE Pacific
Splitnose rockfish	*diploproa*	*dip*	*Allosebastes*	NE Pacific
Greenstriped rockfish	*elongatus*	*elo*	*Hispaniscus*	NE Pacific
Puget Sound rockfish	*emphaeus*	*emp*	*Allosebastes*	NE Pacific
Swordspine rockfish	*ensifer*	*ens*	*Sebastomus*	NE Pacific
Widow rockfish	*entomelas*	*ent*	*Acutomentum*	NE Pacific
Pink rockfish	*eos*	*eos*	*Sebastomus*	NE Pacific
Gulf rockfish	*exsul*	*exs*	*Sebastomus*	NE Pacific
Yellowtail rockfish	*flavidus*	*fla*	*Sebastosomus*	NE Pacific
Bronzespotted rockfish	*gilli*	*gil*	?	NE Pacific
Chilipepper	*goodei*	*goo*	*Sebastodes*	NE Pacific
Rosethorn rockfish	*helvomaculatus*	*hel*	*Sebastomus*	NE Pacific
Squarespot rockfish	*hopkinsi*	*hop*	*Acutomentum*	NE Pacific
Yoroi-mebaru	*hubbsi*	*hub*	*Pteropodus*	NW Pacific
Mebaru	*inermis*	*ine*	*Mebarus*	NW Pacific
Shortbelly rockfish	*jordani*	*jor*	*Sebastodes*	NE Pacific
Togotto-mebaru	*joyneri*	*joy*	*Mebarus*	NW Pacific
Freckled rockfish	*lentiginosus*	*Len*	*Sebastomus*	NE Pacific
Cowcod	*levis*	*Lev*	*Hispaniscus*	NE Pacific
Mexican rockfish	*macdonaldi*	*mac*	*Acutomentum*	NE Pacific

[a]Genus *Sebastes* unless otherwise noted.

Table 1. (Continued.)

Common name	Species[a]	Abbr.	Subgenus	Range
Quillback rockfish	*maliger*	*mal*	*Pteropodus*	NE Pacific
Black rockfish	*melanops*	*mep*	*Sebastosomus*	NE Pacific
Blackgill rockfish	*melanostomus*	*mes*	*Eosebastes*	NE Pacific
Vermillion rockfish	*miniatus*	*min*	*Rosicola*	NE Pacific
Blue rockfish	*mystinus*	*mys*	*Sebastosomus*	NE Pacific
China rockfish	*nebulosus*	*neb*	*Pteropodus*	NE Pacific
Tiger rockfish	*nigrocinctus*	*nig*	*Sebastichthys*	NE Pacific
Goma-soi	*nivosus*	*niv*	*Pteropodus*	NW Pacific
Speckled rockfish	*ovalis*	*ova*	*Acutomentum*	NE Pacific
Bocaccio	*paucispinis*	*pau*	*Sebastodes*	NE Pacific
Chameleon rockfish	*phillipsi*	*phi*	*?*	NE Pacific
Canary rockfish	*pinniger*	*pin*	*Rosicola*	NE Pacific
Northern rockfish	*polyspinis*	*pol*	*?*	NE Pacific
Redstripe rockfish	*proriger*	*pro*	*Allosebastes*	NE Pacific
Grass rockfish	*rastrelliger*	*ras*	*Pteropodus*	NE Pacific
Yellowmouth rockfish	*reedi*	*ree*	*?*	NE Pacific
Rosy rockfish	*rosaceus*	*rsa*	*Sebastomus*	NE Pacific
Greenblotched rockfish	*rosenblatti*	*rsb*	*Sebastomus*	NE Pacific
Yelloweye rockfish	*ruberrimus*	*rbr*	*Sebastopyr*	NE Pacific
Flag rockfish	*rubrivinctus*	*rbv*	*Hispaniscus*	NE Pacific
Bank rockfish	*rufus*	*ruf*	*Acutomentum*	NE Pacific
Stripetail rockfish	*saxicola*	*sax*	*Allosebastes*	NE Pacific
Halfbanded rockfish	*semicinctus*	*sem*	*Allosebastes*	NE Pacific
Olive rockfish	*serranoides*	*srd*	*Sebastomus*	NE Pacific
Treefish	*serriceps*	*srp*	*Sebastocarus*	NE Pacific
Pinkrose rockfish	*simulator*	*sim*	*Sebastomus*	NE Pacific
Spiny-eye rockfish	*spinorbis*	*spi*	*Sebastomus*	NE Pacific
Ezo-mebaru	*taczanowski*	*tac*	*Mebarus*	NW Pacific
Usu-mebaru	*thompsoni*	*tho*	*Mebarus*	NW Pacific
Shima-zoi	*trivitattus*	*tri*	*Pteropodus*	NW Pacific
Honeycomb rockfish	*umbrosus*	*umv*	*Sebastomus*	NE Pacific
Harlequin rockfish	*variegatus*	*var*	*Allosebastes*	NE Pacific
Kitsune-mebaru	*vulpes*	*vul*	*Neohispaniscus*	NW Pacific
Pygmy rockfish	*wilsoni*	*wil*	*Allosebastes*	NE Pacific
Sharpchin rockfish	*zacentrus*	*zac*	*Allosebastes*	NE Pacific
Helicolenus	*Helicolenus hilgendorfi*	*Hh*		NW Pacific
Shortspine thornyhead	*Sebastolobus alascanus*	*Sa*		NE Pacific

Phylogenetic analysis

The rate of nucleotide substitution per nucleotide (d_r) was calculated for all pairs of haplotypes following Nei and Tajima (1981) and Nei and Miller (1990, eq. 4) using REAP (McElroy et al. 1990). Nucleotide substitutions per nucleotide were calculated for all pairs of *Sebastes* spp., between *Sebastes* spp. and *Helicolenus hilgendorfi*, between *Sebastes* spp. and *Sebastolobus alascanus*, and between *H. hilgendorfi* and *Sebastolobus alascanus*. Pairwise restriction site differences were calculated using Arlequin 2.0 (Schneider et al. 2000). One hundred neighbor-joining trees (Saitou and Nei 1987) using PHYLIP 3.57c (Felsenstein 1993) were estimated by using randomized orders of the taxa. Maximum parsimony analyses were performed using heuristic searches with PAUP 4.0b10 (Swofford 1998). Because the likelihood of the loss of a site is higher than the gain of a site, three character-weighting schemes were used. The weight of gaining a site was analyzed as (1) equal to that of losing a site, (2) twice that of losing a site, and (3) four times that of losing a site. The following search parameters were used: exclude uninformative characters, retain minimal tree from each replicate, collapse zero-length branches, tree-bisection-reconnection branch swapping in effect, steepest descent not enforced, and save all optimal trees. One hundred replicates were performed for each of the three weighting schemes, and the multiple maximum parsimony trees generated for each scheme were combined to produce a 50% majority consensus tree.

Results

Restriction site analysis

A total of 215 restriction sites were detected in the ND3/ND4 and 12S/16S regions (Li et al. 2006b). The faster evolving ND3/ND4 region had 141 sites, and 74 sites were in the more conserved 12S/16S region. Of the total 215 sites, 97 were unique to *Sebastes* species, 21 were unique to *Sebastolobus alascanus*, seven were unique to *Helicolenus hilgendorfi*, and one was shared only by *Sebastolobus alascanus* and *H. hilgendorfi*.

Site differences in the two mtDNA regions yielded 132 composite haplotypes (Li et al. 2006b). Individuals of the *Sebastes* species had 127 haplotypes, *Sebastolobus alascanus* had four haplotypes, and *H. hilgendorfi* had a single haplotype. Thirty-four of the 71 species displayed intraspecific variation and were represented by more than one composite haplotype.

In several instances, haplotypes were identical among species. These were (1) a variant of *S. carnatus* and a variant of *S. chrysomelas* were identical; (2) *S. chlorostictus*, *S. eos*, and *S. rosenblatti* shared a haplotype; (3) haplotypes of *S. ciliatus/variabilis*, *S. crameri*, and a vari-

ant of *S. polyspinis* were the same; and (4) *S. emphaeus*, a variant of *S. variegatus*, and a variant of *S. wilsoni* were the same. Also, haplotypes of several species differed by a single restriction site. Single site differences were observed in four instances: (1) between *S. entomelas* and *S. mystinus*; (2) between *S. hopkinsi* and *S. ovalis*; (3) between *S. zacentrus* and the *S. emphaeus/S. variegatus/S. wilsoni* complex; and (4) between *S. reedi* and the *S. ciliatus/variabilis/S. crameri/S. polyspinis* complex.

Differences in restriction sites between haplotypes ranged from 0 between some pairs of species (e.g., *S. carnatus* and *S. chrysomelas*) to 71 sites between *Sebastolobus alascanus* and *S. inermis*, and *Sebastolobus alascanus* and *S. joyneri*.

Nucleotide divergence within variable *Sebastes* species averaged 0.0027 substitutions per nucleotide. Nucleotide divergence between *Sebastes* species averaged 0.0285 substitutions per nucleotide, ranging from 0 (as mentioned above for several pairs of species) to 0.0664 per nucleotide between *S. hubbsi* and *S. jordani*. Nucleotide divergence between *Sebastes* species and *H. hilgendorfi* averaged 0.0767 substitutions per nucleotide. Nucleotide divergence between *Sebastes* species and *Sebastolobus alascanus* averaged 0.1047 substitutions per nucleotide, and the largest was observed between *S. hubbsi* and *Sebastolobus alascanus*, at 0.1226 substitutions per nucleotide. The average nucleotide divergence within subgenera ranged from 0.0089 substitutions per nucleotide for the subgenus *Sebastomus* to 0.0370 substitutions per nucleotide for the subgenus *Sebastodes* (Table 2).

Six new restriction sites in the ND3/ND4 region were detected for the individuals included for investigation of intraspecific variation, which resulted in 10 additional haplotypes for *S. aleutianus* ($n = 39$), four for *S. alutus* ($n = 60$), nine for *S. borealis* ($n = 78$), 10 for *S. carnatus* and *S. chrysomelas* ($n = 98$), and five for *S. caurinus* ($n = 78$).

Phylogenetic analysis

A neighbor-joining tree (NJ) (Fig. 1) was constructed from all haplotypes, including those observed for the additional specimens, to evaluate the influence of intraspecific variation on the tree. Multiple haplotypes for each species formed many short terminal branches, but did not obscure interspecific differences. Each additional haplotype of *S. aleutianus*, *S. alutus*, *S. borealis*, *S. carnatus*, and *S. chrysomelas* clustered with the original haplotypes observed for those species. Haplotypes of *S. aleutianus* separated into two clusters at the tip of a branch.

Subsequent analyses included only the original five specimens of each species so that all species would be represented by about the same number of individuals. In the ND3/ND4 region, 109 sites were polymorphic, six were monomorphic, and 26 were autapomorphic (variation was observed in only a single haplotype). In the 12S/16S region, 45 sites were

Table 2. Number of *Sebastes* species analyzed in each subgenus, total number (Kendall 2000), and average nucleotide divergence (substitutions per nucleotide) within each subgenus. The subgenera are abbreviated in Figs. 1-4.

Subgenus	Abbr.	No. species analyzed in subgenus	No. species in subgenus, Kendall 2000	Average divergence
Acutomentum	*Acuto*	7	7	0.0308
3 species[a]				0.0144
Allosebastes	*Allo*	8	13	0.0203
4 species[b]				0.0028
Auctospina	*Aucto*	2	2	0.0129
Eosebastes	*Eoseb*	3	3	0.0184
Hispaniscus	*Hispan*	3	3	0.0272
Mebarus	*Mebar*	5	7	0.0270
NWP clade[c]				0.0226
Neohispaniscus	*Nhispan*	1	2	N/A
Pteropodus	*Ptero*	9	10	0.0291
NEP clade[d]				0.0124
Rosicola	*Rosi*	3	3	0.0179
Sebastichthys	*Sich*	1	1	N/A
Sebastocarus	*Scar*	1	1	N/A
Sebastodes	*Sode*	3	5	0.0370
Sebastomus	*Stom*	14	15	0.0089
Sebastopyr	*Spyr*	1	1	N/A
Sebastosomus	*Stoso*	5	5	0.0224
3 species[e]				0.0101
Zalopyr	*Zpyr*	2	3	0.0171
Unassigned		3		
5 N. Pacific species[f]				0.0084

[a] *S. hopkinsi*, *S. ovalis*, *S. rufus*.
[b] *S. emphaeus*, *S. variegatus*, *S. wilsoni*, *S. zacentrus*.
[c] w/o *S. atrovirens*.
[d] NEP *Pteropodus* w/*S. atrovirens*, *S. auriculatus*, *S. dalli*.
[e] *S. flavidus*, *S. melanops*, *S. serranoides*.
[f] *S. alutus*, *S. ciliatus/variabilis*, *S. crameri*, *S. polyspinis*, *S. reedi*.
NEP = northeastern Pacific; NWP = Northwestern Pacific.

polymorphic, 25 were monomorphic, and four were autapomorphic. A total of 154 sites provided information for the parsimony analysis.

Three schemes assigned different weights to loss and gain of a restriction site in the parsimony analyses. The 1:1 loss/gain scheme produced 18,529 equally parsimonious trees, each with a total length of 536 steps. The 1:2 scheme produced 11,279 trees, each with a total length of 782 steps. The 1:4 scheme produced 1,324 trees, each with a total length of 1,082 steps. For each scheme, a 50% majority consensus tree was produced (Figs. 2-4).

There were many areas of congruence among the three consensus trees and the NJ tree. The NJ tree and the consensus trees were similar in that members of the subgenus *Sebastomus* formed a tight cluster, as did the northeastern Pacific members of *Pteropodus*, whereas many of the other species did not cluster according to their subgeneric assignments. Rather, species from different subgenera often formed small, separate clusters, and the relationships among the clusters were not always clear.

The species of the subgenus *Sebastomus* generally clustered together except for *S. rosaceus*, which often clustered with the group of species that phenotypically have conspicuous vertical bands: *S. babcocki*, *S. nigrocinctus*, *S. rubrivinctus*, and *S. serriceps*. This group of species formed a cluster near the *Sebastomus* cluster.

The northeastern Pacific *Pteropodus* species, including *S. chrysomelas*, *S. carnatus*, *S. caurinus*, *S. maliger*, *S. nebulosus*, and *S. rastrelliger*, clustered consistently with *S. auriculatus* and *S. dalli* of the subgenus *Auctospina*, and *S. atrovirens* of *Mebarus*. Three species clustered near but not consistently with the *Pteropodus* group: *S. saxicola* and *S. semicinctus* (both subgenus *Allosebastes*), and *S. elongatus* (subgenus *Hispaniscus*). The northwestern Pacific members of *Pteropodus*, *S. hubbsi*, *S. nivosus*, and *S. trivittatus*, as well as the northwestern Pacific members of *Mebarus*, *S. inermis*, *S. joyneri*, *S. taczanowski*, and *S. thompsoni*, did not cluster with their northeastern Pacific counterparts. Instead, they generally clustered with other northwestern Pacific species in the analysis. These results are in agreement with earlier observations (Kai et al 2003, Li et al. 2006a).

As for the species in other subgenera, four small consistent clusters of species representing three subgenera occurred in all phylogenetic trees. They were (1) *S. hopkinsi*, *S. ovalis*, and *S. rufus* (subgenus *Acutomentum*); (2) *S. emphaeus*, *S. variegatus*, *S. wilsoni*, and *S. zacentrus* (subgenus *Allosebastes*); (3) *S. inermis*, *S. joyneri*, and *S. thompsoni* (subgenus *Mebarus*); and (4) *S. saxicola* and *S. semicinctus* (subgenus *Allosebastes*). Each of these clusters was distinct from other species belonging to their subgenera. Two other groups formed with a little less consistency. *Sebastes miniatus* and *S. pinniger* (subgenus *Rosicola*) clustered together in all but the 1:1 consensus tree. *Sebastes flavidus*,

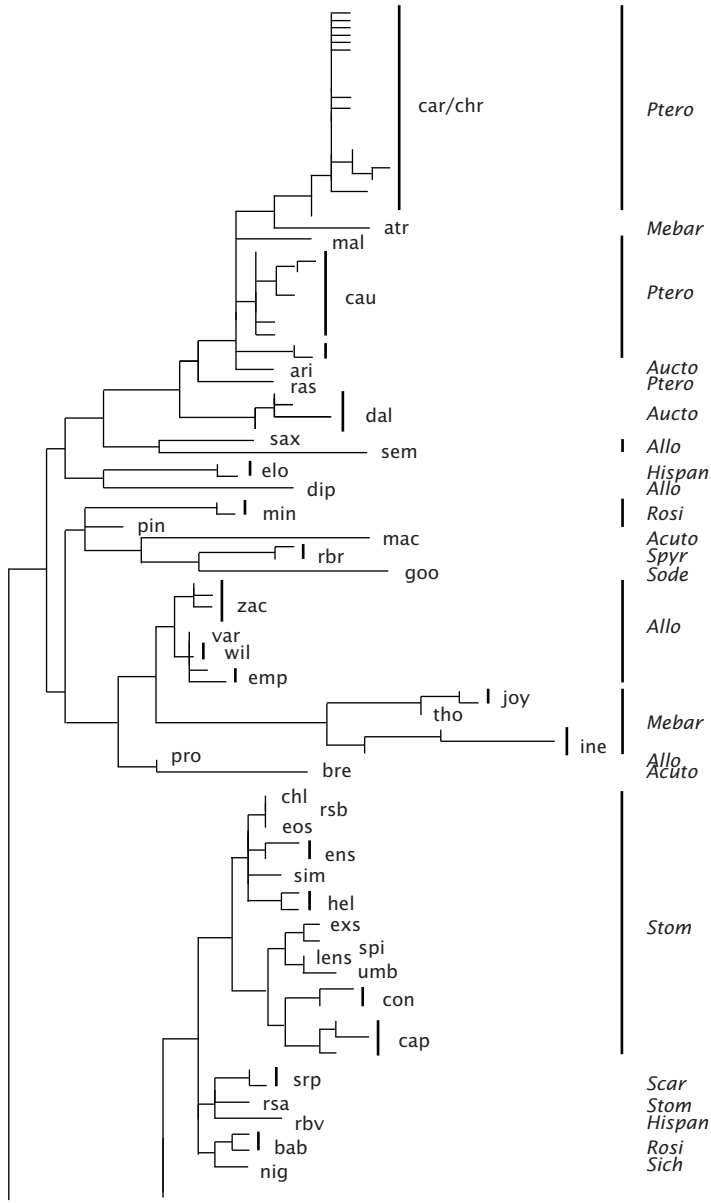


Figure 1. Neighbor-joining tree (Saitou and Nei 1987) based on restriction site variation in *Sebastes*. Haplotypes of additional samples were included for five species to examine the influence of intraspecific variation. Vertical lines reflect multiple haplotypes for a species. Abbreviations are in Tables 1 and 2.

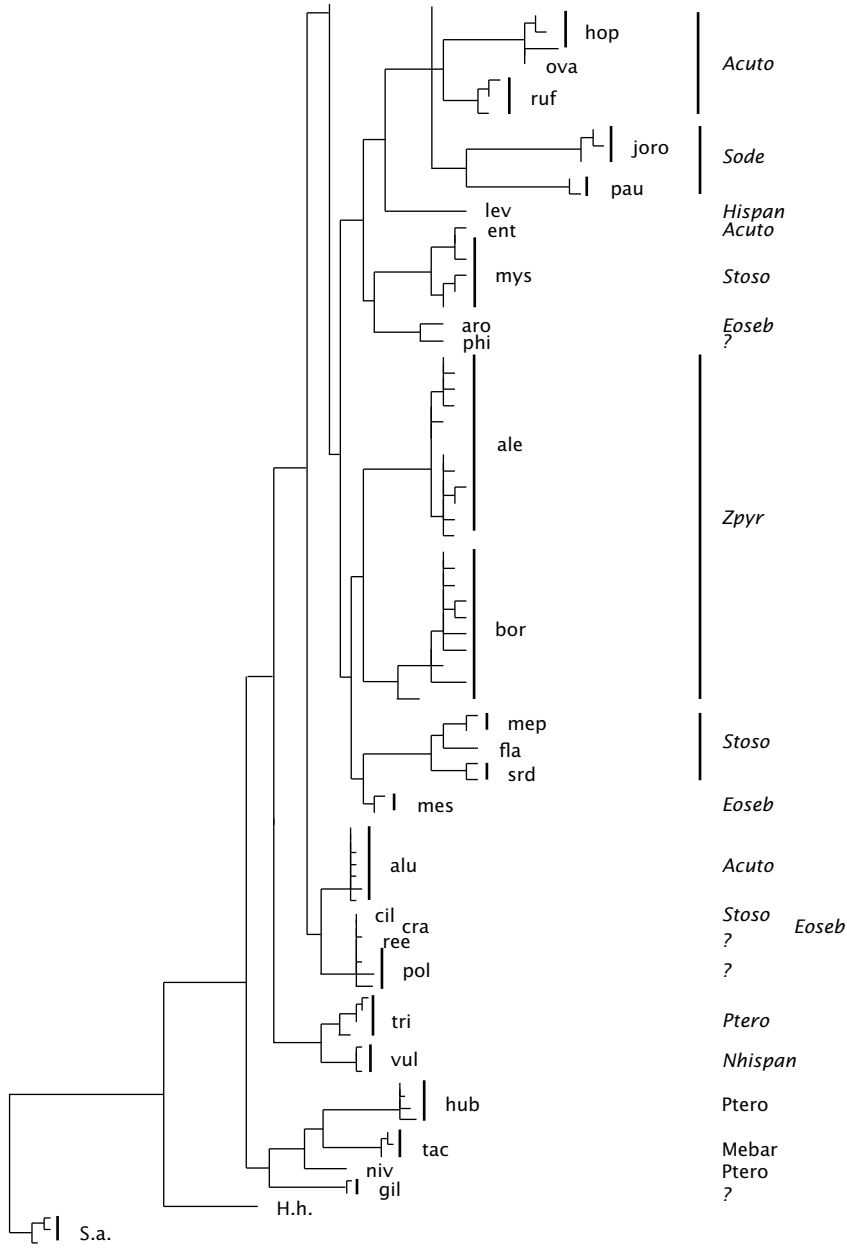


Figure 1. (Continued.)

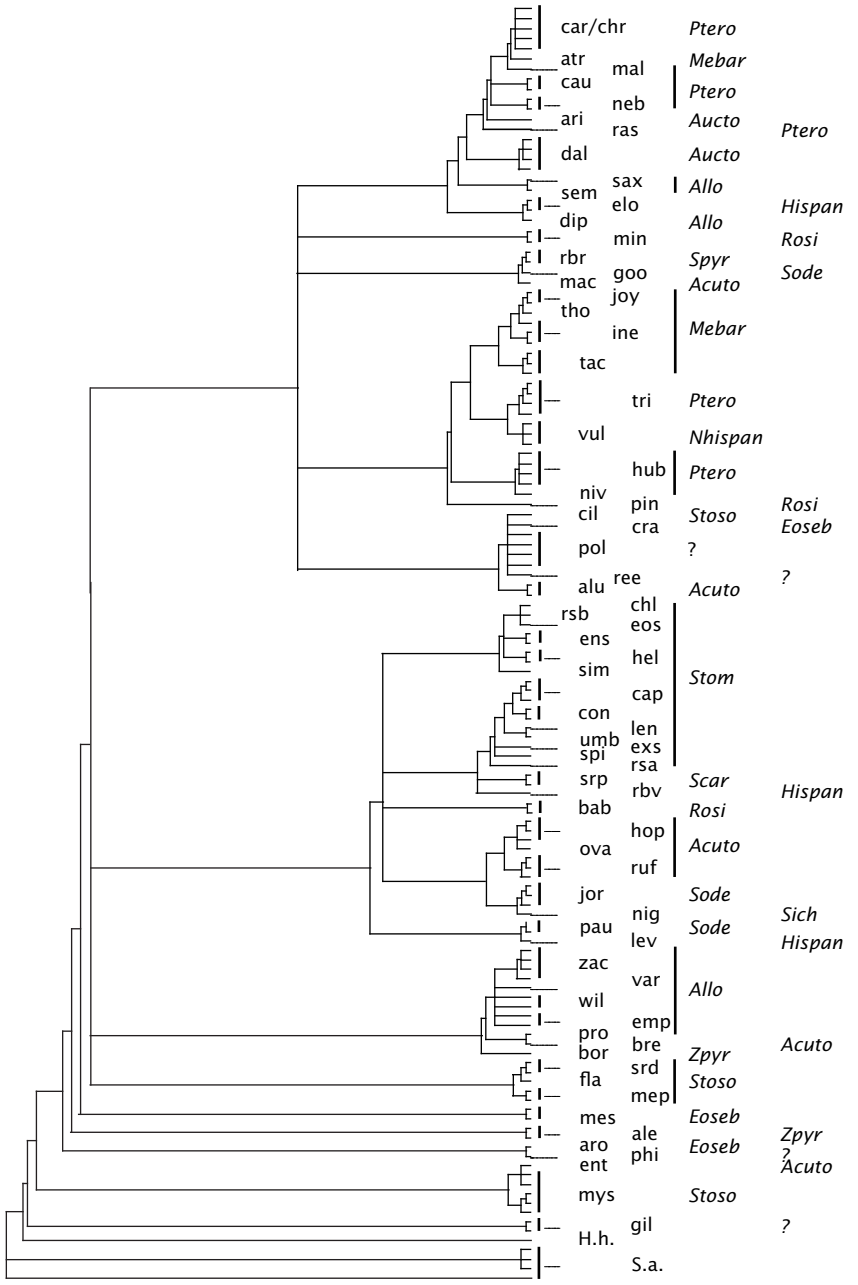


Figure 2. 50% majority consensus tree of 18,529 parsimony trees generated under the 1:1 weighting scheme. Vertical lines reflect multiple haplotypes for a species. Abbreviations are in Tables 1 and 2.

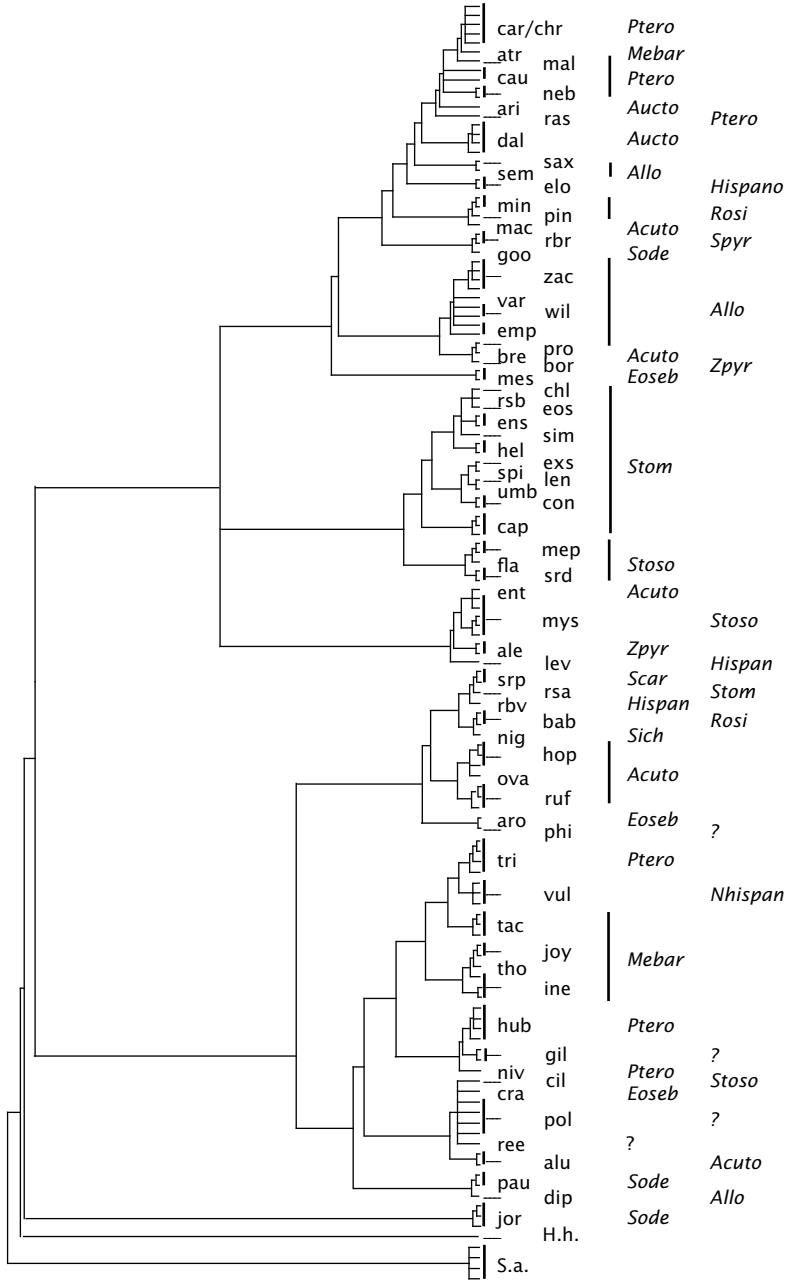


Figure 3. 50% majority consensus tree of 11,279 parsimony trees generated under the 1:2 weighting scheme. Vertical lines reflect multiple haplotypes for a species. Abbreviations are in Tables 1 and 2.

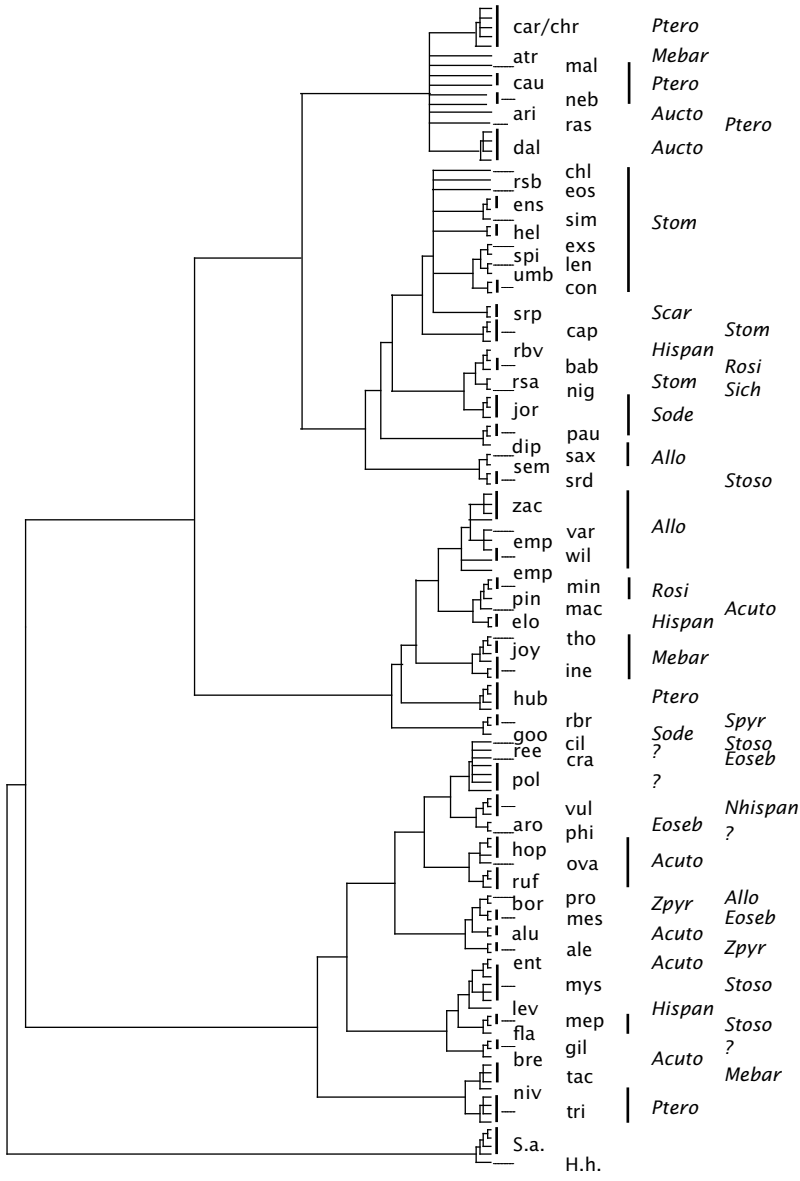


Figure 4. 50% majority consensus tree of 1,324 parsimony trees generated under the 1:4 weighting scheme. Vertical lines reflect multiple haplotypes for a species. Abbreviations are in Tables 1 and 2.

S. melanops, and *S. serranoides* (subgenus *Sebastosomus*) clustered together in all trees except for the 1:4 consensus tree. Other species previously assigned to these subgenera by other authors did not cluster with the species in their assigned subgenera.

Consistent groups were also formed by species from different subgenera. Four clusters appeared in all of the trees: (1) *S. mystinus* (subgenus *Sebastosomus*) and *S. entomelas* (subgenus *Acutomentum*); (2) *S. aurora* (subgenus *Eosebastes*) and *S. phillipsi* (unassigned); (3) *S. ruberrimus* (subgenus *Sebastopyr*) and *S. goodei* (subgenus *Sebastodes*); and (4) *S. ciliatus/variabilis* (subgenus *Sebastosomus*), *S. crameri* (subgenus *Eosebastes*), *S. polyspinis* (unassigned), and *S. reedi* (unassigned). *Sebastes alutus* (subgenus *Acutomentum*) clustered near the latter group in all but the 1:4 consensus tree. *Sebastes babcocki* (subgenus *Rosicola*), *Sebastes nigrocinctus* (subgenus *Sebastichthys*), *S. rubrivinctus* (subgenus *Hispaniscus*), and *S. serriceps* (subgenus *Sebastocarus*) also clustered closely and consistently, often with *S. rosaceus* (subgenus *Sebastomus*).

Discussion

Intraspecific variation

Generally, all variants of a species clustered together, separate from other species in the neighbor-joining tree. In four instances, variants of one species clustered with another species. Variants of *S. carnatus* and *S. chrysomelas* clustered together; variants of *S. mystinus* clustered with *S. entomelas*; variants of *S. polyspinis* clustered with *S. ciliatus/variabilis*, *S. crameri*, and *S. reedi*; and variants of *S. emphaeus* and *S. wilsoni* clustered with *S. variegatus*. In addition, three morphotypes of *S. inermis* have concordant, but small mtDNA and AFLP differences that probably reflect species differences (Kai et al. 2002). These occurrences suggest that the species within the clusters diverged recently. Intraspecific variation did not obscure phylogenetic relationships. The 10 additional haplotypes of *S. aleutianus* formed two separate clusters on the neighbor-joining tree, which is consistent with the existence of two cryptic species (Gharrett et al. 2005).

Phylogenetic analysis

Thirteen subgenera that included more than one species were included in this study. They were *Acutomentum*, *Allosebastes*, *Auctospina*, *Eosebastes*, *Hispaniscus*, *Mebarus*, *Neohispaniscus*, *Pteropodus*, *Sebastocarus*, *Sebastomus*, *Sebastopyr*, *Sebastosomus*, and *Zalopyr*. Based on the subgeneric assignments currently recognized in Kendall (2000) (except for *S. gilli*), our results suggest that only the subgenus *Sebastomus* defined by Chen (1971) is monophyletic. The other subgen-

era are probably polyphyletic, because only a few species clustered with others in their subgenera. The three species in monotypic subgenera all clustered with species from other subgenera. In addition, three species currently not assigned to subgenera consistently clustered with species to which a subgenus had been assigned. Five subgenera will be discussed in detail: *Sebastomus*, *Pteropodus*, *Acutomentum*, *Allosebastes*, and *Sebastosomus*.

Sebastomus

The subgenus *Sebastomus* was erected by Gill (1864) for *S. rosaceus*, and the current species composition mainly follows Chen (1971). From morphology, Chen (1971) concluded that the 13 species *S. capensis*, *S. chlorostictus*, *S. constellatus*, *S. ensifer*, *S. eos*, *S. exsul*, *S. helvomaculatus*, *S. lentiginosus*, *S. notius*, *S. rosaceus*, *S. rosenblatti*, *S. simulator*, and *S. umbrosus*—but not *S. gilli*—form a monophyletic group. He also outlined the relationships among the species (Chen 1971). *Sebastes spinorbis* was described later and considered a close relative of *S. exsul* (Chen 1975). Allozyme patterns (Seeb 1986) of seven of the species included by Chen, and mitochondrial cytochrome *b* sequences (Rocha-Olivares et al. 1999) corroborate the monophyly of the subgenus.

We included all the members of *Sebastomus* except *S. notius* and observed that all the species clustered tightly. The average nucleotide divergence within *Sebastomus* is 0.0089 substitutions per nucleotide. The southern (*S. capensis*, *S. constellatus*, *S. exsul*, *S. spinorbis*, *S. lentiginosus*, and *S. umbrosus*) and northern (all the other species) lineages identified by Rocha-Olivares et al. (1999) were evident in our neighbor-joining tree and the 1:1 consensus tree. Within *Sebastomus*, three species—*S. chlorostictus*, *S. eos*, and *S. rosenblatti*—had identical composite haplotypes; and two pairs of species—*S. exsul* and *S. spinorbis*, and *S. lentiginosus* and *S. umbrosus*—were each separated by two restriction sites, suggesting that these species pairs have recently diverged. These species groupings were also observed by Rocha-Olivares et al. (1999). The type species, *S. rosaceus*, did not consistently group with other members of the subgenus, but instead grouped with the conspicuously banded species, *S. babcocki*, *S. nigrocinctus*, *S. rubrivinctus*, and *S. serriceps*. Rocha-Olivares et al. (1999) suggested that *S. babcocki*, *S. nigrocinctus*, and *S. rubrivinctus* may be a sister clade to *Sebastomus*.

Pteropodus

The northeastern Pacific species of *Pteropodus* (*S. carnatus*, *S. caurinus*, *S. chrysomelas*, *S. maliger*, *S. nebulosus*, and *S. rastrelliger*) clustered with *S. atrovirens*, *S. auriculatus*, and *S. dalli*, but were separate from the northwestern Pacific members of the subgenus (*S. hubbsi*, *S. nivosus*, and *S. trivittatus*) (Li et al. 2006b). The average nucleotide substitution

rate between species within the northeastern Pacific cluster is 0.0124 per nucleotide, the second lowest of all groups considered. The low level of species divergence, as well as the tight cluster these species formed, provides support for the addition of *S. atrovirens*, *S. auriculatus*, and *S. dalli* to the subgenus *Pteropodus*. A possible sister clade of these species is the group *S. saxicola*, *S. semicinctus*, and *S. elongatus*. The northwestern Pacific species of the subgenus did not form any consistent monophyletic groups in the phylogenetic trees (Li et al. 2006a). These results were in agreement with Kai et al. (2003).

Acutomentum

Eigenmann and Beeson (1893) established the subgenus *Acutomentum* for species with "much projecting" lower jaws, among other characteristics. The group originally included *S. ovalis*, the type species, as well as *S. melanostomus*, *S. rufus*, *S. alutus*, and *S. macdonaldi*. Jordan and Evermann (1898) added *S. entomelas*, *S. brevispinis*, *S. hopkinsi*, and *S. proriger*, and moved *S. melanostomus* to the subgenus *Eosebastes*. Chen (1975) moved *S. proriger* to the subgenus *Allosebastes*. Matsubara (1943) added four species from the northwestern Pacific: *S. flammeus*, *S. iracundus*, *S. scythropus*, and *S. baramenuke*. All seven northeastern Pacific species but none of the northwestern Pacific species currently in the subgenus were included in this analysis. The average nucleotide substitution rate within northeastern Pacific *Acutomentum* was 0.0308 per nucleotide (Table 2), among the highest of all subgenera considered.

Species of the subgenus *Acutomentum* that we examined formed several distinct clusters, some with species in the subgenus, others with species from other subgenera. Three species, *S. hopkinsi*, *S. ovalis*, and *S. rufus*, consistently clustered together in all of the phylogenetic trees, indicating they are monophyletic. The average nucleotide substitution rate among these three species was 0.0144 per nucleotide; and the rate between *S. hopkinsi* and *S. ovalis* was extremely low, at 0.0031 substitutions per nucleotide. A pair of species, *S. entomelas* and *S. mystinus* (subgenus *Sebastosomus*), clustered consistently together, and the nucleotide divergence between them was also low, at 0.0055 substitutions per nucleotide. Rocha-Olivares et al. (1999) also observed the close relationship between *S. hopkinsi* and *S. ovalis*, and between *S. entomelas* and *S. mystinus*. *Sebastes brevispinis* and *S. proriger* (subgenus *Allosebastes*) clustered together in all but the 1:4 consensus tree. *Sebastes macdonaldi* occurred in various positions in the trees; it is unclear to which species it is most closely related. *Sebastes alutus* clustered near four northerly species, *S. ciliatus/variabilis* (*Sebastosomus*), *S. crameri* (*Eosebastes*), *S. polyspinis* (unassigned), and *S. reedi* (unassigned), in all but one of the trees but was distal from other *Acutomentum* species.

Allosebastes

The subgenus *Allosebastes* was erected for *S. sinensis* by Hubbs (1951), who regarded the "most notable character of this subgenus" to be "the reduction of the anal soft-rays to 5." Hubbs also described other distinct characters of *S. sinensis*, among them "the smooth, mostly cycloid scales; the swollen lower pectoral rays; the excessively long anal spines." *Sebastes sinensis* remained the only member of the subgenus until Chen (1975) added 11 northeastern Pacific species—*S. dalli*, *S. diploproa*, *S. emphaeus*, *S. proriger*, *S. rufinanus*, *S. saxicola*, *S. semicinctus*, *S. variegatus*, *S. wilsoni*, and *S. zacentrus*—and one northwestern Pacific species—*S. scythropus*. Chen (1971) considered *S. cortezi*, *S. peduncularis*, and *S. varispinis* relatives of the subgenus, and added them to the subgenus in 1985. Currently *S. dalli* is assigned to *Auctospina* (also see under *Pteropodus*) (Jordan and Starks 1895, Kendall 2000), and *S. scythropus* is assigned to *Acutomentum* following Matsubara (1943).

Chen (1975) gave a brief description of the characters shared among the species, including the cranial spine patterns, a banded color pattern, and the morphology of the gas-bladder muscles. However, these characters were not those considered by Hubbs (1951), and did not seem specific enough for subgeneric assignments (e.g., Kendall 2000). In addition, some species were described from few specimens (only two *S. peduncularis* and two *S. rufinanus* have ever been collected) or from samples of juveniles (*S. peduncularis* and *S. varispinis*). Chen admitted that the phylogenetic relationships he proposed were speculative. Our results do not support the monophyly of *Allosebastes*. We observed close relationships within two groups of species: *S. emphaeus*, *S. variegatus*, *S. wilsoni*, and *S. zacentrus* consistently clustered together and *S. saxicola* and *S. semicinctus* clustered with each other near the *Pteropodus* clade. *Sebastes proriger* clustered near the *S. emphaeus* group, relationships also suggested by Seeb (1986). *Sebastes diploproa* clustered with *S. elongatus* in the 1:1 consensus tree and the neighbor-joining tree, and clustered with *S. paucispinis* in the 1:2 and 1:4 consensus trees. From our data, it is unclear to which species *S. diploproa* is most related. Because a sample of the type species, *S. sinensis*, was unavailable for this study, it is difficult to determine which species added by Chen should be retained in the subgenus.

Sebastosomus

Three of the five members of *Sebastosomus*, *S. flavidus*, *S. melanops* (the type species), and *S. serranoides*, clustered together in three of the phylogenetic trees, suggesting that some species assigned to the subgenus are monophyletic. This group was also observed by Seeb (1986) and Rocha-Olivares et al. (1999). The other two *Sebastosomus* members, *S. crameri* and *S. mystinus*, were associated with complexes formed by species from other subgenera. *Sebastes crameri* consistently grouped with *S.*

ciliatus/variabilis, *S. polyspinis*, and *S. reedi*, which indicates that these species are closely related, and may warrant assignment to a single subgenus. *Sebastes alutus* appeared to be closely related to this group. The ranges of these species overlap off British Columbia and Southeast Alaska, and are all categorized as continental slope species. Love et al. (2002) reported that *S. reedi* are commonly taken with *S. alutus* and *S. crameri*. *Sebastes mystinus* clustered with *S. entomelas* in all trees, suggesting that they are closely related. Seeb (1986) and Rocha-Olivares et al. (1999) observed this grouping as well.

Other groups

Other notable groupings included *S. aurora* and *S. phillipsi*, and *S. ruberrimus* and *S. goodei*, both of which appeared in all of the phylogenetic trees. *Sebastes aurora* and *S. phillipsi* resemble each other morphologically, overlap in ranges, and are both deepwater species (Love et al. 2002). They appear to be closely related. Although *S. ruberrimus* and *S. goodei* cluster consistently, they differ from each other in coloration and body shape and differ at 11 restriction sites (0.021 substitutions per nucleotide). *Sebastes miniatus* and *S. pinniger* (both *Rosicola*) clustered together in all trees except for the 1:4 consensus tree. These species resemble each other in having a mottled pattern and prominent white markings along the lateral line, and they differ mostly in coloration. They are most likely closely related. This group was also observed by Rocha-Olivares et al. (1999).

Two subgenera in this study, *Pteropodus* and *Mebarus*, contain species from both the northeastern Pacific and the northwestern Pacific. The results provide strong evidence that the northeastern Pacific and northwestern Pacific members of these subgenera are not monophyletic. This may prove true for other trans-Pacific subgenera as well. Analysis of more northwestern Pacific species needs to be done to resolve the relationship between northeastern Pacific and northwestern Pacific species.

Although many consistent species groups were revealed in this study, relationships among other species remained unresolved, as are the relationships among the existing subgenera. Northeastern Pacific species that did not cluster consistently with any other species included *S. aleutianus*, *S. borealis*, *S. gilli*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, and *S. paucispinis*. In addition, species within several groups have identical composite profiles. These observations point to the need to explore other mtDNA regions and that comparison of nuclear genes is needed to corroborate the results from analysis of mtDNA variation.

Our results were generally similar to those of Seeb (1986) from allozyme analysis and to those of Rocha-Olivares et al. (1999) and Kai et al. (2003) from sequence analysis of the mtDNA cytochrome *b* gene.

In many instances the results were identical. The concordance in results of the three studies gives strong support to some of the phylogenetic relationships we suggested, because they were observed using three different methods that examined different parts of the genome. The similarities also indicate that both sequencing and restriction site analysis can provide data for phylogenetic comparisons. Each method has its advantages and disadvantages. DNA sequencing can provide data that can be analyzed using a wider array of analytical tools and provide more detail; however, restriction site studies can efficiently survey longer spans of DNA at a relatively low cost. In this study, an estimated 901 nucleotides were recognized by the restriction enzymes, equivalent to about 19% of the 4,815 nucleotides examined in the two mtDNA regions, and 5.4 % of the mtDNA genome. In Rocha-Olivares et al. (1999), the stretch of DNA sequenced was about 750 bp.

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Use of Otolithometry to Determine Asian Shortraker Rockfish Population Structure

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Abstract

The shortraker rockfish, *Sebastes borealis*, is an important target of bottom trawl and longline fisheries in the North Pacific Ocean. Its population structure is still uncertain, and there are two different theories on the life history of this species. Some authors think that shortraker rockfish is a non-migrating species, which forms many local populations within its range. Other investigators suggest that currents may transport pelagic larvae and juveniles of this species far from their spawning grounds and then, after reaching maturity, they undergo lengthy reverse migrations. Otolith studies may be useful to improve our knowledge of the population structure of shortraker rockfish. Otoliths of these fish were sampled in nine different geographic areas of the northwestern Pacific (northern Kuril Islands, southeastern Kamchatka, six large Kamchatka bays, and the Koryak slope) to define possible distinctions among fish. Length, width, and weight of otoliths of shortraker rockfish were measured from about 1,500 fish. Results are presented of a comparative statistical analysis of the relationship between these otolith characteristics for the fish of different areas. The otolith analysis did not yield any conclusive results about shortraker rockfish population structure.

Introduction

Recently in the North Pacific Ocean, more importance is being attached to harvesting species that have a relatively low abundance, but that are in demand at markets. This is especially true for the shortraker rockfish, *Sebastes borealis*, which is broadly distributed in the North

Pacific. This species used to be of importance for Russian fisheries in the Bering Sea in the 1960s and 1970s, when the exploitation of continental slope resources was being developed on a large scale. In recent decades, shortraker rockfish were harvested near the northern Kurils, eastern Kamchatka, and in the western Bering Sea, as well as in the Gulf of Alaska and near the Aleutian Islands. The large range of the shortraker rockfish includes the continental shelf and slope extending from the Pacific coast of Honshu, Japan (Iwate Prefecture), eastward to southern California at 36ºN, and includes the area of the Bering Sea and the southwestern Sea of Okhotsk, the Pacific waters near northern Japan, the Kuril Islands, Kamchatka, the Commander and Aleutian islands, and the Gulf of Alaska (Barsukov 1981, Mecklenburg et al. 2002).

Rational exploitation of a species is not possible without a clear understanding of its population structure. However, the population structure of shortraker rockfish is uncertain, and there have been two opposite points of view regarding the life history of this species. Some authors (Barsukov 1981, Parker et al. 2000) believe that the shortraker rockfish's mode of life is sedentary, and they make no extensive geographic migrations. Others (Orlov 2001, 2002) suggest that this species' larvae and pelagic juveniles are transported long distances by currents and that later in life they undergo reverse migrations to reproduction sites.

Various methods have been used to investigate the population structure of this rockfish, which have included a study of parasites (Moles et al. 1998) and genetic analysis (Matala et al. 2004, Hawkins et al. 2005). None of these studies, however, provides a definitive answer as to the stock structure of shortraker rockfish.

The method of otolithometry has been increasingly used in recent years in fishery research to ascertain the population structure of various fish species. This technique involves the comparison of parameters of fish otoliths taken from various parts of the geographic range. This method has been used to determine the population structure of a number of fish species, including Pacific cod *Gadus macrocephalus* (Vinnikov and Davydenko 1998); saffron cod *Eleginus gracilis* (Lyogen'kaya 1999); walleye pollock *Theragra chalcogramma* (Pashchenko and Gritsai 2001, Nishimura and Yanagimoto 2001); round sardinella *Sardinella aurita* (Chesheva and Zimin 2004); haddock *Melanogrammus aeglefinus* (Begg and Brown 2000, Begg et al. 2001); and redfish *Sebastes mentella* (Stransky 2002).

The main purpose of this paper is to attempt to resolve intraspecific differences in shortraker rockfish populations of the northwest Pacific on the basis of otolith analysis.

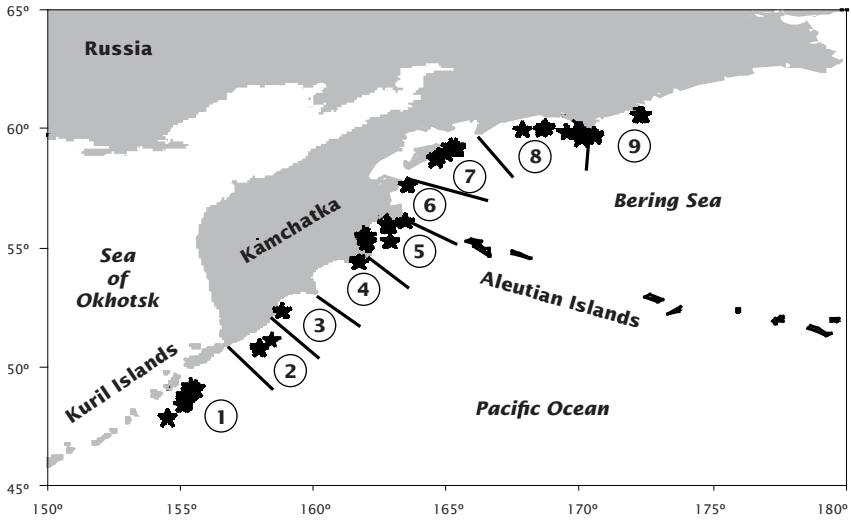


Figure 1. Sites of otolith samples (numbers of areas as in Table 1) of shortraker rockfish in the northwestern Pacific.

Material and methods

Otoliths of shortraker rockfish, which were collected from bottom trawl and longline catches on Japanese trawlers in 1992-1999 and on Russian longliners in 1993-1994, were used as material for this paper. Otoliths were sampled from nine different sites of the northwest Pacific (Fig. 1) including waters of the (1) North Kurils, (2) Southeast Kamchatka, (3) Avacha Bay, (4) Kronotsky Bay, (5) Kamchatsky Bay, (6) Ozernoi Bay, (7) Karaginsky Bay, (8) Olyutorsky Bay, and (9) the Koryak slope. A total of 1,438 pairs of otoliths from fish ranging in length from 11 to 100 cm were gathered during the period of research (Table 1). Fork lengths of fish were measured throughout the study. The lengths and heights of otoliths were measured to within 0.1 mm; the weight of otoliths was determined to within 0.001 g. A previous study observed no statistically valid differences in measurements between the right and left otoliths in rockfishes (Munk and Smikrud 2002). Consequently, only one otolith (left or right) was measured. Data processing and analysis were made with statistical programs of the Microsoft Excel software package based on the procedures of Ivanter and Korosov (2003).

Table 1. Data on shortraker rockfish body length and otolith size and weight in different areas of the northwestern Pacific.

Area	Latitude, N	Longitude, E	Number of fish examined	Fork length, cm	Otolith length, mm	Otolith height, mm	Otolith weight, g
1 Northern Kuril Islands	47°49'-49°08'	154°31'-155°34'	287	11-58 34.58±10.94	5.5-16.8 13.046±2.969	3.1-11.7 7.712±1.838	0.005-0.521 0.227±0.120
2 Southeastern Kamchatka	50°45'-51°06'	157°58'-158°25'	41	21-70.5 45.27±10.93	9.0-24.5 15.914±3.117	5.5-12.8 9.502±1.550	0.081-1.011 0.391±0.186
3 Avachinsky Bay	52°19'	158°49'	47	38-86 68.02±12.41	14.0-26.2 20.379±2.922	8.9-14.8 12.132±1.530	0.269-1.249 0.745±0.242
4 Kronotsky Bay	54°24'	161°44'	50	41-92 72.94±10.71	12.1-26.5 21.832±2.761	7.2-15.0 12.518±1.577	0.183-1.371 0.913±0.269
5 Kamchatsky Bay	55°14'-56°07'	161°54'-163°26'	285	31-100 68.77±8.61	12.1-26.3 20.957±2.218	7.3-17.9 12.031±1.255	0.197-1.464 0.817±0.220
6 Ozernoy Bay	57°36'	163°31'	42	47-93 69.69±11.35	15.2-16.8 20.767±2.618	10.0-15.8 12.259±1.450	0.386-1.618 0.793±0.287
7 Karaginsky Bay	58°40'-59°12'	164°37'-165°24'	291	37-99 67.52±10.42	13.5-27.6 20.471±2.550	8.8-15.0 11.891±1.454	0.275-1.598 0.765±0.227
8 Olyutorsky Bay	59°36'-60°02'	167°51'-170°35'	291	32-90 58.58±8.36	12.0-25.8 18.574±2.133	8.0-14.8 10.994±1.064	0.208-1.579 0.695±0.138
9 Koryak slope	60°33'-60°35'	172°16'-172°21'	104	44-79 61.39±7.12	14.5-24.0 19.105±1.951	9.2-14.0 11.257±0.971	0.302-1.224 0.624±0.175

Note: underlined is range of variations, not underlined are mean and standard deviation (±SD).

Table 2. Mean values of otolith length/height (LO/HO) ratios and standard errors (±SE) of shortraker rockfish in different areas of the northwestern Pacific (numbers of areas as in Table 1).

Area	Mean LO/HO value	Standard error	Number examined
1 Northern Kuril Islands	1.6990	0.0058	287
2 Southeastern Kamchatka	1.6699	0.0167	41
3 Avachinsky Bay	1.6814	0.0214	47
4 Kronotsky Bay	1.7502	0.0223	50
5 Kamchatsky Bay	1.7495	0.0102	285
6 Ozernoy Bay	1.6978	0.0222	42
7 Karaginsky Bay	1.7234	0.0096	291
8 Olyutorsky Bay	1.6910	0.0079	291
9 Koryak slope	1.6996	0.0131	104

Results

Otolith collections of rockfish from various regions were heterogeneous (Table 1); samples differed greatly in mean body length of fish, size, and weight of otoliths. Therefore, we used characteristics that do not depend on body length for comparative analysis of otoliths from various regions. The otoliths were compared using two different methods: variance and regression analysis. Results were corrected for multiple pairwise comparisons using Student's *t*-test, which is frequently used in biological studies (Plokhinsky 1970), with further adjustment of Bonferroni correction as described by Westfall and Wolfinger (1997).

Variance analysis

The relationship between the fork length (FL) and the otolith length/weight ratio (LO/WO), otolith height/weight ratio (HO/WO) and otolith length/height (LO/HO) ratio were analyzed in order to determine which of these relationships were independent of body length. The first two relationships clearly showed a strong, nonlinear correlation to fork length (Fig. 2a,b) and were not appropriate for the comparative analysis. Only the otolith length/height ratio appeared independent of body length (Fig. 2c), which made it possible to use this ratio to compare otoliths of shortraker rockfish from the different sites. The average values of this ratio and associated standard errors were calculated for each area studied (Table 2). Additional subsequent variance analysis was based on them, and was used for a matrix (Table 3), which shows

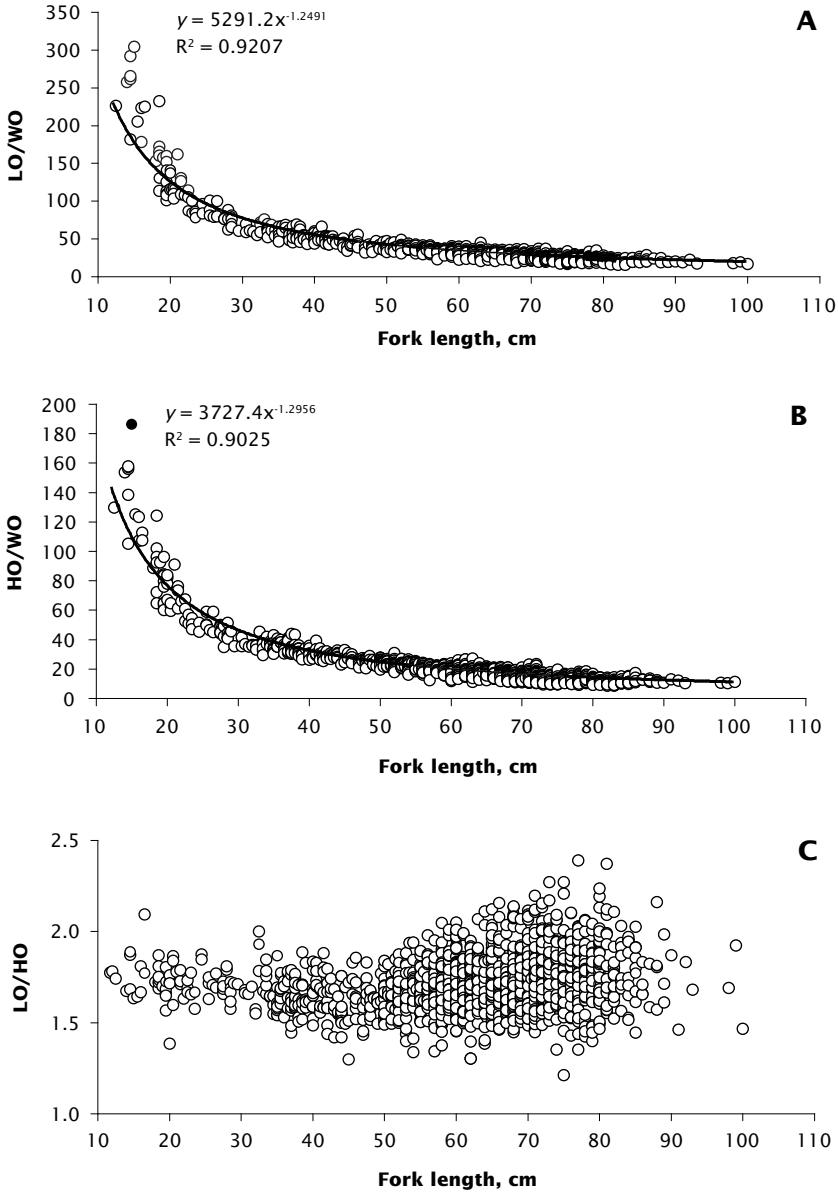


Figure 2. Relation between fork length and otolith (A) length/weight, (B) height/weight, and (C) length/height ratios.

Table 3. ***P*-values of multiple pairwise comparison of shortraker rockfish otolith length/height ratio in different areas tested using Student's *t*-test with 95% confidence interval.**

Area	1	2	3	4	5	6	7	8	9
1 Northern Kuril Islands									
2 Southeastern Kamchatka	0.07687								
3 Avachinsky Bay	0.28293	0.67789							
4 Kronotsky Bay	**0.00279**	**0.00676**	**0.02911**						
5 Kamchatsky Bay	**0.00002**	**0.00429**	**0.01101**	0.97968					
6 Ozernoy Bay	0.91999	0.32071	0.59843	0.10283	0.06522				
7 Karaginsky Bay	**0.03542**	**0.04401**	0.10109	0.28516	0.06353	0.33992			
8 Olyutorsky Bay	0.32840	0.36370	0.96422	**0.00481**	**0.00000**	0.72621	**0.00773**		
9 Koryak slope	0.98154	0.20552	0.45223	**0.04247**	**0.00850**	0.93529	0.19299	0.52174	

Bold values = significantly different, non-bold = not different, underlined = significantly different after Bonferroni correction.

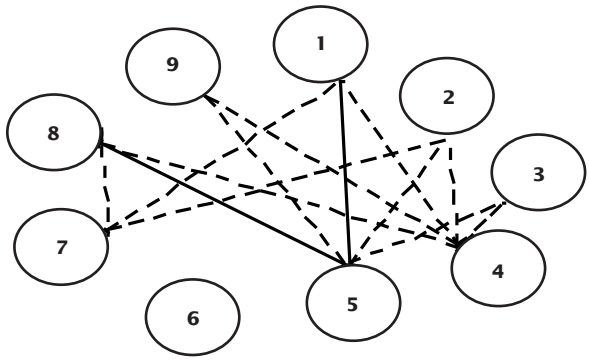


Figure 3. Schematic diagram of differences of shortraker rockfish otolith samples from different areas of the northwestern Pacific (numbers of areas as in Table 1; dashed lines showed significant differences with $\alpha = 0.05$; bold lines = after Bonferroni correction with $\alpha = 0.00139$).

the disparities among otoliths taken from the different areas. To better perceive these results, the matrix was also transformed into a schematic diagram (Fig. 3). Overall, an unequivocal interpretation of these data is difficult. On one hand, in some individual cases the data indicated that there are significant differences between fish from contiguous areas, e.g., in the Southeast Kamchatka (2), Avacha Bay (3) and Kronotsky Bay (4) or in Karaginsky Bay (7) and Olyutorsky Bay (8). On the other hand, the data showed similarities of fish from regions distal from one another, for example, Avachinsky Bay (3) compared with Karagadinsky Bay (7), Olyutorsky Bay (8), and Koryal slope (9); and the North Kurils (1) compared with Olyutorsky Bay (8) and Koryal slope (9). The group of rockfish from Ozernoy Bay (6) stands out because it does not differ from all the other samples in the characteristics compared. It should be noted that the results described are based on the level of statistical significance $\alpha = 0.05$. After Bonferroni correction (Table 3, Fig. 3) only differences between Kamchatsky Bay (5) and both North Kurils (1) and Olyutorsky Bay (8) are statistically significant. On the one hand, this observation would support Orlov's (2001, 2002) hypothesis if the shortraker rockfish that inhabit Kamchatsky Bay (5) are represented by mixed stocks from the Bering Sea and the Pacific. On the other hand, the similarity between rockfish from different geographic areas of the northwestern Pacific and western Bering Sea does not support any existent idea about shortraker rockfish population structure. Consequently, because of these generally inconsistent results, it appears that the variance analysis was unsuccessful in detecting the population structure of the shortraker rockfish in the northwest Pacific Ocean.

Regression analysis

It is well known that there is often a high degree of correlation between body length and the sizes and weights of the otoliths in fish, especially rockfish (Wyllie Echeverria 1987, Pawson 1990). To investigate this correlation for our shortraker rockfish data, we used simple regression analysis. The analysis showed linear relationships between fork length and each of the otolith parameters for every area sampled (Fig. 4), which has a moderate to high degree of correlation ($R = 0.47 - 0.97$). Hence, the differences among the rockfish from different areas can be evaluated using the differences among the coefficients of the regression equations. As in the case of the variance analysis, the results do not provide definitive patterns of similarity or difference between the fish taken at the different sites. For example, dependence between the length of fish and otolith height in the regressions are close to one another both in adjacent sites (1 and 2) and in sites that are geographically far apart (4 and 8). As another example, the regression values for body length versus otolith height were very similar from the adjoining sites 5 and 6, but were also similar for sites 3 and 8, which are quite far from each other. As was the case in the variance analysis, the sample from Ozernoy Bay (6) generally differed from those from the other sites, especially in terms of the regression values for body length versus otolith height and for body length versus otolith weight. However, the Ozernoy Bay samples proved to be close to the samples from sites 5 and 9 in terms of the relationship between the body length and the height of otolith. In some cases (FL/HO and FL/WO regressions) the North Kuril (1) sample also differed from the other sites. Taking into consideration all the results of the regression analysis, it appears these results were inconclusive regarding the population structure of shortraker rockfish within the areas sampled.

Discussion

Studies of shortraker rockfish population structure have been undertaken using different methods. The most powerful method is the traditional tag-and-release experiment. Unfortunately, that method is not feasible for deepwater rockfishes (including shortraker) because they cannot survive the barotrauma of initial capture. Studies of parasite incidence are more practical for detecting population structure for rockfishes (Yanulov 1962). In the 1990s, the parasite incidence of shortraker rockfish, in samples from five different areas of the Gulf of Alaska, suggested that parasites may be naturally occurring tags that reflect rockfish population structure (Moles et al. 1998). Occurrence and abundance of several parasite species differed distinctly among sample sites, which may indicate existence of population structure. On the other hand, there is considerable variation in fish length between the

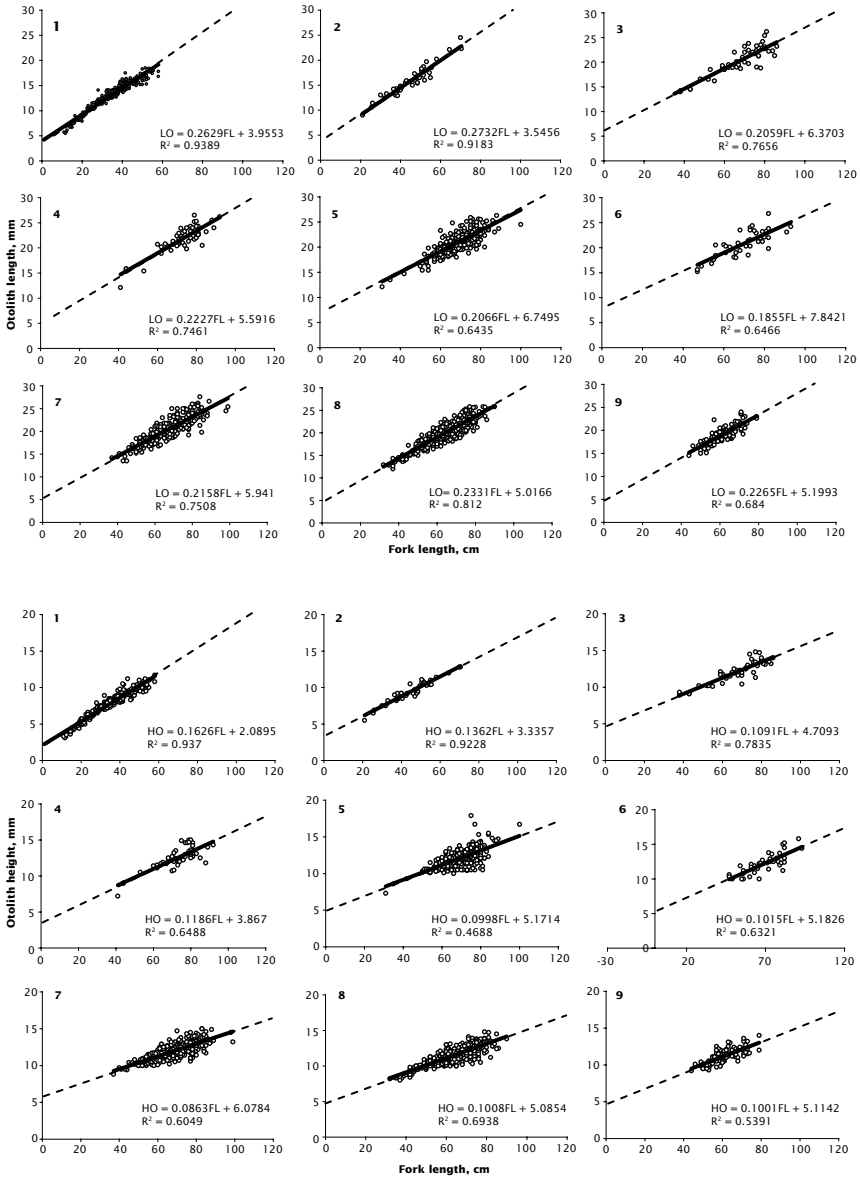


Figure 4. Regression lines and equations of relations between fork length (FL), otolith length (LO), height (HO), and weight (WO). Each graph is numbered and corresponds to one of the areas in Table 1.

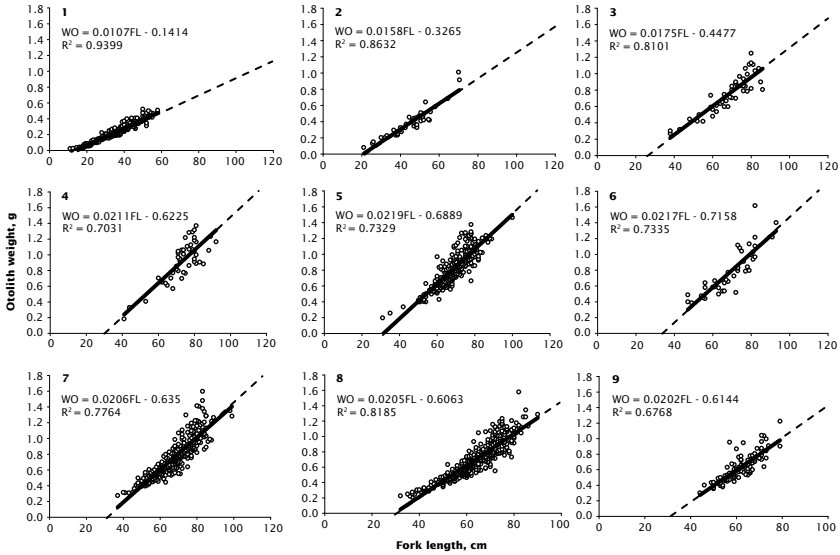


Figure 4. (Continued.)

areas surveyed; and distinctions in the parasite prevalence and abundance observed may relate to different age compositions of shortraker rockfish in each area.

Orlov (2001, 2002) analyzed size composition, relative abundance, and distributions of adult and benthic juveniles of shortraker rockfish in different areas of the North Pacific Ocean and compared these data with ocean current patterns. Based on these comparisons, he formulated a hypothesis that three super-populations of species occur within the Bering Sea, the western subarctic, and the Alaska gyres, as well as local populations that occur within eddies, which often form along the Kuril and Aleutian islands. This hypothesis can be confirmed or denied only with factual data, for instance, the results of genetic studies.

Hawkins et al. (2005) examined variation at allozyme loci and found no genetic heterogeneity among shortraker rockfish throughout sampled regions that included the west coast of North America from British Columbia waters to the central Aleutian Islands and western Bering Sea. However, they suggested that other genetic markers, such as microsatellite loci, may provide finer resolution of population structure.

In contrast, Matala et al. (2004) analyzed population structure of Alaska shortraker rockfish by examining allelic variation at eight microsatellite loci. Results of that study showed that the collection from

the southern end of the range differed from all remaining collections at three loci, i.e., provides evidence for genetic structure along the Pacific Rim from Southeast Alaska to the Aleutian Islands, which is a geographically based one. On the one hand, this may be associated with the mixed character of the fish inhabiting waters off the central Aleutian Islands that originated from different populations (southern Bering Sea and Aleutians). Microsatellite data typically provide more resolution than allozyme data. On the other hand there is significant variation of shortraker rockfish size in different geographic areas (decreasing from eastern to western Gulf of Alaska), and that pattern may be related to genetic differences among sites.

Otolithometry is another promising method for examining population structures for different species. Vinnikov and Davydenko (1998) used four otolith parameters (length, height, thickness, and weight) of the Pacific cod to investigate their population structure in the northwestern Pacific and used cluster analysis and pairwise comparison adjusted for multiple testing using Student's *t*-test. Since this species does not perform lengthy migrations and forms local populations, the method of otolithometry is probably applicable to the purpose considered.

Lyogen'kaya (1999) attempted to investigate population structure of saffron cod in the northwestern Pacific using regression analysis that involved relationships between fish length and otolith length, height, and weight. The results of that analysis are ambiguous. In some cases significant differences occurred among fish from neighboring sites, while in other cases similarity was found between samples from distant areas.

Pashchenko and Gritsai (2001) compared relationships between walleye pollock body length and otolith length, height, and weight in different areas of the Sea of Okhotsk and western Bering Sea. They observed significant differences in otolith morphology between different sites and concluded that otolithometry could be applied to resolution of population structure of walleye pollock.

Seven otolith measurements and weights were taken for population structure studies of the round sardinella in the central-eastern Atlantic (Chesheva and Zimin 2004) based on the comparison of fish of the same age classes. Results of this study provide evidence of the homogeneity of the West African population of round sardine and do not support the idea about existence of subspecies *S. aurita terrasae* in waters off Western Sahara, Mauritania, and Senegal.

Identification of haddock stocks on Georges Bank was conducted with the use of different techniques. In the paper of Begg and Brown (2000) four morphometric characteristics (area, length, width, and

perimeter), and two shape indices (circularity and rectangularity) were used. Potential confounding sources of variation (fish length, otolith position, age group, and year class) were examined and accounted for in the analyses before interpretation of stock differences. In the paper of Begg et al. (2001) the structure of otolith sections was described for individual haddock samples by using a combination of linear morphometrics, shape characteristics, and growth increments. Analyses were structured to account for the effects of size, sex, age, and year class.

Otolith shape analysis for stock and species separation for *Sebastes* species have been used by Stransky (2002) and Stransky and MacLellan (2005). Results of the first paper do not provide evidence of the heterogeneity of redfish *S. mentella* in the Irminger Sea on vertical (depth) or horizontal scale, and therefore do not support the idea about existence of oceanic and pelagic deep-sea populations of this species. Results of the latter study allow successfully separating different *Sebastes* species and showed strongest affinity of the North Pacific *S. alutus* to the North Atlantic species.

Neither of the techniques applied in this study allowed us to make any specific conclusions on the similarity or disparity of shortraker rockfish population structure at nine sites in the Northwest Pacific. The results neither favored the existence of local stocks for this species, nor supported the idea that shortraker rockfish are composed of large populations within the Bering Sea and western subarctic gyres. Obviously, the method we used provided no information about population structure for shortraker rockfish. Otolithometry as the tool for population structure of shortraker rockfish might be effective if more otolith measurements were available. We suggest that an analysis that takes into account the effects of length, sex, and age might be more informative. However, such an analysis will requires a larger number of otolith samples than we had at our disposal. Of the available methods for applying otolith differences to studies of population structure, otolith shape analysis is probably the most powerful, but the method requires special equipment and software.

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Changes in Growth and Recruitment of the Puget Sound Rockfish (*Sebastes emphaeus*) in Northern Puget Sound

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Abstract

Age composition and growth rates of Puget Sound rockfish in northern Puget Sound, Washington, were compared between 1994, 2001, and 2002. A rapid population expansion began in 1990 and 1991, at a time when several important predators had been reduced through overfishing. Growth (length at age) of Puget Sound rockfish slowed significantly between 1994, 2001, and 2002 ($p < 0.001$). El Niño events resulted in relatively poor recruitment success for Puget Sound rockfish, and could also result in reduced growth rates for adults. Observation of the changing role of Puget Sound rockfish in the local food web appears useful in understanding broader community changes.

Introduction

The northern Puget Sound fish community has undergone substantial changes in the last 30 years (Fig. 1). Recreational fishing and environmental changes have resulted in reduced populations of lingcod (*Ophiodon elongatus*), copper (*Sebastes caurinus*), and quillback (*Sebastes*

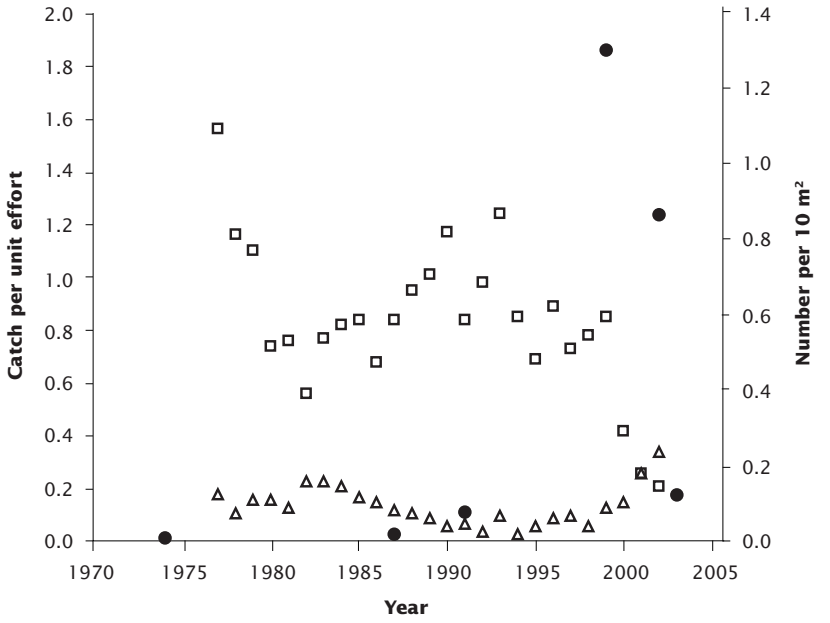


Figure 1. Abundance indices for lingcod (catch per angler trip, open triangles), Puget Sound rockfish (number per 10 m² in scuba surveys, solid circles), and larger rockfish (catch per angler trip, open squares).

maliger) rockfish in the area, and an almost complete disappearance of black rockfish (*Sebastes melanops*) and yellowtail rockfish (*Sebastes flavidus*) in the San Juan Channel. During this same time period, the abundance of Puget Sound rockfish (*Sebastes emphaeus*) has increased substantially.

Initial research on the basic biology of Puget Sound rockfish was done in 1975 and it was then stated to be a rarely reported species (Moulton 1975). Scuba surveys near a transect line at Point George, Shaw Island (Fig. 2), estimated average densities of 12, 21, 80, 1,300, 865, and 125 fish per hectare in 1974-75, 1987, 1991, 1999, 2002, and 2003 respectively (Moulton 1977, Caselle 1987, Bruce S. Miller unpubl. data 1991, Eisenhardt 2001, Sausman 2002, Toran 2003). Systematic video camera surveys were conducted throughout the San Juan Islands in 1994 and 2000 by the Washington State Department of Fish and Wildlife. These surveys were relatively precise (95% confidence intervals ±37-42%), and indicated that Puget Sound rockfish were at high levels of abundance in 1994, since mean counts per station in rocky habitats were 2.6 times higher in 1994 than in 2000. These sets of survey data combined indi-

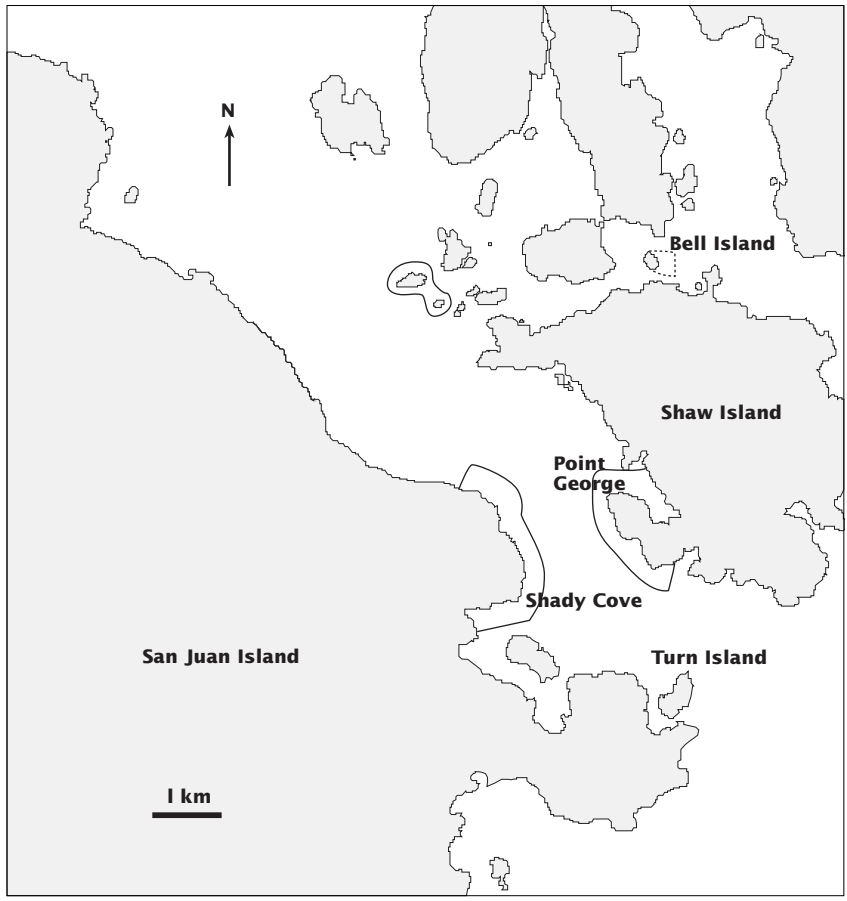


Figure 2. Sampling sites in San Juan Channel. Mandatory marine reserves are indicated by solid lines and the voluntary compliance reserve by the dotted line.

cate that Puget Sound rockfish underwent a rapid population increase in the San Juan Islands of northern Puget Sound between 1991 and 1994 and have declined in abundance since then. Age and length data collected in 1994, 2001, and 2002 allow examination of changes in growth rates and recruitment, features of Puget Sound rockfish biology that may suggest reasons for their dramatic increase in abundance.

Puget Sound rockfish have a more *r*-selected life history strategy than most rockfish (genus *Sebastes*). They are relatively small, reaching a maximum size of 180 mm and a maximum age of 13 years in Puget Sound (Beckmann et al.1998). Female Puget Sound rockfish are repro-

ductively mature at an average of 2 years of age and parturition occurs in late August and early September, later than the spring parturition period of other *Sebastes* species in Puget Sound (Beckmann et al. 1998). Like other rockfish, young Puget Sound rockfish feed on invertebrate plankton but because of their small size, they do not graduate to a piscivorous diet, although they may eat larval fish. Studies of the diet of Puget Sound rockfish in the spring and fall have shown that it is an opportunistic feeder, choosing the most abundant plankton of an appropriate size such as euphausids, calanoid copepods, and crab zoeae (Nelson 1996, O'Connor 1999).

The objective of this research is to examine how the abundance patterns of Puget Sound rockfish near San Juan Island relate to broader community dynamics, using analysis of age structure, growth, and mortality. Growth and recruitment of *S. emphaeus* will also be discussed in relation to recent El Niño events.

Materials and methods

In 1994, 353 fish were collected during 23 sampling trips. Samples were caught at two San Juan channel sites (Fig. 2), Turn Island (90%) and Shady Cove (4%), and two west-side sites, Deadman Bay (5%) and Henry Island (1%) (Beckmann et al. 1998).

In 2001, 227 Puget Sound rockfish were collected by hook and line and two were caught during scuba diving using hand nets. Fish were collected in 13 sampling trips between October and November at four San Juan Channel sites: Point George (20% of sample), Shady Cove (36%), Bell Island (26%), and Turn Island (18%).

Between October and November 2002, 10 sampling trips were made and 195 Puget Sound rockfish were collected by hook and line at three San Juan Channel sites: Shady Cove (61% of samples), Bell Island (18%), and Turn Island (11%). The remaining 10% of the 2002 samples were collected at Pile Point, which is located on the west side of San Juan Island.

Most fish were caught using a variety of herring jigs (sizes 4, 5, and 10) to assure a wide range of ages. Fish were placed in an ice bath to anesthetize them. At the Friday Harbor Labs they were counted, put into plastic bags, and placed in a freezer for later processing. Samples were thawed, and sex, total length (cm), fork length (cm), standard length (cm), and weight (g) were determined. Otoliths were removed and stored in 50% ethanol.

Otoliths were aged using the break and burn method (Chilton and Beamish 1982). An experienced rockfish reader provided training in ageing otoliths to researchers in 1994 and 2001 and provided support in age determination methodology throughout the study period. After age

determination was complete, a 20% subsample was sent to the rockfish reader to verify results in all three sampling years.

The function Solver in Excel was used to fit the data to the von Bertalanffy growth equation:

$$L_t = L_\infty \left[1 - \exp^{-K_{(t-t_0)}} \right]$$

Where:

L_t = length of fish at age t

L_∞ = asymptotic length

K = growth coefficient

t_0 = age at onset of growth

Tests for the reduction in the error sum of squares (Draper and Smith 1981) were performed to test for the statistical significance of differences in length at age between all year combinations.

There is no recreational or commercial fishery for Puget Sound rockfish, and natural mortality was estimated using the catch curve (Ricker 1975):

$$Y = M_t + a$$

Where:

Y = ln (number caught at age x)

M = instantaneous rate of natural mortality

t = age of fish

a = constant

Mortality calculations used fish that were 3 years of age or older to counter size-selective bias of the hook and line sampling method. The age classes used in mortality calculations varied between years based on the availability of young fish in the sample (Table 1). Mortality calculations were made for females and males separately when permitted by sample size, as well as for sexes combined.

Temperature data were compiled from the Fisheries and Oceans Canada hydrographic station at Race Rocks (48.19ºN, 122.84ºW), 48 km southwest of the study area, and the Washington Department of Ecology station at Admiralty Inlet (48.29ºN, 123.54ºW), 35 km southeast of the study area.

Table 1. Instantaneous natural mortality (*M*) rates for Puget Sound rockfish, by year.

	Females			Males			Sexes combined		
	M	SE	Age range	M	SE	Age range	M	SE	Age range
1994	0.401	0.123	3-11	0.330	0.100	3-12	0.426	0.083	3-13
2001	0.343	0.107	4-12	NA	NA	NA	0.317	0.104	4-12
2002	0.234	0.037	5-11	NA	NA	NA	0.304	0.038	5-11

Results

Results of the comparison between age readers showed an average percent error of 10.5% in 1994, 2.9% in 2001, and 14.0% in 2002.

A chi square test for homogeneity in age composition across sites sampled in 2001 (Fig. 3) failed to detect any significant differences ($p = 0.076$). The von Bertalanffy growth curves between the sites in 2001 were highly variable, though the data showed no obvious trends and size tended to converge with increasing age (Fig. 4). The similarity in age composition and growth between fishing sites in 2001 was such that we treated them as coming from a single population. This allowed a comparison of data between 1994, 2001, and 2002, by pooling data collected from different sites around San Juan Island.

The 95% confidence limits (±2SE) for mortality estimates all overlapped and none of the differences in mortality were statistically significant. The average *M* for all years and sexes combined was 0.35.

In 1994, three and four year old fish (1990 and 1991 year classes) were most abundant within the population with a secondary mode for eight year olds (Fig. 5). Four and five year old fish (1996 and 1997 year classes) made up a large portion of the 2001 population with relatively high numbers of fish in the ten and eleven year old age groups. Fish that were 10 and 11 years old in 2001 represent the survivors of the 1990 and 1991 year class observed in 1994.

Five and six year old fish from the 1996 and 1997 year classes were again abundant in the 2002 sample, and two year olds (2000 year class) were also abundant. We would not expect that the 2000 year class would be well represented by one year old fish in 2001 due to the difficulty in catching small individuals by hook and line.

Von Bertalanffy growth curves for male and female fish were fitted separately (Table 2). The data for males conformed poorly to the von Bertalanffy model, particularly in 2001 (Fig. 6, Table 2). Growth between 1994 and 2001 was significantly different ($p < 0.001$) for both sexes. Female length (FL) at a given age was consistently about 10 mm

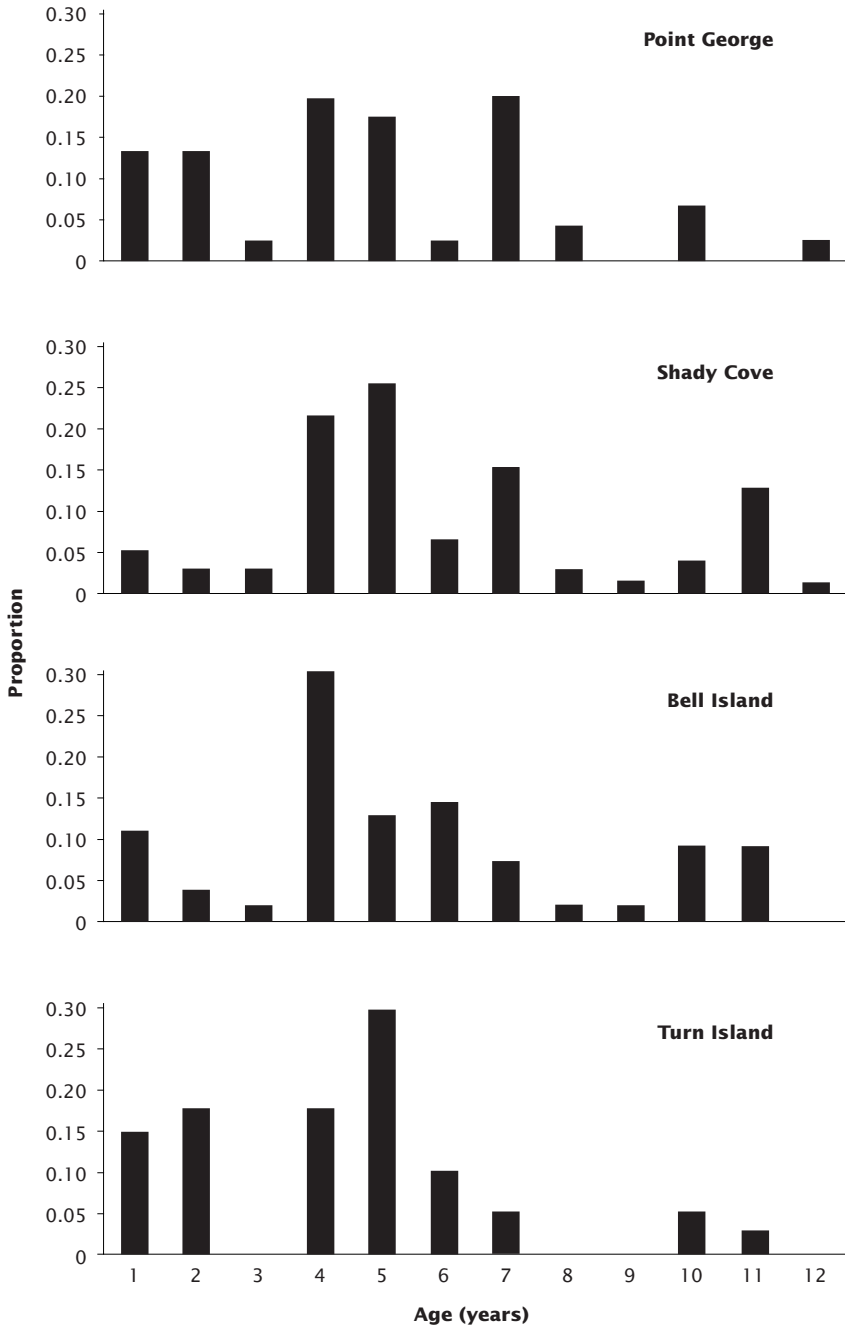


Figure 3. Age composition (sexes combined) by sampling site in 2001.

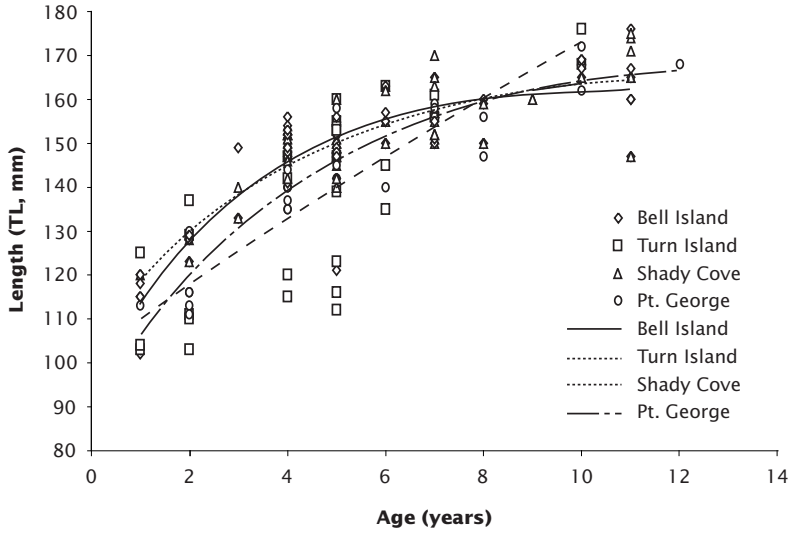


Figure 4. Female length at age in 2001 compared between sampling sites. Growth predicted by the Von Bertalanffy growth equation is indicated by lines.

Table 2. Von Bertalanffy growth parameters for *S. emphaeus*, by year.

Year	Sex	L_∞	K	t_0
1994	Female	168.200	0.414	–1.712
	Male	151.401	0.124	–9.947
2001	Female	168.238	0.222	–3.647
	Male	243.677	0.032	–15.675
2002	Female	159.321	0.263	–3.034
	Male	151.725	0.087	–13.339

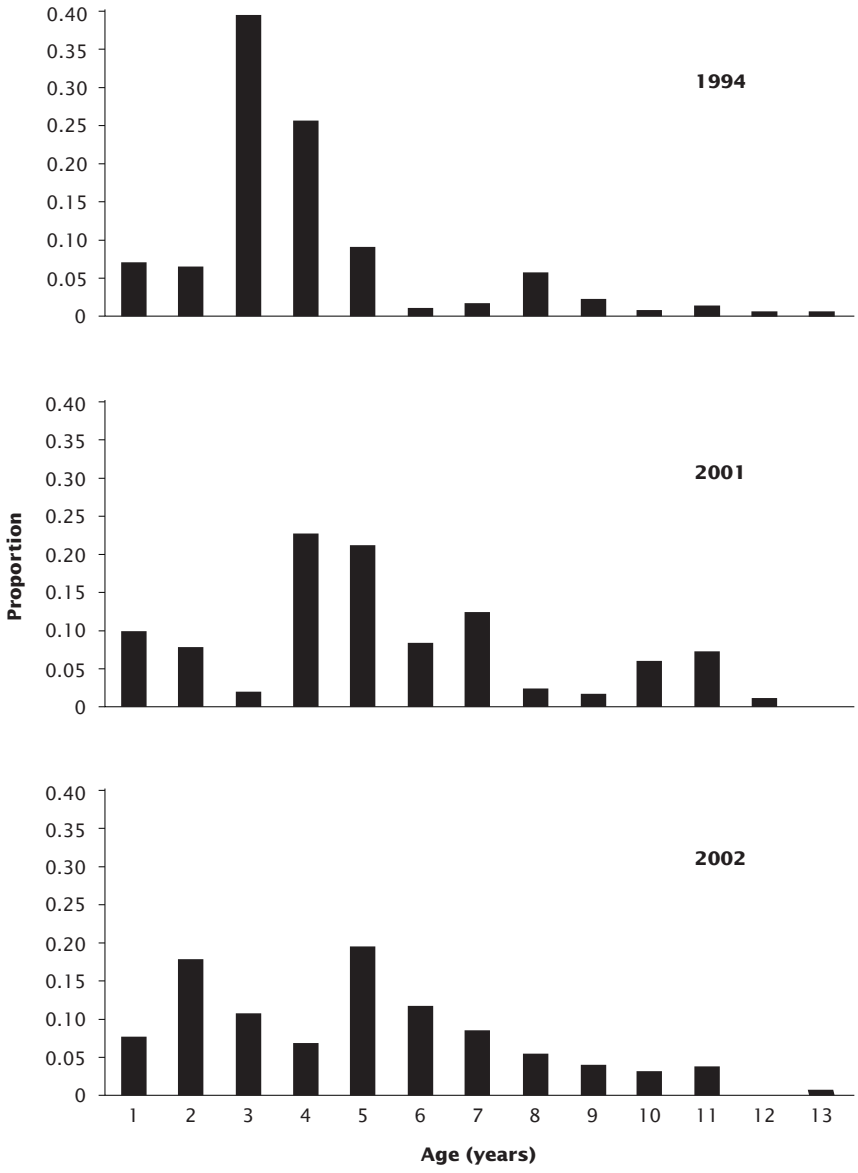


Figure 5. Age composition (sexes combined) by year.

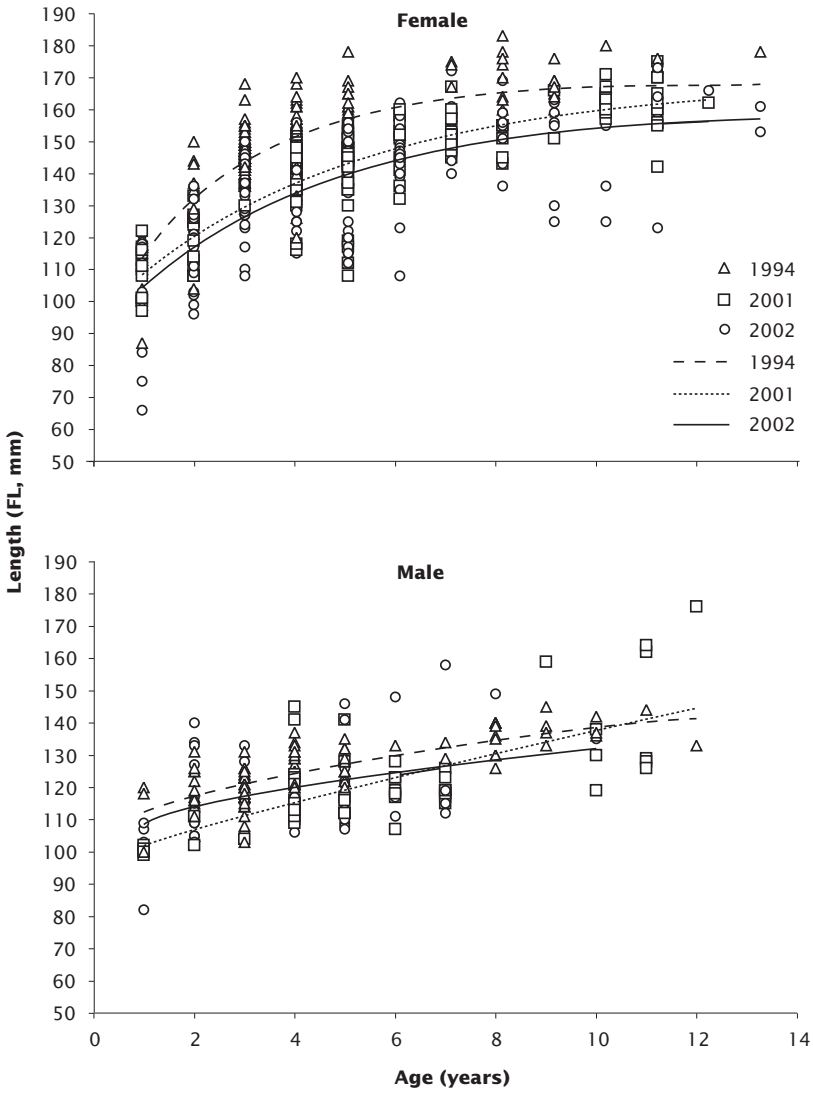


Figure 6. Length at age by sex and year. Growth curves predicted by the Von Bertalanffy growth equation are indicated by lines.

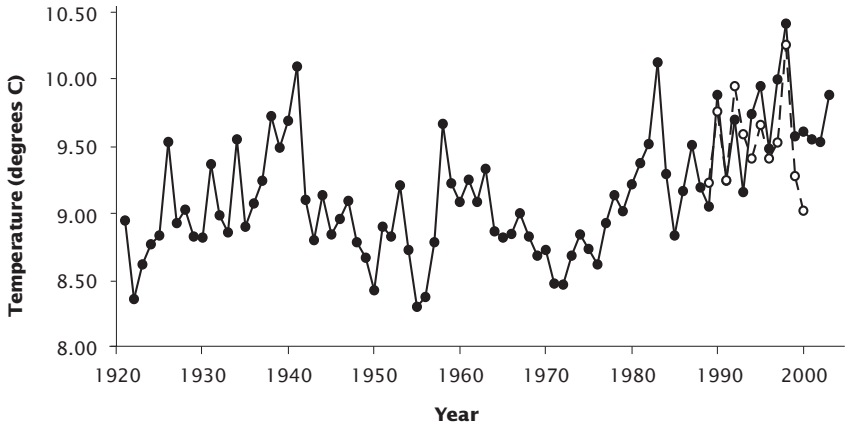


Figure 7. Average annual temperature at Race Rocks (solid line) and Admiralty Inlet (dashed line) from 1990 to 2000.

greater for fish caught in 1994. Length at age for males also declined significantly between 1994 and 2001. The trend of reduced growth in length appears to have continued in the females caught in 2002 (Fig. 6), with fish being significantly smaller (about 1mm less) for a given age in 2002 ($p < 0.001$). There were no significant differences in growth of males between 2001 and 2002 ($p = 0.282$).

Water temperatures from both the Race Rocks and Admiralty Inlet locations show that the average annual water temperature from 1990 to 2000 has remained between 9ºC and 10ºC, with the exception of a strong El Niño signal in 1998 when the average temperature was 10-10.5ºC (Fig. 7).

Discussion

It is apparent from the strong contribution of certain age classes in the Puget Sound rockfish population that the success of recruitment in a given year will greatly affect population abundance. The effect of a strong recruitment year is sustained in the population over long periods of time. Evidence for this is seen in the high numbers of fish from the 1990 and 1991 year classes, which appear to have initiated the rapid increase in abundance that occurred between 1991 and 1994. These cohorts were represented by 3 and 4 year old fish in 1994, then as 10 and 11 year old fish in 2001.

The 1998 year class (3 years old in 2001, 4 in 2002) was spawned during an El Niño year, and was characterized by extremely low recruit-

ment (Fig. 5). In coastal waters of Southern British Columbia (near the entrance to the Straits of Juan De Fuca), an El Niño is characterized by high sea surface temperatures, a deep thermocline, decreased upwelling, and low nutrient content in water above the thermocline (Whitney and Welch 2002). The timing and strength of upwelling is known to influence the recruitment of rockfishes off California (Ralston and Howard 1995) and has been related to decreased abundance of zooplankton (Hayward et al. 1994) and unfavorable larval transport at critical times of settlement (Johnson et al. 2001). Strong El Niños also occurred in 1982-83 and 1997-98 in the region surrounding San Juan Island as seen by average surface temperature (Fig. 7), and the effect on *S. emphaeus* recruitment was apparent (Fig. 5).

The increase in abundance of *S. emphaeus* was concurrent with a decrease in abundance of several larger predatory fish species in the region, suggesting that *S. emphaeus* increased in number due to release from predation. Recreational catch per unit effort for rockfish other than *S. emphaeus* in the San Juan Islands declined from 1.6 fish per trip in 1977 to 0.7 fish per trip in 1980. Despite bag limit reductions in 1994 (from 10 fish to 5) and 2000 (to 1 fish), landings per trip did not increase (Fig. 1). Lingcod (*Ophiodon elongatus*) were also heavily fished by recreational fishermen, and catch per trip has undergone a steep decline in the San Juan Islands. During 1977-1983 an average of 0.17 lingcod per targeted trip was caught, which dropped to about 0.04 lingcod per trip by 1992. More stringent bag limit and fishing season restrictions were imposed in 1992 and lingcod caught per trip had increased to 0.15 by 2000 and 0.34 by 2002. Puget Sound rockfish are an important part of the lingcod diet (Gregory 2004; Ann Beaudreau, Univ. of Washington, pers. comm.).

Several mandatory marine reserves established in the San Juan Islands in 1990, including four in the San Juan Channel (Fig. 2) and eight voluntary compliance reserves added in 1997, could also have contributed to the recovery of lingcod stocks. Eisenhardt (2001) compared three paired, mandatory reserve and non-reserve sites and found that reserves had higher densities of copper rockfish (*Sebastes caurinus*), kelp greenling (*Hexagrammos decagrammus*), and lingcod (*Ophiodon elongatus*), and lower densities of Puget Sound rockfish than non-reserve sites. Mean sizes of copper rockfish and lingcod were significantly higher within marine reserves.

There are many possible reasons for the significant reduction in growth between 1994 and 2001-2002. Given what is known from dive transects, this reduced growth could be the result of the increase in population density. Our data indicate that the major increase in the abundance of Puget Sound rockfish occurred between 1991 and 1994. Given this, fish older than about 3 caught in 1994 had spent most of their lives in conditions of much lower population density that those

caught in 2001 and 2002. One possible explanation for a reduction in growth with increased population density would be competition for food or space.

Temperature is also a factor, although there were no apparent long-term trends during 1990-2000 (Fig. 7). However, elevated temperatures, associated with the 1997-1998 El Niño, were evident in 1998 (Fig. 6). During the 1982-1983 El Niño, growth of juvenile (1-4 year old) widow rockfish declined by 12.6%, and juvenile yellowtail rockfish by 20.5% off central and northern California (Woodbury 1999).

Exploitation in northern Puget Sound appears to have contributed to a decline in the abundance of predators and an increase in forage species such as *S. emphaeus*, and reductions in fishing activity and the establishment of marine protected areas could be reversing this trend. The recent decline in Puget Sound rockfish abundance may indicate a return to pre-disturbance conditions and is coincident with the recovery of lingcod. The abundance, recruitment, and growth of Puget Sound rockfish appear to reflect major changes in the Puget Sound ecosystem, and continued monitoring of this population will be an important factor in understanding ecosystem dynamics.

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Using Radiometric Ages to Develop Conventional Ageing Methods for Shortraker Rockfish (*Sebastes borealis*)

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Abstract

Whole otoliths from a previous radiometric ageing study were thin sectioned using a modified preparation technique. Growth rings on the thin sections were counted using three different ageing strategies with different levels of banding (i.e., grouping fine growth zones). Ages generated from the different ageing strategies were compared with the radiometric ages to select the "best" ageing strategy. A comparison of ageing strategies and radiometric ages suggests that the "best" strategy had a transition age of approximately 20 years below which fine growth zones should be grouped into bands, and above which finer marks should be counted. Otoliths from additional specimens were thin sectioned and aged using this "best" strategy, and also radiometrically aged. Using the "best" ageing strategy, von Bertalanffy growth parameters for female shortraker rockfish were estimated to be (L_{∞} = 83.2 cm., K = 0.04, and t_0 = 4.68 years). These parameters, plus the length at maturity were used to estimate an age range at 50% sexual maturity of between 18 to 28 years which is similar to the probable transition age of 20 years.

Introduction

Shortraker rockfish (*Sebastes borealis*) occur over the continental slope of the North Pacific ocean, from Japan, the Okhotsk Sea, southeast-

ern Kamchatka, to the Bering Sea and Aleutian Islands, and south to California, at depths of 25 to 875 m. Rockfish (*Sebastes* spp.) are an important commercial species in the North Pacific because of their high market value with multiple species being harvested either directly or indirectly as retainable incidental catch. To ensure better management, it is important to understand rockfish life history characteristics such as longevity, growth, and age at maturity.

Otoliths are the most common structure used for fish ageing. Otoliths are good structures to use because they are made of a hard material called aragonite, a form of calcium carbonate crystal, which stands up to different preparation techniques and the deposition of otolith material appears to occur each year without resorption (Chilton and Beamish 1982). A standard preparation for reading otoliths is the break and burn method (Christensen 1964). In this method the otolith is snapped or sawed through its core on the transverse plane and then burned over an alcohol flame. The burning darkens the slow growth (dark translucent) zone distinguishing it from the fast growth (light opaque) zone when viewed under a dissecting microscope with reflected light. Ageing is accomplished by counting these growth zones. A set of guidelines or ageing criteria is used to help age the fish.

Radiometric ageing has been used to validate ageing criteria for rockfish species such as splitnose rockfish (*S. diploproa*), rougheye rockfish (*S. aleutianus*), Pacific ocean perch (*S. alutus*), northern rockfish (*S. polyspinus*), and yelloweye rockfish (*S. ruberrimus*) (Bennett et al. 1982, Kastelle et al. 2000, Andrews et al. 2002). This method measures the disequilibrium of daughter/parent isotope pairs found in otolith cores to independently determine age.

The Alaska Fisheries Science Center's (AFSC) Age and Growth Program has been able to age a number of different species using the break and burn method. However, shortraker rockfish has not been aged because of the difficulty of interpreting the growth zones and the presence of "glassy areas" (Fig. 1) on the burnt half of the otolith. In the "glassy areas" the growth zone are obscured. Therefore no ageing criteria have been set for shortraker rockfish at the AFSC.

The goal of this study was to obtain an otolith preparation method to elucidate growth patterns, to examine three very different ageing strategies, and determine the best ageing criteria from these strategies. This was accomplished by modifying an existing thin section technique to generate ages that could be compared to $^{210}Pb/^{226}Ra$ radiometric ages. Validated ages generated by the thin section method were then used to estimate von Bertalanffy growth parameters which were applied to length at maturity data (McDermott 1994) to estimate age at maturity for female shortraker rockfish. We provide detailed information of the methods used because these are new methods for obtaining ageing criteria using radiometric results.

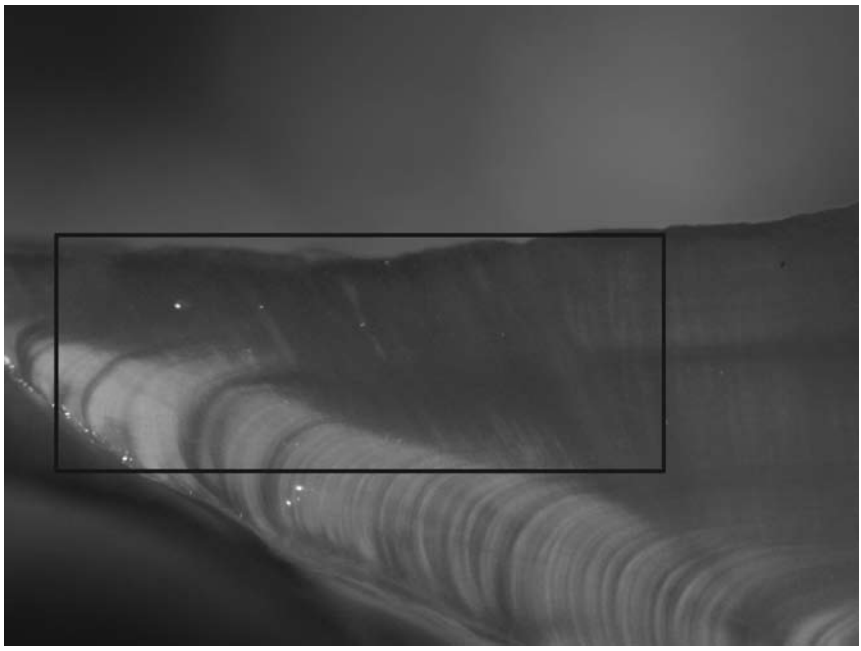


Figure 1. Photograph of a shortraker rockfish break and burn otolith half with presence of a "glassy area" highlighted within the box outline. In the "glassy areas" the growth zones are obscured.

Materials and methods

Shortraker rockfish thin sectioning

A production thin sectioning method used at the Central Ageing Facility in Queenscliff, Victoria, Australia was adapted for use with shortraker rockfish otoliths (Smith et al. 1995). Using a pencil, otoliths were lightly marked transversely through the middle of the first year. Otoliths were embedded in resin blocks using a polyester resin (i.e., Artificial Water [trade name not necessarily endorsed by NOAA]). A bottom layer of resin for the blocks was poured into silicone molds and allowed to cure for 40 minutes. Marked otoliths were then placed on the semi-cured resin which had been scored. In this way the otoliths were lined up evenly in a row and did not lose alignment by sinking into the resin. Another layer of resin was applied encasing the otoliths in resin and allowed to cure for 2 days. The block was cut using a high speed Tyslide saw that made thin sections approximately 0.4 mm thick. Three to five thin sections were cut from each specimen to ensure that a thin section contained a cross section of the first year. Next the thin sections were mounted on

a glass slide using a UV curing adhesive, Loctite 349®. The adhesive was cured by exposure to UV light for 20 minutes. Finally the mounted thin sections were reduced in thickness by grinding on a Hillquist® grinding wheel to a thickness of 0.2 mm.

Development of age determination strategies

The shortraker rockfish otolith sections contain many fine dark growth zones punctuated by occasional major or thick dark growth zones when viewed under reflected light. Thus, the question for the age reader was to determine which zones represent yearly growth.

Previous results for orange roughy (*Hopostethus atlanticus*) indicate that a transition age occurs when a fish's somatic growth slows due to the production of reproductive material as a fish matures, and is usually close to the age at 50% maturity (Francis and Horn 1997). Three age determination strategies were developed: strategy 1 focused on counting major growth zones or lumping together of finer growth zones. If only the major growth zones were counted, the age reader obtained a young age. Strategy 2 focused on counting fine growth zones and if all of the fine growth zones were counted, the age reader obtained a much greater age. Strategy 3 was a combination of strategies 1 and 2 and included a "transition age," below which fine growth zones should be grouped into bands, and above which finer growth zones should be counted. We used radiometric ages to determine which strategy was best.

First radiometric experiment: determination of transition age

The first experiment involved ageing the remaining whole otoliths from a radiometric ageing study conducted by Kastelle et al. (2000). The otoliths were collected from the 1993 AFSC summer trawl surveys. Kastelle et al. (2000) used radiometrics to age seven length categories of shortraker rockfish since no ages (i.e., ages that were generated by the break and burn method) were available. To help establish the ageing criteria for shortraker rockfish, the remaining otoliths from that radiometric study were thin sectioned as previously described. The thin sections from each of these length categories were then aged (i.e., counting growth zones) using strategy 1 and strategy 2 and the ages averaged for each length category used in the radiometric study. The averaged thin section age was compared to the average radiometric age for each length category (Table 1).

To compare the previous radiometric ages (Kastelle et al. 2000) with the possible strategy 3 ageing criteria, we posited that a transition age occurred at each of the strategy 1 ages for each length category (Table 1). A matrix of estimated strategy 3 ages, for each assumed transition age and length category combination, was calculated using the follow-

Table 1. Radiometric age, strategy 1 and 2 ages, and strategy 3 ages based on different posited transition ages. Arranged by length groups used by Kastelle et al. (2000).

Ave length (cm)	Radiometric age[b]	Strategy 1 average age	Strategy 2 average age	Incremental increase in strategy 2 ages	Posited transition age for strategy 3						
					8.5	13.7	22.6	23.2	25.3	26.1	36.0
					Estimated strategy 3 age[c]						
40.0	22.4	8.5	65.0	0.0	8.5	8.5	8.5	8.5	8.5	8.5	8.5
43.0	36.6	13.7	51.2	-13.8	-5.3	13.7	13.7	13.7	13.7	13.7	13.7
61.0	30.8	22.6	63.1	11.9	6.6	25.6	22.6	22.6	22.6	22.6	22.6
76.0	51.3	23.2	59.1	-4.0	2.6	21.6	18.6	23.2	23.2	23.2	23.2
81.7	57.3	25.3	58.8	-0.3	2.3	21.3	18.3	22.9	25.3	25.3	25.3
83.7	56.2	26.1	79.6	20.8	23.1	42.1	39.1	43.7	46.1	26.1	26.1
97.0	92.6	36.0	117.0	37.4	60.5	79.5	76.5	81.1	83.5	63.5	36.0
SS residuals[a]					10,080	3,308	3,942	3,060	2,796	4,364	6,721

[a]Sum of squared (SS) residuals between radiometric ages and posited transition ages.

[b]Kastelle et al. (2000).

[c]Estimated ages for the length groups for a given transition age are derived by adding the strategy 2 incremental increases to the transition age starting with next larger length group after the transition age.

ing procedure: first, an incremental increase in strategy 2 ages was calculated for each length category. Next, from the diagonal the lower left half of the matrix was filled by adding the incremental increase to the assumed transition age and then to each following strategy 3 age. In this way, the strategy 3 ages in successive length categories, once above the assumed transition age, were increased by an amount equal to the incremental increase of strategy 2 ages. Finally, for the upper right half of the matrix, the estimated strategy 3 age can not be above the strategy 1 age by definition when using the strategy 1 age as the assumed transition ages. For example, for the 43 cm length grouping, these specimens were found to have an average of 13.7 major growth zones using strategy 1 and an average of 51.2 fine growth zones using strategy 2. For the next length category 61 cm, strategy 2 gave an average fine growth zone count of 63.1. For strategy 3, if we posited a transition age of 13.7 years, the estimated average age for the 61 cm category fish would be 13.7 + (63.1 − 51.2) = 25.6 years. The value 63.1 − 51.2 = 11.9 shows up in Table 1 under the category "incremental increase in strategy 2 ages," and 25.6 shows up under the strategy 3 ages with an assumed 13.7 year transition age for the 61 cm length category. Negative incremental ages used in the calculations were the result of sampling variability, averaging the strategy 2 ages from each group of fish, and ageing error.

The sum of squared residuals was calculated between the radiometric and the estimated strategy 3 ages for each of the assumed transition ages (Table 1). A parabola was fit to the sum of squares with the assumed transition age as the independent variable. The lowest point on the parabola was solved using calculus to obtain a least squares estimate of the transition age, which yielded thin section ages closest to the radiometric ages. Using the least squares estimate of the transition age as a guideline, the original radiometric sample was reaged. Prior to reaging the thin sections, the specimen identification numbers were randomly rearranged to prevent the reader's knowledge of previous ages obtained using strategies 1 and 2 from affecting results. The reader did not have access to any sample data, including fish size. Apparent transition ages were recorded. Upon completion of re-ageing the radiometric sample, recorded apparent transition ages were averaged.

Second radiometric experiment: testing strategy 3

A new set of otoliths was used to test strategy 3 with the averaged apparent transition age. For this part of the experiment, otoliths from summer trawl survey cruises were used with samples collected from areas around the Aleutian Islands. Otolith data collection and storage methods followed standard AFSC procedures. One otolith from each fish was thin sectioned and aged using strategy 3. The remaining otoliths were used for radiometric analysis.

In this radiometric analysis, we used otolith material laid down in the first 3 years of the fish's life (cored otoliths). Previous radiometric studies have shown that young fish or cored otoliths are less likely to violate assumptions associated with radiometric ageing. Because approximately 1 gm of otolith material was needed for each sample, this meant that otoliths of the same nominal age needed to be grouped into pools. Samples were chosen for three pools (designated SR1, SR2, and SR3) based on age availability, experimental design, and time concerns. The initial step in the radiometric work for the pooled otoliths was to core (i.e., remove all material beyond the third year) each otolith. This was accomplished by mechanically removing the material using a Buehler® low speed cutting saw and grinding wheel. The cored otolith size was determined by taking measurements of the first 3 years on whole and thin-sectioned otoliths from samples being processed for radiometric analysis. Early growth zones were distinguishable in shortraker rockfish otoliths, especially when layers were first ground off of the distal side in the coring process. The visual location of the third year served as a coring guide in addition to the third year measurements. Cores were rinsed with distilled water, dried, and weighed. Cores were then stored in a clean, acid-washed vials containing 60% ethanol until further processing. The samples were cleaned and processed to measure the activity of ^{226}Ra and ^{210}Pb as described in Kastelle et al. (2000).

The measured ^{210}Pb/^{226}Ra in the otoliths can be used to predict a radiometric age from the curve:

$$\frac{A_2}{A_1} = 1 - \exp\left(-\lambda_2 t\right) + R^* \exp\left(-\lambda_2 t\right)$$

Here A_1 is the activity for ^{226}Ra, A_2 and λ_2 are the activity and decay constant, respectively, for ^{210}Pb, t is time (age in years), and R^* is the initial ratio of ^{210}Pb/^{226}Ra incorporated into the otolith cores. In this study, two R^* values were used: an assumed value of $R^* = 0.0$, and from rougheye rockfish, $R^* = 0.0636$ (Kastelle et al. 2000).

Sources of error associated with the radiometric ages came from counting statistics involved in measuring decays of radionuclides, reagent blanks, background measurements, and yield tracers. Errors were propagated through all calculations to estimate errors in radiometric age. The radiometric ages from the pooled otoliths were adjusted to take into account the time between date of capture and date of analysis and average age of material in the 3 year core.

Estimation of age at 50% sexual maturity

All female shortraker rockfish from the 1993 radiometric study and females (37 cm or less) from the 2000 AFSC cruises were used to estimate age at 50% sexual maturity. Otoliths were aged using strategy 3

with the averaged apparent transition age. A total of 150 specimens were used: 60 from the 1993 cruise and 90 from the 2000 cruise.

Female shortraker growth parameters were determined from the von Bertalanffy growth equation:

$$L_t = L_\infty \left\{1 - \exp\left(-k\left[t - t_0\right]\right)\right\}$$

Here L_t is the length at age t, L_∞ is the theoretical length at age infinity, t_0 is the theoretical age at length zero and k is the growth rate. The von Bertalanffy curve was solved for t to estimate age at 50 % sexual maturity:

$$t_{50} = t_0 - \left(1/k\right)\ln\left(1 - \frac{L_{50}}{L_\infty}\right)$$

Here, t_{50} is the estimated age at 50% sexual maturity using the length at 50% sexual maturity (L_{50}), previously estimated to be 44.9 cm by McDermott (1994).

The likelihood method (Kimura 1980) was used to estimate von Bertalanffy growth parameters, and to estimate the covariance matrix of parameter estimates. The delta method (Seber 1973) was used to construct 95% confidence levels for age at 50% female sexual maturity.

Results

First radiometric experiment: determination of transition age

Comparison of ageing strategies to the radiometric ages in the first radiometric experiment yielded the following results: strategy 1 (major or thick growth zones) gave ages that were younger than the radiometric ages. Strategy 2 (fine growth zones) gave ages that were older. Strategy 3 produced ages closest to the radiometric ages. Strategy 3 ages included the averaged apparent transition age.

The least squares estimate of the transition age was obtained from the calculated sum of squared residuals between the radiometric and the strategy 3 ages (Table 1) was 23±3.2 years (±2 SE). The average apparent transition age was 20.7 years.

Second radiometric experiment: testing strategy 3

Estimated radiometric ages for pooled sample SR1, for both initial ratios, were younger than average thin section ages. Estimated radiometric ages for pooled samples SR2 and SR3, for both initial ratios, were older than average thin section ages (Table 2). The 95% confidence intervals for mean radiometric age ranges for both initial ratios included the mean thin section ages for all three samples (Fig. 2) except for SR3 with the initial ratio of 0.0.

Table 2. Comparison of average ages for SR1, SR2, and SR3 samples from the thin section (using strategy 3) and radiometric ageing methods. Ninety-five percent confidence intervals are shown for radiometric ages.

Pools	Ave thin section age (yr)	Initial ratio	Radiometric age (yr)	95% CI
SR1	20	0.0000	18.3	±5.9
		0.0636	16.2	±5.9
SR2	30	0.0000	59.8	±36.4
		0.0636	57.7	±36.4
SR3	20	0.0000	33.2	±12.9
		0.0636	31.1	±12.9

Estimation of age at 50% sexual maturity

Growth parameters and age at 50% sexual maturity were estimated for female shortraker rockfish (Table 3). The age at 50% sexual maturity of female shortraker rockfish ranged from 21.4 to 23.2 years.

Discussion

Growth zones in the otoliths of shortraker rockfish are difficult to interpret. The light and dark growth zones may have irregular spatial patterns that bring into question whether they are annual marks. The otoliths exhibit major or thick dark growth zones that can be split into finer dark growth zones. This is seen from the nucleus to the edge on the reading surface of a shortraker rockfish otolith. Experienced age readers know that for short-lived species such as Pacific cod, only major marks need to be counted (Roberson et al. 2002). However, for long-lived species such as shortraker rockfish, counting only major marks may not be the correct strategy because once growth slows fine marks could represent annual zones (Beamish 1979). The "correct strategy" might be to count major marks up to a "transition age," and then count fine marks past this point. A unique (and difficult) aspect of shortraker rockfish otoliths is that occasionally major marks are visible past a transition age. The problem for the age reader is to determine the location of this transition age when there are several apparent possibilities in the pattern of growth zones. The comparison between thin section ages and radiometric ages from a previous radiometric study dismissed strategy 1 (counting only major marks) and strategy 2 (counting all fine marks) and found strategy 3 to be best (incorporating an averaged apparent transition zone around 20 years).

Table 3. Von Bertalanffy growth parameters and age at 50% sexual maturity for female shortraker rockfish.

Samples	N	L_∞ cm	k	t_0	50% maturity[a]	95% CI
1993 sample	60	83.2	0.042	4.68	23.22	±4.40
2000 sample	90	69.1	0.043	−2.89	21.55	±4.12
Combined	150	84.6	0.030	−3.62	21.42	±3.60

[a]All samples were aged using the thin section method and strategy 3 with the averaged apparent transition age.

The second radiometric experiment performed on new samples was designed to test the observed transition age. The agreement between the radiometric ages and the thin section ages supported the hypothesis of a transition age of around 20 years. The pool of older fish (SR2) strengthened the ageing criteria by extending ages past the transition age and confirming that all growth zones should be counted after the transition age.

Although there was fair agreement between radiometric and thin section ages using strategy 3, with the transition age of around 20 years, caution should be observed. Confidence intervals for radiometric ages can encompass a wide age range. The radiometric analysis that tested the transition age was based on only three pools and limited age ranges were used. More testing is needed to examine the accuracy of the ageing criteria over a wider age range and to study the possibility of underestimating ages. One limitation of radiometric ageing is that otolith cores need to be pooled and these results yield an average age rather than an individual age. As fish age, the variability in length at age may increase and length may become less correlated with age. Therefore, the pooled fish analyzed by Kastelle et al. (2000), which were length-based, may represent a broad age range.

This study suggests that the initial ratio (R^*) of 0.0 produced slightly better agreement than 0.0636. The use of an initial ratio of 0.0 can be rationalized because previous rockfish radiometric studies have found initial ratios that were close to 0.0 or assumed a value of 0.0 (Bennett et al. 1982, Campana et al. 1990, Fenton and Short 1995, Kastelle et al. 2000, Andrews et al. 2002).

Age at 50% maturity was determined from the 1993 and 2000 samples and also from the samples combined, indicating that age at maturity is approximately 22 years. The reduction in somatic growth is related to narrower spacing between translucent growth zones on the otolith. This study used ages generated by strategy 3 to estimate age at 50% sexual maturity. Although this is somewhat circular, the estimated

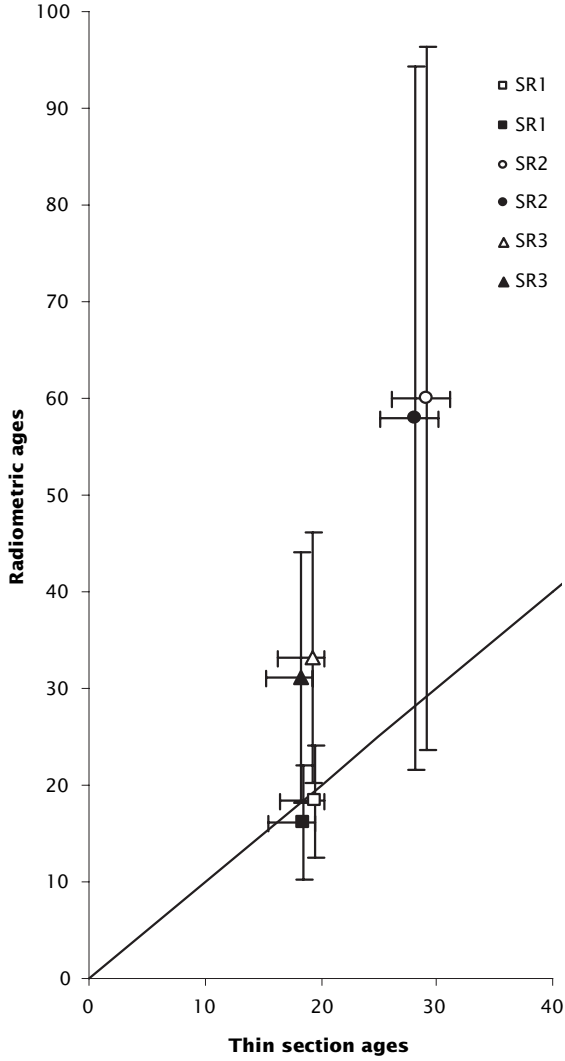


Figure 2. Radiometric ages for SR1, SR2, and SR3 for initial ratios (R^*) of 0.0 (shown in clear symbols) and 0.0636 (shown in solid symbols) plotted against thin sections ages. The error bars on the x-axis represent thin section age range in the samples. The y-axis error bars represent two standard errors for the radiometric ages. Point estimators for each sample on the x axis are offset (by 1 year) for a clearer view of error bars. Dark solid line represents line of agreement.

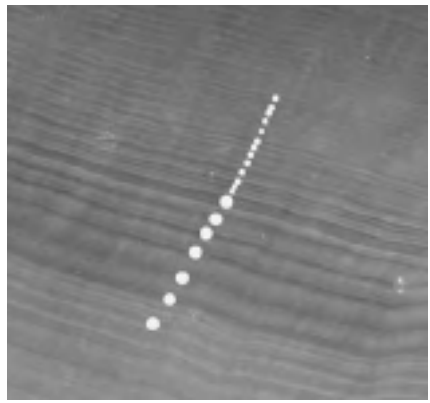


Figure 3. Thin section of shortraker rockfish aged using Strategy 3. First small dot represents transition age. Large dots indicate major or banded zones and small dots indicate fine growth zones.

age at 50% sexual maturity is consistent with the averaged apparent transition age of 20.7 years.

Under strategy 3 ageing, the transition age in the otolith growth pattern signals a shift in otolith growth indicated by a reduced distance between dark or translucent growth zones. The comparison between radiometric and thin section ages indicated that a transition zone was present around the age of 20 years. This was useful because a clear demarcation between fast and slow growth patterns was lacking in many otolith specimens. This result provided a rationale for using a 20 year transition age when the transition age was not apparent. Although specimens could be found that exhibited apparent transition zone ages between 10 to 30 years (Fig. 3), most transition zone ages occurred around 20 years. The criteria became more subjective when the transition year was not apparent. This will lead to a lower precision between age readers. Munk (2001) aged shortraker rockfish up to 157 years, while the oldest age we generated using strategy 3 was 102 years. A future goal will be to work with other age readers to establish a set of ageing criteria that will produce ages with reasonable precision.

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Modeling Larval Dispersion of Rockfish: A Tool for Marine Reserve Design?

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Abstract

Marine reserves have been suggested as an important tool for rockfish management and conservation in the northeast Pacific Ocean. One issue confronting effective reserve design is to ensure that larvae released within a reserve system are not lost through dispersal but actually contribute to the population within the reserve areas and beyond. As a first attempt to address this issue for marine reserves in the Aleutian Islands (AI) and Gulf of Alaska (GOA), we modified the particle-tracking module of a three-dimensional circulation model for the northeast Pacific to incorporate simple larval behaviors such as diel vertical migration. We used the model to simulate dispersal of rockfish larvae during peak months of larval release from a suite of potential reserve locations in the AI and GOA. Because larval behavioral patterns are unknown for most rockfish species, we incorporated several alternative behavioral models in the simulations. We also addressed intra- and interannual variation in dispersal by repeating the simulations with larval release occurring during several different months for two different years. Model results indicate that retention of larvae near release sites is greatest for sites in the AI and least for sites in the GOA. However, we regard these results as preliminary and as a demonstration of the modeling approach rather than as an actual basis for selecting reserve areas.

Introduction

Rockfishes (*Sebastes* spp.) represent one of the most diverse (over 70 species) and economically valuable multispecies resources for commercial and recreational fisheries along the Pacific coast of the United States and Canada (Love et al. 2002). Rockfish have been taken commercially since 1875 in California and since the early 1900s off Alaska. In Alaska waters, a large fishery for Pacific ocean perch (POP, *Sebastes alutus*) by the USSR and Japan developed in the early 1960s. Catches quickly peaked in the mid-1960s at nearly 500,000 t, but were followed by a precipitous decline at the end of the 1960s that continued into the next decade (Love et al. 2002). More recently, estimated stock abundance has rebounded to ~50% of that in the early 1960s, apparently due to a shift to environmental conditions that favor recruitment success (Heifetz et al. 1999, Ito et al. 1999, Hanselman et al. 2005, Spencer et al. 2005). Directed fisheries currently exist in Alaska for POP, northern rockfish (*S. polyspinis*), and dusky rockfish (*S. ciliatus*). All other rockfish species are considered nontarget species and can only be retained as certain percentages of the targeted species catch. Under current harvest strategies, no federally managed rockfish species in Alaska are considered to be overfished (NPFMC 2004a,b).

However, there is concern that existing harvest strategies for rockfishes may be inadequate (e.g., Clark 2002, Dorn 2002, Ianelli 2002, Berkeley et al. 2004). The life history characteristics of many rockfish species make individual stocks particularly vulnerable to overexploitation and slow to recover. In particular, many species mature slowly (age at 50% maturity greater than 5-10 years) and are long-lived (50-150 years) (Love et al. 2002). Recruitment success can be exceedingly intermittent (Ralston and Howard 1995, Love et al. 2002). Further, at least some species show evidence of genetic divergence and stock structure on small spatial scales (Withler et al. 2001, Buonaccorsi et al. 2002, Matala et al. 2004).

Marine reserves (i.e., harvest refugia) have been suggested as an important tool for rockfish management and conservation in the Aleutian Islands (AI) and Gulf of Alaska (GOA), as well as along the West Coast of the United States (Murray et al. 1999, Soh et al. 2001, Berkeley et al. 2004). Potential advantages posited for the use of marine reserves in conjunction with existing harvest strategies include protection from stock depletion and prevention of serial overfishing of substocks (Soh et al. 2001), maintenance of complex population age and spatial structure (Berkeley et al. 2004), and conservation of essential fish habitat (O'Connell et al. 1998).

The criteria for designating areas as marine reserves depend on the management goals the reserves are intended to address. For reserves whose purpose is to protect a species from depletion, one element

of effective design is to ensure that local populations protected in reserves are self-sustaining; that is, they remain viable in the absence of recruitment from outside the reserve system. Consequently, larvae released within the reserve system must not be completely lost through dispersal, but must contribute to the population within reserve areas as adults (Roberts 2000, Warner et al 2000). In this respect, areas that display a high degree of larval retention may be preferred as reserve sites to areas that have low larval retention.

As a demonstration of one approach to address the issue of larval retention for rockfish stocks in the AI and GOA, we coupled an individual-based model (IBM) that incorporated simple larval behaviors such as vertical migration to a three-dimensional circulation model for the northeast Pacific to assess the extent of local retention at potential sites of larval release. We used the model to simulate dispersal of rockfish larvae during peak months for larval release (i.e., parturition) from a suite of potential reserve locations in the AI and GOA. We addressed temporal variation in dispersal by simulating hydrodynamic currents for two different years and three different release periods within each year. Also, because larval behavioral patterns are uncertain for most rockfish species, we repeated model runs using several alternative behavioral models. Among the sites considered, we regarded release sites that exhibited strong retention patterns that were robust to variation in release period and larval behavior as the best candidates for reserve location. We regard the results presented here as a demonstration of the modeling approach and preliminary at best. They should not be used as the basis for reserve selection.

Materials and methods

The early life history of rockfishes in Alaska waters is generally characterized by a lack of species-specific information for most species, and information is sparse even for the best-studied species. Difficulty in identifying larval *Sebastes* to species level confounds understanding of species-specific patterns and behavior (Matarese et al. 2003). As such, our simulation model reflects an amalgam of details drawn from studies of disparate individual species or from early life history characteristics of rockfishes classified only to the generic level.

Larval IBM

We developed a very simple IBM for rockfish larval behavior that incorporated the ability to actively migrate vertically to occupy a preferred depth range. Modeled larvae that were outside their preferred depth range at any time immediately began to swim vertically (up or down) at a prescribed rate until they entered their preferred depth range. In the current IBM configuration, preferred depth ranges could differ between

daytime and nighttime to model diel vertical migration, a type of active larval behavior that could result from feeding behaviors, light sensitivity, or predator avoidance but could also enable larvae to utilize vertical current shear to modify dispersal patterns from those of passive particles (Neilson and Perry 1990).

Unlike many marine fish species, rockfish do not undergo a planktonic egg stage. Rockfish are a primitive viviparous group, with females extruding larvae rather than eggs in a process known as "parturition" (Love et al. 2002). Extruded larvae are ready to begin feeding and, at 3-7 mm standard length, are comparable in size to first-feeding larvae of species with planktonic eggs (Kendall and Lenarz 1987). In Alaska waters, parturition occurs primarily during the spring and summer for most species (see references in Wyllie Echeverria 1987, Love et al. 2002). Depending on species, larvae may be released near the bottom or in midwater (Love et al. 2002). Recent studies of POP in British Columbia suggest that, for this species, adult females migrate to the mouths of submarine canyons and release their larvae at depth (500-700 m); the larvae subsequently remain at depth for a month or more prior to moving to shallower water (Love et al. 2002). However, most rockfish larvae are typically found above the pycnocline at relatively shallow depths (Ahlstrom 1959, Boehlert et al. 1985, Sakuma et al. 1999, Matarese et al. 2003). Matarese et al. (2003) give the duration of the larval stage as 1-2 months (see also Kendall and Lenarz 1987, Laidig et al 1991, Sakuma and Laidig 1995, Plaza Pasten et al. 2003). After completion of the larval stage following growth to 20-30 mm SL, most rockfish species undergo a pelagic juvenile stage lasting several weeks to months before transitioning to a demersal existence (Love et al. 2002).

Little is directly known of larval behavior of rockfish species in the AI and GOA. Studies that examined rockfish larvae focused on temporal patterns of larval abundance or on broad spatial patterns, not on vertical position or diel behavior (e.g., Doyle et al. 2002, Matarese et al. 2003). Complicating these studies is an inability to distinguish most rockfish larvae at the species level (Matarese et al. 2003). More work has been done along the west coast of North America. Ahlstrom (1959) found rockfish larvae off California and Baja California above or in the thermocline (<100 m) with no consistent day/night differences in vertical distribution. Barnett et al. (1984) and Moser and Boehlert (1991) obtained similar results off southern California. Boehlert et al. (1985) found *Sebastes* larvae off Oregon distributed from 5 to 40 m during the day and from the surface to 30 m, as well as below 50 m, at night. Shenker (1988) found rockfish larvae in the neuston off Oregon. Sakuma et al. (1999) found that postflexion rockfish larvae off central California were generally above the pycnocline. They found *Sebastes* spp. larvae most abundant between 20 and 40 m, regardless of diel time period, although mean depth of capture was 40 m; postflexion *S. jordani* were

found somewhat deeper (mean depth of capture was 50-70 m). Sakuma et al. (1999) also found little evidence for diel vertical migration in postflexion *Sebastes* spp. or *S. jordani* larvae.

Thus, evidence from the west coast of North America suggests that rockfish larvae occupy the near-surface layers of the water column and do not migrate on a diel basis. However, the regional hydrography of the west coast is dominated by strong upwelling, whereas the GOA is dominated by downwelling (Ware and McFarlane 1989). Because local adaptations for successful recruitment may favor different behavioral strategies for larvae in the two regions, we regarded the vertical behavior of rockfish larvae in the GOA and AI as reasonably uncertain.

To address this perceived uncertainty in rockfish larval behavior, we considered three different behavioral scenarios in our models based on assumed depth preference:

1. "Near Surface" (NS);
2. "At Depth" (AD); and
3. "Vertical Migration" (VM).

Under the NS behavior, the preferred depth range for larvae was 5-20 m. Under the AD scenario, the preferred depth range was much deeper, at 80-100 m. The preferred depth range was static and did not change with time for these two scenarios. Under the VM scenario, larvae underwent diel vertical migration, preferring to be at depth (80-100 m) during the daytime but rising to near the surface at night (5-20 m). The NS and AD scenarios bracket the depth ranges over which rockfish larvae have been observed on the west coast; the NS scenario is probably closest to the truth.

Larval release sites

Direct information on areas of rockfish parturition in the AI and GOA is lacking. Thus, modeled larvae were released from locations that have been identified as areas of persistent, high abundance of rockfish species (Fig. 1). In the AI, areas were chosen that exhibited persistent aggregations of a complex of rockfish species (rougheye, *S. aleutianus*; shortraker, *S. borealis*; and POP) over multiple years in data from trawl surveys conducted tri- and biennially by the National Marine Fisheries Service (NMFS; Reuter and Spencer 2007). In the GOA, areas were chosen that exhibited persistently high fishery catches of northern rockfish (Clausen and Heifetz 2002). However, the trawl survey and the fishery are not temporally coincident with the period of peak parturition, so areas of high abundance identified from these data sources may not correspond to areas where parturition actually occurs. However, in lieu of more specific information, we assumed these areas broadly coincided with sites where parturition occurs.

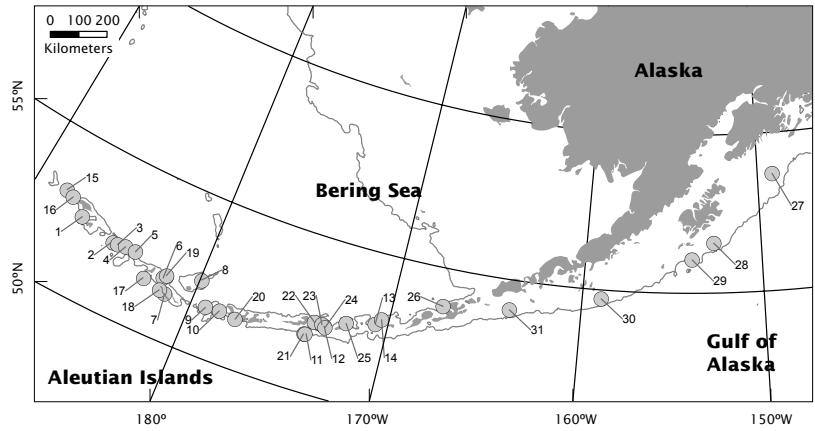


Figure 1. Locations of modeled larval release sites (circles). The 500 m isobath is also shown.

The timing of parturition at these sites was based on reported parturition dates summarized in Wyllie Echeverria (1987) and Love et al. (2002). Parturition occurs during April and May in the GOA for POP (Westrheim 1975 and Lyubimova 1965, cited in Wyllie Echeverria 1987). It occurs during April in British Columbia for shortraker and rougheye (Westrheim 1975 cited in Wyllie Echeverria 1987), and probably occurs somewhat later in the AI and GOA. Northern rockfish parturate throughout the spring (Love et al. 2002). As such, we considered larval release times of April-June in the model runs.

Hydrodynamic model

Dispersal of meroplanktonic larvae in the AI and GOA can be influenced by several large-scale current patterns, as well as smaller-scale gyres and eddies. The GOA is bounded to the east, north, and west by the mountainous coast of Alaska and is open to the south (Fig. 2). The bottom topography is complex, with many deep canyons intruding onto the continental shelf. Regional meteorology is dominated by strong storms, the frequency of which varies on seasonal to decadal timescales. These storms impact oceanic current patterns in the region. Circulation in the GOA is dominated by two current systems, the subarctic gyre in the ocean basin and the Alaska Coastal Current (ACC) on the continental shelf (Fig. 2; Stabeno et al. 2004). The subarctic gyre consists of the eastward-flowing West Wind Drift in the south, the northerly flowing Alaska Current to the east, and the southwestwardly flowing Alaskan Stream to the north. The latter flows at speeds up to 50 cm per s along the slope

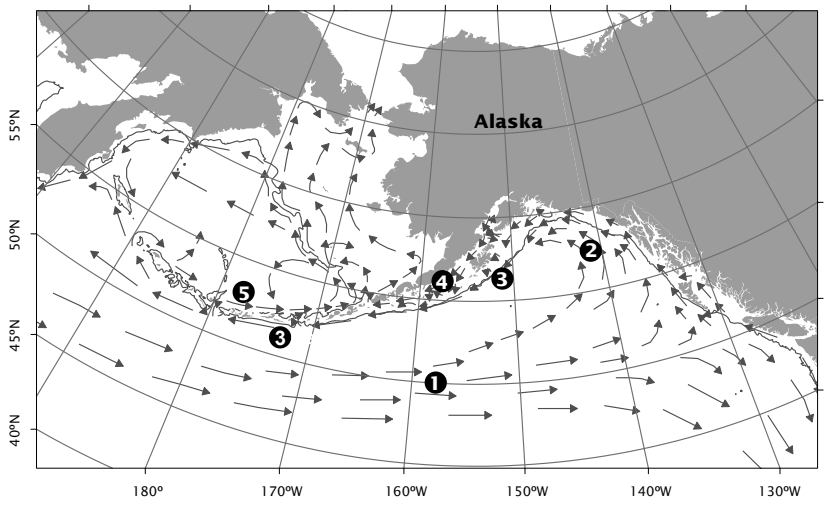


Figure 2. General current pattern near the Aleutian Islands and Gulf of Alaska. Major features include (1) the West Wind Drift, (2) the Alaska Current, (3) the Alaskan Stream, (4) the Alaska Coastal Current, and (5) the Aleutian North Slope Current. The 500 m isobath is also shown.

of the Alaska Peninsula and the AI (Reed and Stabeno 1989). The ACC is driven by winds and freshwater runoff and dominates circulation on the shelf (Stabeno et al. 1995).

To the west of the GOA, the AI and Aleutian Archipelago stretch over 2,000 km from the Alaska Peninsula west to the Commander Islands off the Kamchatka Peninsula in eastern Asia. Passes between the islands connect the North Pacific Ocean and the Bering Sea (Fig. 3). They vary from wide, deep channels bordered by small islands (e.g., Amchitka and Buldir Passes) to narrow, shallow channels between large islands (e.g., Unimak and Seguam Passes; Ladd et al. 2005). Flows in the passes are dominated by tides, and strong tidal currents mix the water column over the shallow sills (Stabeno et al. 2005). The shelf is generally narrow (<10 km) on the northern side of the islands; on the southern side, as one travels west, the shelf is initially wide (~100 km) near the Alaska Peninsula, but narrows to 25 km at Samalga Pass (Hunt and Stabeno 2005). The Aleutians are affected by three major current patterns: the Alaskan Stream and the ACC flowing westward from the GOA along the southern side of the archipelago and the eastward-flowing Aleutian North Slope Current (ANSC) north of the islands from Amchitka Pass (Hunt and Stabeno 2005 and references therein). The inshore portion

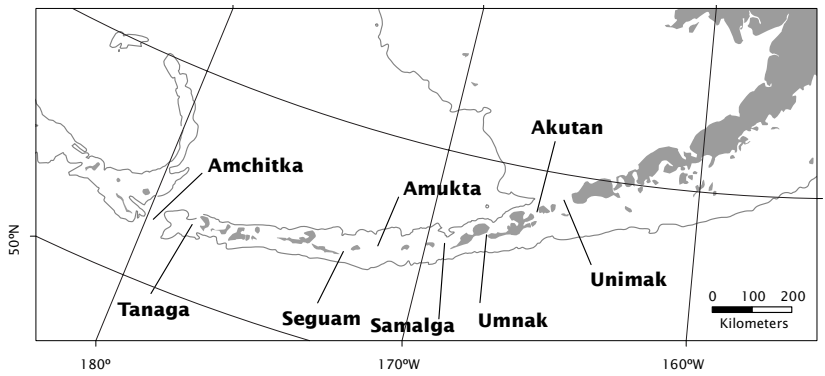


Figure 3. Major passes in the eastern and central Aleutian Islands. The 1,000 m isobath is also shown.

of the ACC enters Unimak Pass and flows into the southeast Bering Sea, while the offshore portion continues east to Samalga Pass before turning north through the pass to join the ANSC. The Alaskan Stream flows eastward along the shelf break to Amchitka Pass, where the archipelago turns to the northwest and the stream separates from the slope and broadens, resulting in the formation of eddies and meanders (Stabeno and Reed 1994).

The hydrodynamic model utilized in the study is part of a suite of basin-, regional-, and local-scale circulation models which are linked via one-way coupling (Curchitser et al. 2005; also see www.pmel.noaa.gov/people/dobbins/nep.html). These include a basin-scale model encompassing the North Pacific at 20-40 km resolution (NPac), a regional model at ~10 km resolution spanning the Northeast Pacific (NEP; Fig. 4), and, finally, local models at ~3 km resolution in regions of specific interest. One-way nesting of the models was implemented using a hybrid of nudging and radiation approaches, as described in Marchesiello et al. (2001).

The nested models utilize the Regional Ocean Modeling System (ROMS), a free-surface, hydrostatic primitive equation ocean circulation model. ROMS is a terrain-following, finite difference (Arakawa C-grid) model with the following advanced features: extensive restructuring for sustained performance on parallel computing platforms; high-order, weakly dissipative algorithms for tracer advection; a unified treatment of surface and bottom boundary layers, based on the Large et al. (1994; KPP) and Styles and Glenn (2000) algorithms; and an integrated set of procedures for data assimilation. The NEP version of ROMS also includes a Lagrangian particle tracking algorithm, which uses a fourth-order

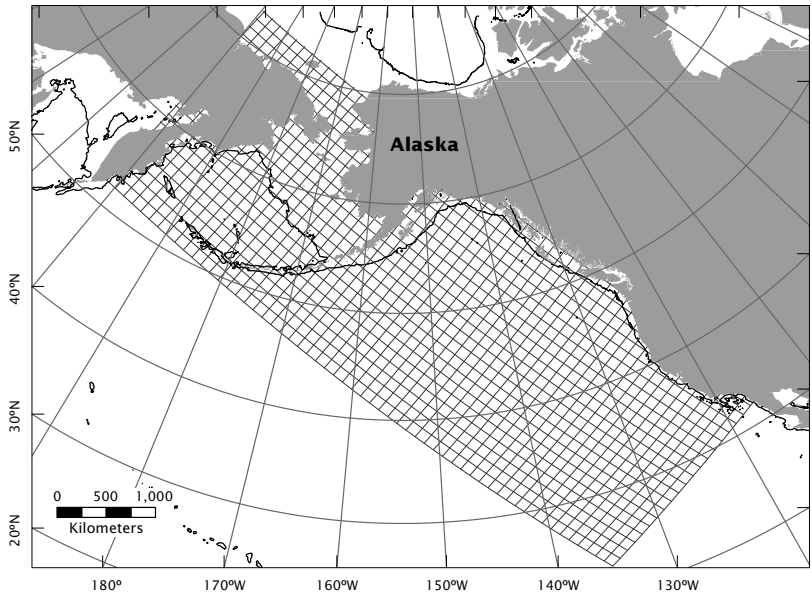


Figure 4. Extent of horizontal grid for the Northeast Pacific (NEP) three-dimensional hydrodynamic model. Model grid spacing is ~10 km. Illustrated grid cells correspond to 10 × 10 model cells. The 500 m isobath is also shown.

predictor-corrector scheme to determine instantaneous positions for released passive particles. Numerical details for ROMS can be found in Haidvogel et al. (2000), Moore et al. (2004), and Shchepetkin and McWilliams (2005), as well as on the ROMS Web site (www.myroms.org/index.php).

Hindcasts of the nested circulation models were forced by atmospheric reanalysis products and data (NCEP, COADS, QuickScat), with freshwater runoff time series (T. Royer, Old Dominion University, pers. comm.; also USGS data) applied to the NEP. Surface fluxes of heat and momentum were calculated from the atmospheric data using bulk formulae (Fairall et al. 1996), which include the instantaneous model sea surface temperature (SST). To reduce the computational burden, tidal forcing was not applied. Although formal validation of the NEP model has not yet been completed, the output reproduces the major current patterns in the northeast Pacific. It also captures the spatial and temporal characteristics of mesoscale features such as eddies and gyres in a statistical sense.

For the present study, NEP model output was utilized to provide time-varying three-dimensional current fields in which to embed the larval IBMs. NEP model output consisted of 3-day averages of instantaneous model current fields. We enhanced an "offline" version of the ROMS Lagrangian particle tracking algorithm to incorporate the larval IBMs. This version was "offline" because it read in pre-computed flow fields rather than computing the flow fields simultaneous to tracking the IBMs. Because the flow fields were calculated only once, this approach substantially reduced computer memory and time requirements when different IBM scenarios were run using the same hydrodynamic scenario. In an informal test of the offline tracking algorithm, we found reasonable qualitative agreement between the tracks of real drifters deployed in the GOA in 1998 and 2001 and model drifters simulated over the same time frames.

Model cases

Each model run consisted of releasing 25 "larvae" in a small 5×5 grid at each of 31 release sites along the Aleutian Islands or in the Gulf of Alaska (Fig. 1). Once released, larvae acted as Lagrangian drifters embedded in the NEP circulation flow fields and were tracked for 60 model days. Larvae whose movement would have taken them beyond the model grid were flagged and were not tracked further. Since the duration of the larval stage is typically between 1 and 2 months for many rockfish species in the northeast Pacific Ocean (Matarese et al. 2003), we scored each larva as being retained near its release site if, at any time after 30 days following its release, it was within 50 km of that site. Larvae that left the grid were included in the scoring.

We conducted 18 model simulations in all. For each of the three larval behavior scenarios, we repeated model runs for release times at the beginning of the months of April, May, and June for two different years. NEP model output was available for 1996-2002; we haphazardly elected to use output for 1998 and 2001. Using only two years allowed us to incorporate some measure of interannual variability into our results, while not being computationally overburdensome (each model simulation took approximately 12 hours). To evaluate retention for each release site, we calculated the mean fraction of larvae retained near the site over the two model years and three within-year release times.

Results

IBM tracks

From the perspective of individual model larvae, the model results exhibited substantial complexity and variability with respect to larval behavior type, time of parturition with a year, and year of parturition (Figs. 5-7). Spatial patterns in individual tracks reflect the cumulative

effect of complex current features predicted by the NEP hydrodynamic model. Numerous eddies and gyres are evident in the model currents near the Aleutian Islands, leading to larval tracks in the same area that exhibit numerous loops and whorls (e.g., those from site 23, NS case, Fig. 5). Somewhat larger-scale gyres are also predicted by the hydrodynamic model off the shelf in the GOA (e.g., as exhibited by tracks from site 27, NS case, Fig. 7), but not on the shelf where flow is dominated by the ACC (as exhibited by the tracks from sites 28 and 29, Fig. 7). The effects of the gyres appear to be greatest for larvae that prefer to remain near the surface (NS behavioral scenario), with lesser effects on larvae that prefer to remain at depth (AD scenario) or migrate on a diel basis (VM scenario).

Substantial variation in the tracks also occurred depending on the date of parturition. Larvae following the NS scenario that were released in April 1998 on the GOA shelf (sites 27-31) tended to move south off the shelf into deep water (Fig. 5). In contrast, larvae released in June 1998 from the same sites moved southwest along the shelf and into the AI (Fig. 6). Also, more larvae were advected into the Bering Sea along the 500 m isobath when released in June (Fig. 6) than in April (Fig. 5).

Finally, there was also substantial interannual variation in the tracks. Larvae released in the GOA in April 2001 tended to move along the shelf break to the southwest (Fig. 7), while those released in April 1998 from the same sites moved offshore more to the south (Fig. 5). More larvae were also advected into the Bering Sea in 2001 (Fig. 7) than in 1998 (Fig. 5).

Larval retention

Taking the modeled larvae in aggregate, the highest retention of larvae occurred in the western AI under all three behavioral scenarios at sites in the vicinity of Amchitka and Tanaga passes (Fig. 8). Conversely, the lowest retention occurred for sites in the GOA. The fraction of larvae retained at each site was generally highest under the AD scenario (mean of 27% retention among sites) and lowest under the NS behavioral scenario (17%), while retention under the VM scenario was generally intermediate between the two (24%). However, results at individual sites did not always follow this pattern (e.g., the easternmost site in the GOA, site 27, had NS > VM ≈ AD).

Discussion

To maximize the potential for long-term population persistence and sustainability, marine reserves should protect self-recruiting local populations—that is, local populations within the reserve should not have to rely on recruitment from beyond the reserve to remain in existence (Roberts 2000, Warner et al. 2000). Here, we tested the concept of

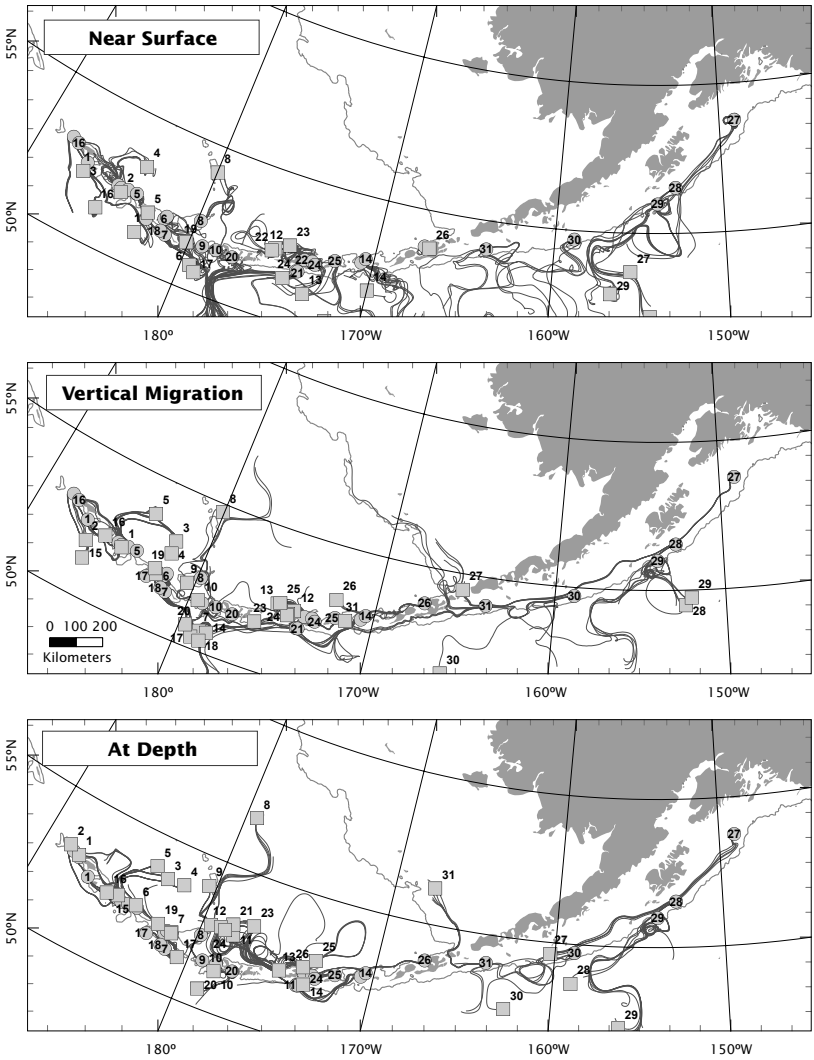


Figure 5. Sample IBM tracks for larvae released on April 1, 1998. Numbered circles denote release locations; numbered squares denote final location of one track from the corresponding release location. The 500 m isobath is also shown.

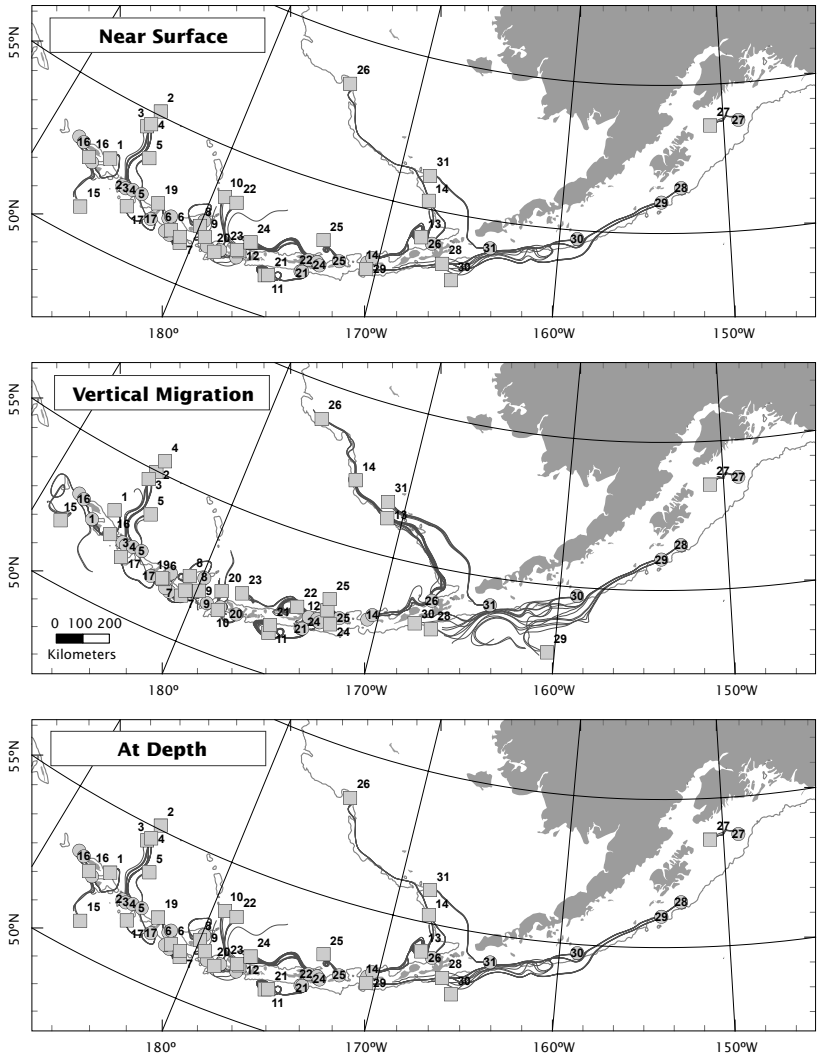


Figure 6. Sample IBM tracks for larvae released on June 1, 1998. Numbered circles denote release locations; numbered squares denote final location of one track from the corresponding release location. The 500 m isobath is also shown.

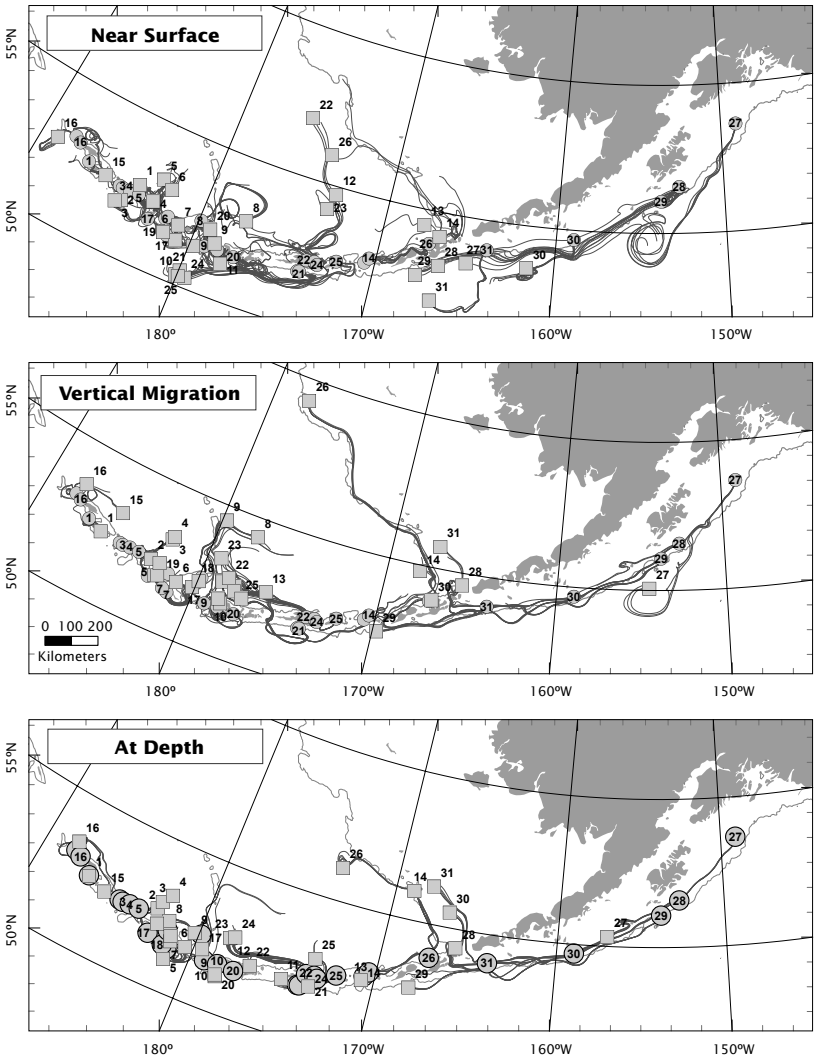


Figure 7. Sample IBM track larvae released on April 1, 2001. Numbered circles denote release locations; numbered squares denote final location of one track from the corresponding release location. The 500 m isobath is also shown.

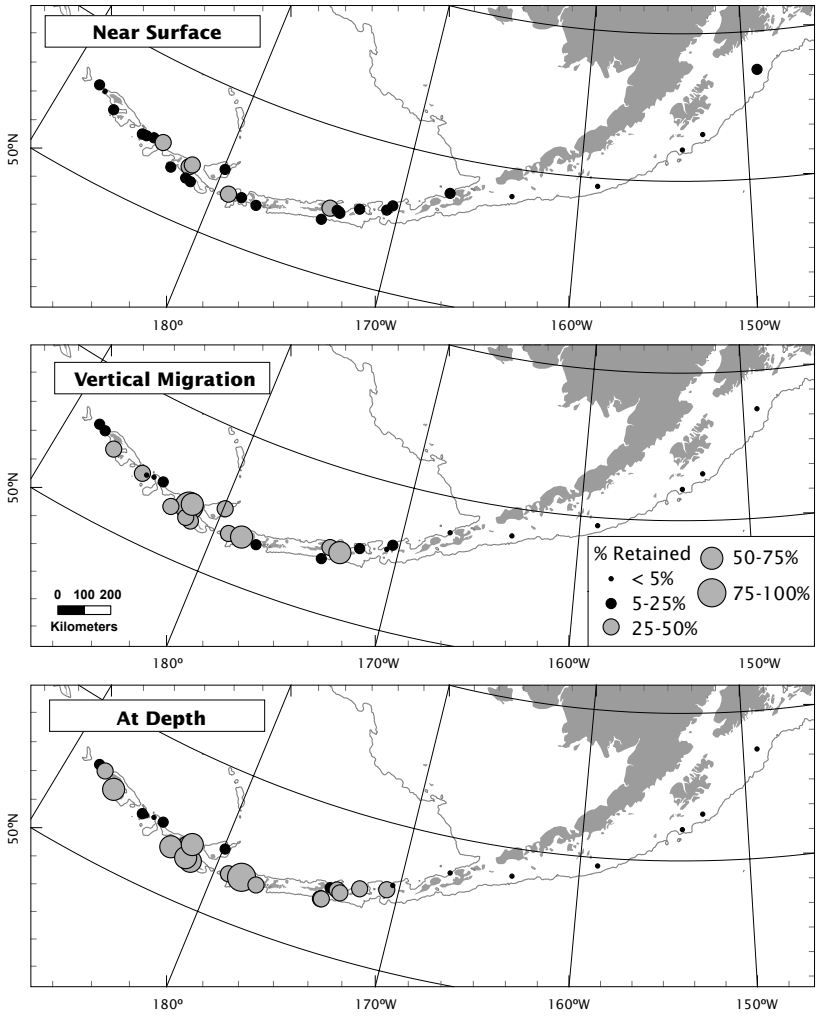


Figure 8. The fraction of larvae retained at each site for the three larval behavior scenarios considered. The retained fraction is calculated over all model year and month combinations. The 500 m isobath is also shown.

using models of larval behavior coupled with an oceanographic current model of the northeast Pacific to evaluate potential reserve locations in the AI and GOA. These sites were selected on the basis of historic patterns of adult abundance of several rockfish species (northern rockfish in the GOA; POP, shortraker and rougheye in the AI). Our model results indicated that, over the range of larval behaviors, parturition times, and years we considered, local retention of simulated larvae was greatest in the western AI and essentially negligible in the GOA.

The greater retention within the AI was apparently due to the existence of numerous small-scale (<100 km) eddies and gyres in that area in all of our hydrodynamic scenarios. Larvae became entrained in these eddies and were not dispersed far from their release sites. A secondary mechanism also contributed to the greater degree of retention in the AI. The Aleutian North Slope Current (flowing eastward) and the Alaskan Stream (flowing westward) serve as oppositely directed currents on opposite sides of the Aleutian chain. Larvae that are swept along the island chain in one direction by one of these currents may "reverse course" simply by being advected through one of the island passes to the other side of the island chain where they would be entrained in the reverse-flowing current. While this mechanism accounted for some larvae in the AI returning to near their release locations, the mechanism for the majority of those retained was entrainment in an eddy or gyre.

Although gyres were also evident in the GOA, their spatial scales were larger (>200 km) and they tended to be advected to the southwest by the Alaskan Stream, whereas gyres in the AI exhibited little tendency to drift. Thus, entrainment of larvae in a gyre in the GOA was no guarantee of retention. However, if larvae were not entrained in a gyre, they were certain not to be retained near their release site; rather, they were swept far downstream by the ACC and the Alaskan Stream toward the AI.

Although we have probably not captured the true range of interannual variability in larval dispersal with our simulations (only two years were simulated), our results suggest that the high abundances of adult northern rockfish caught by the fishery in the central and western GOA (sites 27-31, Fig. 1; Clausen and Heifetz 2002) may not be part of local self-sustaining populations spanning 10s to 100s of kilometers, but rather may be part of a much more extended population spanning hundreds to thousands of kilometers. Larval dispersal appears to be on the order of 1,000 km west along the Alaska Peninsula, and possibly into the Aleutians. An eastward contranatant migration by juveniles and subadults is one mechanism that could replenish adult abundances in the central GOA. An alternative mechanism is seeding by recruits from sub-stocks farther to the east in the GOA than those we have modeled (but this, of course, simply raises the issue of how these easterly stocks are maintained). Unfortunately, little information currently exists to

test either of these hypotheses. It is clear, however, that under either hypothesis the issue of local retention is moot and reserve design must focus on creation of a network of reserves connected by recruitment over large spatial scales.

In terms of reserve design, we note that our results address the issue of larval retention while the design criterion we selected to emphasize addressed the issue of self-sustaining recruitment. Measures of larval retention are relative—and probably nonlinear—indices of self-recruitment. The level of larval retention that corresponds to a self-sustaining level of recruitment is unknown without modeling the dynamics of subsequent life history stages. For the purpose of selecting among otherwise equivalent reserve sites, higher larval retention may be presumed to indicate higher self-recruitment—and thus to indicate areas that would be more likely to support self-sustaining local populations in the absence of outside recruitment. However, other life history factors (e.g., quality and quantity of nursery habitat) may alter the relationship between retention and self-recruitment by altering survival rates on a site-specific basis. Thus, the degree of larval retention alone may be a misleading index of self-recruitment among sites of varying quality. Rather, reserve selection criteria should also include factors that are related to subsequent survival to the reproductive adult stage, such as habitat quality.

Our retention results can certainly be criticized on a number of grounds, and we regard them simply as a test-of-concept at this point. Most significantly, the definition of "retention" used to evaluate parturition sites was rather arbitrary: a simulated larva that was within 50 km of its parturition site at some time after 30 model days was regarded as being retained near the site. This definition reflected two considerations, the first was that extruded larvae are not immediately capable of transition to a benthic existence and must undergo development in the plankton for some minimum time period. We chose a minimum developmental period of 30 model days, based on rockfish larval durations that are generally assumed to be 1-2 months (Matarese et al. 2003). The second consideration was that older larvae and early juveniles are typically capable of sustained swimming and may be capable of orientation toward nursery habitats. Thus, settlement-competent larvae need only be "close" to natal locations in order to recruit to the local population. We chose 50 km as a reasonable distance. As a check on the sensitivity of our results, we re-analyzed our model results using two alternative criteria: (1) 45 days and 50 km, and (2) 30 days and 25 km. As one would expect, retention rates declined at most sites under the two alternative criteria (they could not increase). The five sites exhibiting the highest retention were generally consistent across the criteria for the VM and AD behavioral scenarios, but were less so for the NS scenario.

The characterization of retention for rockfish is somewhat complicated beyond mere distance of dispersal from a parturition site, though. Many rockfish utilize nursery habitats that are not coincident with adult habitats; nursery habitats tend to be inshore of and shallower than adult habitats, being linked by an ontogenetic shift to deeper water (Love et al. 2002). Our use of a 50 km distance implies that suitable nursery habitat is located within 50 km of each parturition site. This may be true at most sites in the AI, given the narrow width of the continental shelf there, but may not be true at sites in the GOA, given its much wider shelf. Ideally, it would be better to characterize local retention using the geographic coverage of nursery habitats that are connected to a given parturition site through ontogenetic migration rather than using a simple distance from the parturition site. This is not currently feasible for the AI and GOA, however, because little information exists regarding the location of nursery habitats there.

Another criticism of the retention results is that they are only based on two years of simulated currents. Given the intermittent nature of rockfish recruitment, the temporal coverage used to evaluate sites should include a much wider range of years to incorporate more realistic temporal variability in the current fields and improve confidence in the robustness of the model results. Output from the NEP hydrodynamic model for the period 1958-2004 will be available sometime in 2007 to allow us to address this particular issue.

Finally, we considered retention only from the perspective of individual locations, not as a potential network of sites. Considering the sites as a network of potential marine reserve locations would allow for inter-site connections through larval dispersal; consequently retention within the network would be greater than retention at any single site.

Our models can also be criticized from a number of perspectives, including inadequacy of the hydrodynamic model current fields and lack of biological realism. The most significant inadequacy in the hydrodynamic model was the lack of tidal forcing. Tidal forcing was not included in the hydrodynamic model to reduce computational ($\times$ 2) and storage ($\times$ 24) requirements; consequently the interaction between tidal excursions and vertical migration cannot be captured in our simulations. This interaction would have most effect within the passes and channels of the AI and thus may be an important physical transport process missing from our simulations. Tidal currents could be expected to increase horizontal dispersion of larvae that do not vertically migrate, but might provide a retention mechanism for larvae capable of selective tidal stream transport (Forward and Tankersley 2001). Because rockfish larvae do not appear to undergo diel migration (Sakuma et al. 1999, Love et al. 2002), our model results may overestimate retention in the AI. Additionally, because the spatial resolution of the hydrodynamic model grid is ~10 km, smaller-scale bathymetric features that might

promote retention (e.g., canyon walls) are not adequately resolved by the hydrodynamic model.

From a biological perspective, the simple larval IBM we developed seems adequate to represent what is known of larval rockfish behavior, which principally consists of observations that *Sebastes* larvae occupy the upper layers of the water column above the pycnocline (e.g., Ahlstrom 1959, Sakuma et al. 1999), although some information on growth rates is also available (e.g., Kendall and Lenarz 1987, Plaza Pasten et al. 2003) that is not captured in the model. While the models of larval behavior we considered are certainly simplistic, even these models are pushing the bounds on what is known of the behavior of larval rockfish in the AI and GOA—information required to develop more sophisticated models is simply not available at the present time. However, our model only tracked dispersal through the larval stage. For many rockfish species, transition to a less-dispersive demersal life style does not occur at the end of the larval stage. Rather, these species undergo a pelagic juvenile stage during which further dispersal may occur. This stage may last a few weeks to months prior to transition to a more benthic existence. A more complete model of the pelagic dispersal of rockfish would incorporate this stage as well.

So, is modeling larval dispersion a tool for the design of marine reserves for rockfish? We think the results presented here show that such models can certainly inform the reserve design process. However, given the model deficiencies acknowledged above, as well as the uncertainties associated with early life history information for rockfish in the AI and GOA, the model presented here requires further refinement and validation before it can be useful as such a tool. We also emphasize the need for more information concerning the early life history of rockfish species, particularly those most vulnerable to overexploitation.

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Trawl Effort Distribution off the U.S. Pacific Coast: Regulatory Shifts and Seafloor Habitat Conservation

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Abstract

The U.S. West Coast groundfish trawl fishery currently operates under a variety of management measures designed to rebuild depleted rockfish (*Sebastes* sp.) populations. Regulatory measures can shift or reduce trawling over seafloor habitats and thus act as a tool to protect the long-term sustainability of groundfish by conserving Essential Fish Habitat (EFH) from fishing impacts. Our analysis reviews the spatial and temporal extent of trawl fishing effort over the Pacific coast seafloor in the framework of complex fishery management from 1999 to 2004. Coastwide trawl effort declined over these years, yet the remaining fishing effort changed in spatial extent and intensity and shifted between habitat types. The proportion of annual trawl effort on the continental shelf has increased. In recent years, trawl fishing effort has intensified along boundaries of depth-based spatial closures. This study emphasizes the benefits of increasing the spatial resolution of fishery data to better understand how fishing impacts on habitat are minimized, identifying locations of potential habitat recovery, and the implications of fishery management measures on EFH conservation.

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Introduction

Regional fishery management councils are responsible for drafting fishery management plans to describe and identify Essential Fish Habitat (EFH) and address adverse effects of fishing on EFH, to the extent practicable and based on the best available science (Magnuson-Stevens Fishery Conservation and Management Act 1996). The incorporation of EFH provisions into fisheries management has been challenging (Rosenberg et al. 2000), but remains a critical component for the recovery and long-term sustainability of depleted rockfish species and other habitat-associated groundfish. Rockfish are associated with hard-bottom, high-relief rocky areas (Love et al. 2002, McCain 2003) which are particularly sensitive to fishing impacts from mobile trawl gear that reduce habitat complexity, biogenic structures, and benthic community diversity (Auster and Langton 1999, Kaiser et al. 2002, NRC 2002). It has also been suggested that this loss of essential fish habitat is equivalent to increased mortality on the stocks that utilize these habitats (Mangel 2000). The reduction of bottom trawling over these habitats is an important outcome of fishery management to achieve a degree of EFH conservation for depleted rockfish.

Groundfish bottom trawling off the U.S. Pacific coast operates under a host of management measures aimed at reducing the catch of depleted rockfish species, but rarely are these measures evaluated as to their benefit or impact on EFH. Some of these management strategies were solely designed to reduce bycatch of depleted species, while others in recent years intend to spatially shift fishing effort away from depths where depleted species are thought to be most abundant. Understanding how management strategies, including in-season management, gear modification, and depth-related spatial closures, influence either the spatial extent or intensity of trawl effort over different seafloor habitat types, provides the connection for evaluating the extent and severity of fishing impacts. Similarly, this understanding also provides fundamental knowledge of where and to what degree recovery from fishing impacts may be occurring for rockfish EFH.

The objectives of this study were to (1) increase the spatial resolution of trawl fishing effort data on a coast-wide basis (Washington, Oregon, and California) to obtain a better understanding of where fishing impacts occur and where habitat recovery from impacts may be occurring, (2) identify significant fishing effort shifts (extent and intensity, by habitat or depth), and (3) evaluate the role of recent depth-related spatial closures for habitat conservation and the habitat implications of resulting shifts in fishing effort.

This analysis combines three types of data: the spatial distribution of trawl effort, seafloor habitat maps, and spatial management measures. The spatial scale (resolution) of data required to examine trawl effort shifts and methods of analyses were initially defined and tested through

previous research (Bellman et al. 2005). Trawl towlines, modeled as a straight line between the tow start and end location, demonstrated a substantial improvement in the resolution of fishing effort data relative to the use of start point locations alone. The towline model was initially used to demonstrate that the 2000 Pacific Fishery Management Council footrope restriction, with associated landing limits, effectively reduced trawling over Oregon rocky banks. The use of towlines enhanced representation of spatial fishing patterns to detect changes or shifts in fishing patterns and provided a measurable metric for trawl effort or intensity. However, trawl end point location information did not yet exist in electronic databases for the creation of towlines to review effort shifts on a coast-wide basis over multiple years.

Seafloor habitat maps have been compiled by Goldfinger et al. (2003) and Romsos (2004) of both geologic (surficial lithology) and geophysical (physiography) data off the Washington and Oregon coast and by Greene and Bizzarro (2003) of geophysical data off the California coast, using a classification code modified after Greene et al. (1999). In this study, the structural substrate component is used as a proxy for associated fish communities (Hixon et al. 1991, Stein et al. 1992, Yoklavich et al. 2000) and does not encompass other ecological or abiotic factors defining fish habitat.

Spatial information associated with recent management strategies, including depth-related closures, has not been readily available in a format for spatial analysis or review. However, the tracking and processing of this spatial management data is essential to those agencies responsible for carrying out fishery management objectives. Depth-related spatial closures are referred to as Rockfish Conservation Areas (RCA). Boundaries differ between latitudinal areas along the Pacific coast. RCAs have associated gear regulations, such that large footrope configurations are only allowed west of the closure and small footrope configurations are only allowed east of the closure. Each winter from approximately November to February, the westward boundary of the trawl RCA is modified to open particular fishing grounds to allow for targeted fishing of petrale sole (*Eopsetta jordani*). We assembled spatial management information for the RCA closures into a format that allowed us to review different management efforts and the spatial distribution of trawl fishing effort on the Pacific coast.

This study resolves the deficiency in coast-wide fishing location information, utilizes the most updated data available on seafloor habitat, and provides a synopsis of spatial fishery management. The resulting information and data of trawl fishing effort, spatial management measures, and seafloor habitat areas experiencing change represent the best available science for informing decision-making and evaluating the implications of management decisions for rockfish EFH. It also provides the basis for identifying specific locations where habitat impact and recovery studies can be conducted.

Methods

Logbook data were obtained for the limited entry (LE) groundfish trawl fishery (1998-2004) from state databases maintained by the Oregon Department of Fish and Wildlife, the Washington Department of Fish and Wildlife, and the California Department of Fish and Game. Traditionally, only tow start locations, referred to as the set of a tow, have been entered into electronic databases from the paper logbooks completed by fishermen. Through our previous work with the Oregon Department of Fish and Wildlife (Bellman et al. 2005), a subset of tow end locations, referred to as the haul of a tow, were entered into the state database and provided the key for improving the spatial resolution of trawl fishing effort. Subsequently, Oregon and Washington state agencies began entering all tow haul locations in 2003 and Oregon elected to enter several additional years of haul location data retroactively (concluding with 1999). The California Department of Fish and Game had begun entering tow haul locations in their state database in 1997 and these were readily available in an electronic format. Therefore, our data retrieval efforts focused on manually retrieving tow end locations for 1999-2002 from paper logbooks held by the Washington Department of Fisheries and Wildlife. This provided complete annual fishing location information on a coast-wide basis from 1999 to 2004.

Logbook data were then processed to create a single logbook record corresponding to each individual trawl tow, which included information pertaining to the vessel, date, time, and location of tow, the gear used, and the catch. Logbook records were removed from the analysis if the fisherman used mid-water or Danish seine gear, the tow haul was reported as the exact location of the tow set, or if either the set or haul location were incorrectly noted over a landmass. Logbook records that did not contain haul location information were also removed from the analysis.

Spatial analysis and mapping were conducted with ArcGIS Desktop version 9.1 (Environmental Systems Research Institute, Redlands, California). Trawl towlines were created using a Visual Basic script that draws a straight line from each set location to each corresponding haul location. Trawl towlines were removed from the analysis if they overlaid a landmass, extended beyond a depth of 2,000 meters, extended outside of the Exclusive Economic Zone (EEZ) of the United States (0-200 miles), or if projected vessel speed was greater than 5 knots (1 nautical mile = 1.85 km).

Seafloor habitat polygons based on surficial lithology (boulder, gravel, mix sand/gravel, mud, rock, rock/sand, sand, sand/mud, tuff) mapped off of Washington and Oregon (v1.5.2: Romsos 2004, Goldfinger et al. 2003), as well as coast-wide geophysical habitat type (Greene and Bizzarro 2003), were used to compute the geometric intersection of trawl

towlines and the seafloor habitat where that fishing occurs. Results for coast-wide geophysical habitat types were grouped into basic categories (shelf, slope, basin, ridge) and subcategories (rocky, sedimentary) to simplify the original 37 separate geophysical habitat descriptions. An overlay of trawl towlines across seafloor habitat type subsequently split each towline into multiple segments at each habitat boundary and joined the attributes of the underlying habitat type to each towline segment. The length of each resulting towline-habitat segment was measured and segment lengths were then summarized according to habitat type annually or within in-season management time periods. Temporal patterns of trawl towlines were examined through the production and review of video files using the Tracking Analyst extension based on two-week time frames.

To observe the spatial shift in fishing effort between years or between management time periods, trawl towline layers were converted to a continuous surface (raster) layer based on line density and then subtracted between time periods to observe areas of increased and decreased fishing effort. A kernel density calculation per square kilometer was used with a 3 km search radius and an output cell size of 1 km^2.

Depth-related spatial management measures (2002-2004) were compiled from the Federal Register and tabulated for review and analysis. Coordinate files related to these measures were obtained from the NOAA Northwest Regional Office and verified against the information published in the Federal Register. Polylines for each depth boundary were created and these boundary lines (≤6 polylines) were then used to create a single coast-wide polygon for each particular configuration of the closure area. Seafloor habitat data were extracted (using a clip function) for the area entirely within closure area boundaries and the attributes of the underlying habitat type and closure were joined. The area of each resulting habitat-closure polygon was calculated and summarized by habitat type to evaluate the spatial extent of each management closure configuration.

Patterns of trawl towlines were reviewed in both a spatial and temporal context related to the closure areas by dividing them into time periods during which each closure configuration existed, summarizing by geologic habitat (based on the previous towline-habitat overlay), and normalizing the results to effort (km towed) per day.

Fishing effort resulting from exempted fishing permits (EFP) was difficult to identify due to the fact that this effort is included in state agency databases, but the databases contain no identification field to separate them from regular trawl tows. EFP trawling is often governed under very different spatial and catch limit regulations and can be allowed within areas closed to the remainder of the fleet. In 2003, Oregon and California participated in an EFP to test selective flatfish

trawls (68 FR 19518, 68 FR 32731) and Washington participated in an EFP to test net configurations to selectively harvest arrowtooth flounder (*Atheresthes stomias*) while avoiding overfished rockfish species (68 FR 4162). In 2004, California again conducted an EFP for a selective flatfish net and small footrope configuration (69 FR 51812). Washington participated in several 2004 EFP trawl fisheries, one for testing an experimental net for selectively harvesting arrowtooth flounder and another to identify gear configurations for more selective harvest of nearshore flatfish species in the nearshore using a large footrope (69 FR 2324). Initial efforts were made to identify which vessels participated in the 2003 EFP fishery during which time period, such that all tows made by those vessels during the EFP time frame could be removed from the analysis of 2003 data. This alone did not accurately identify all of the targeted trawl fishing effort within the closed areas. Therefore, trawl towlines that were completely contained by the closure boundaries were assumed to reflect EFP trawl efforts and were selectively removed from the towline-closure area analysis in both 2003 and 2004.

Results

Overall trawl effort (distance trawled) declined coast-wide from 1999 to 2004 (Table 1), yet the remaining fishing effort shifted between habitat types over time. Analysis of coast-wide fishing effort demonstrates that the majority of annual trawl effort occurs in sedimentary continental slope habitat, followed by sedimentary continental shelf habitat. Trawl effort patterns over hard habitat on both the continental shelf and slope fluctuate each year. Trawl effort over hard continental shelf habitat decreased sharply in 2000; although it rose again in 2001. The proportion of annual trawl effort that occurred on the continental shelf decreased slightly in 2000 and has been rising since that time. The highest proportion of annual trawl effort over both sedimentary and hard continental shelf habitat is observed in 2004. In 2002 and 2004, the increase in proportion of annual trawl effort on the continental shelf correlates with a decrease of effort on the continental slope.

In Washington and Oregon offshore waters, annual trawl effort is greatest in mud habitats, followed by sand, and then sand/mud (Table 1). Trawling in sand habitats was higher in the last three study years (2002-2004), and was highest in 2004. Trawl effort over rock habitat markedly decreased between 1999 and 2000, although it rose again slightly in 2001. Trawl effort over boulder habitat was highest in 2002. The proportion of annual trawl effort over rock habitat also rose markedly between 2003 and 2004.

The ratio of annual trawl fishing effort to geophysical and geologic habitat type can highlight trends relative to differences in the total area of each habitat type (Figs. 1 and 2). The proportion of trawl effort in

Table 1. The distribution of trawl fishing effort over geologic and geophysical habitat type by distance trawled (km) and the proportion of annual distance trawled by habitat type. Geologic habitat type (surficial lithology) is mapped off of Washington and Oregon only, while geophysical habitat type (physiographic) is mapped coast-wide (Washington, Oregon, and California).

	1999	2000	2001	2002	2003	2004
Geophysical Habitat Type - Coast-wide						
Distance Trawled (km)						
SHELF_hard	3737	2194	3158	2808	1722	2194
SHELF_soft	117602	79013	103493	109856	77268	85276
SLOPE_hard	3943	2708	2877	1787	2253	1270
SLOPE_soft	237042	205272	178928	151317	148293	95959
BASIN_hard	5	1	3	2	1	6
BASIN_soft	967	722	735	657	700	356
RIDGE_hard	3335	2358	1870	2349	3258	1464
RIDGE_soft	6689	7460	6656	6124	7636	3859
Total	373320	299727	297718	274899	241130	190285
Proportion of Annual Distance Trawled (km)						
SHELF_hard	0.01001	0.00732	0.01061	0.01022	0.00714	0.01153
SHELF_soft	0.31502	0.26362	0.34762	0.39962	0.32044	0.44815
SLOPE_hard	0.01056	0.00903	0.00966	0.00650	0.00934	0.00668
SLOPE_soft	0.63495	0.68486	0.60100	0.55044	0.61499	0.50377
BASIN_hard	0.00001	0.00000	0.00001	0.00001	0.00000	0.00003
BASIN_soft	0.00259	0.00241	0.00247	0.00239	0.00290	0.00187
RIDGE_hard	0.00893	0.00787	0.00628	0.00855	0.01351	0.00770
RIDGE_soft	0.01792	0.02489	0.02236	0.02228	0.03167	0.02028
Geologic Habitat Type - Washington and Oregon						
Distance Trawled (km)						
MUD	129985	115761	122963	85179	98559	65523
SAND	17709	14547	19868	25261	21887	23579
SAND/MUD	17605	17506	14783	14772	14495	9730
ROCK	3032	1509	2090	1292	901	1225
BOULDER	1151	822	1192	1236	755	532
GRAVEL	0	2	0	1	0	8
MIX SAND/GRAVEL	52	7	8	0	2	1
ROCK/SAND	0	1	1	1	0	0
Proportion of Annual Distance Trawled (km)						
MUD	0.75238	0.75627	0.75078	0.65509	0.70647	0.64253
SAND	0.10250	0.09503	0.12131	0.19428	0.15689	0.23122
SAND/MUD	0.10190	0.11437	0.09026	0.11361	0.10390	0.09542
ROCK	0.01755	0.00986	0.01276	0.00994	0.00646	0.01201
BOULDER	0.00666	0.00537	0.00728	0.00950	0.00541	0.00521
GRAVEL	0.00000	0.00001	0.00000	0.00000	0.00000	0.00008
MIX SAND/GRAVEL	0.00030	0.00004	0.00005	0.00000	0.00001	0.00001
ROCK/SAND	0.00000	0.00001	0.00001	0.00001	0.00000	0.00000

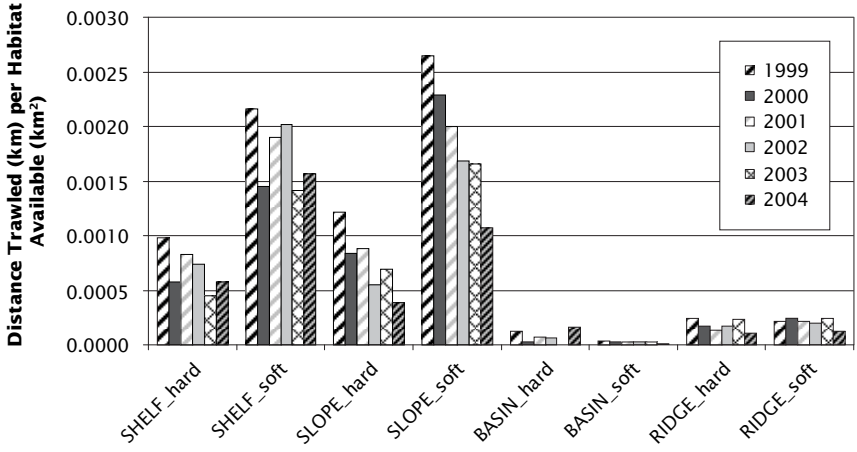


Figure 1. The ratio of annual trawl fishing effort to geophysical habitat type (km of distance trawled per km² of total habitat area mapped). Geophysical habitat type (physiographic) is mapped coast-wide (Washington, Oregon, and California).

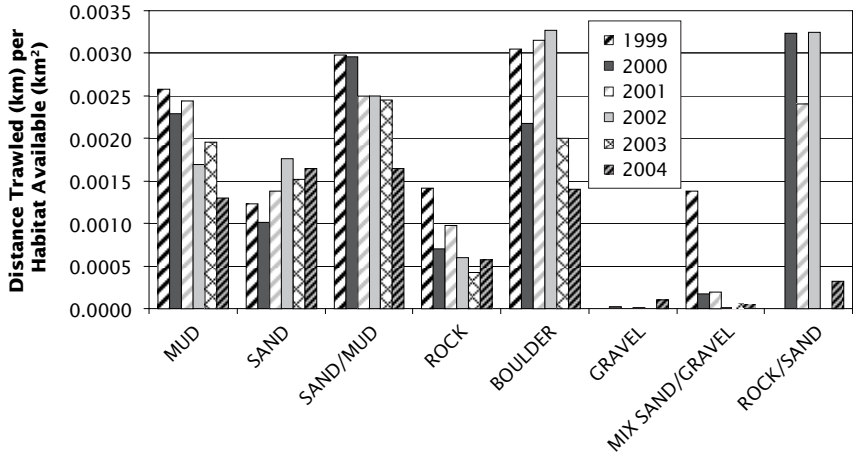


Figure 2. The ratio of annual trawl fishing effort to geologic habitat type (km of distance trawled per km² of total habitat area mapped). Geologic habitat type (surficial lithology) is mapped off of Washington and Oregon only.

areas of hard habitat on the continental shelf and slope is lower in comparison to the proportion in soft habitats. Off Washington and Oregon an increasing trend in the proportion of trawl fishing effort in sand habitat is evident (Fig. 2). Also, the proportion of trawl effort in habitat types with very minimally mapped areas can emerge much higher, such as the case with sand/mud and boulder, or have more erratic trends (e.g., rock/sand).

A compilation of 2002-2004 limited entry (LE) trawl fishery management measures established distinct time periods of in-season management changes that were not solely based on increases or decreases in catch limits. The changes in management measures between these periods were specifically intended to produce particular changes in the spatial distribution of fishing to reduce catch of depleted species.

In July and August 2002 (two months of high fishing effort during summer fair-weather conditions), a measure was passed to avoid catch of darkblotched rockfish (*Sebastes crameri*) that required all LE bottom trawling north of 40º10'N to use a small footrope configuration (≤20.5 cm diameter; 67 FR 44778). This corresponded with a major shift of trawl fishing effort onto the continental shelf. From September 1 to September 9, all bottom trawling north of 40º10'N was closed in an effort to further protect darkblotched rockfish. For the remainder of the year, LE trawling south of 40º10'N was prohibited for all groundfish except for deepwater complex, minor slope rockfish, and specified flatfish and grenadier taken incidentally in those fisheries.

The first depth-related spatial closure north of 40º10'N began on September 10, 2002, and had boundary lines approximating the 100 and 250 fathom (~183 and 457 m) contours. This created the Darkblotched Rockfish Conservation Area (DCBA) (67 FR 57973). Until September 30, trawling was also prohibited shoreward of the 100 fathom boundary due to concerns about incidental catch during this time period. When fishing re-opened shoreward of 100 fathoms in October and for the remainder of the year, a small footrope configuration was required along with reduced flatfish limits during October to keep incidental catch of darkblotched rockfish to a minimum.

Depth-related closures continued and are now referred to as Rockfish Conservation Areas (RCA). In this study, we focused on RCA closures north of 40º10'N (Table 2). In 2003, the spatial configuration of RCA closures changed eleven times, both due to coordinate corrections and actual changes to depth boundaries. The majority of coordinate corrections did not appear to have any effect on fishing effort in the area of correction, with the exception of the July coordinate correction to the 75 fathom boundary line off the Washington coast. This boundary correction created access to a sizeable area of the seafloor and in response an increase in fishing effort was observed.

Table 2. Timeline of 2003 and 2004 depth-based spatial closures for the limited entry trawl fishery north of 40°10'N, referred to as Rockfish Conservation Areas (RCA). Depth boundaries in bold indicate a coordinate correction from the previous management period or previously published coordinates.

2003								
Actual Timeline	Jan 1-Jan 26		Jan 27-Feb 28		Mar 1-Apr 14		Apr 15-Apr 30	
FR Citation	68 FR 908		68 FR 4719		68 FR 11182		68 FR 18166	
Latitude (North)	(west)	(east)	(west)	(east)	(west)	(east)	(west)	(east)
46°16' to Canada	250 fm **	100 fm	**250 fm ** **	**100 fm**	**250 fm**	**100 fm**	250 fm	**100 fm**
40°10' to 46°16'	250 fm **	100 fm	**250 fm ** **	**100 fm**	**250 fm**	**100 fm**	250 fm	**100 fm**
Actual Timeline	May 1-May 27		May 28-Jun 30		Jul 1-Jul 21		Jul 22-Aug 31	
FR Citation	68 FR 23901		68 FR 32680		68 FR 40187		68 FR 43473	
Latitude (North)	(west)	(east)	(west)	(east)	(west)	(east)	(west)	(east)
46°16' to Canada	250 fm	shoreline	**200 fm**	**50 fm**	200 fm	**75 fm**	200 fm	**75 fm**
40°10' to 46°16'	250 fm	shoreline	**200 fm**	**50 fm**	200 fm	**75 fm**	200 fm	**75 fm**
Actual Timeline	Sep 1		Sep 2-Oct 31		Nov 1-Nov 20		Nov 21-Dec 31	
FR Citation	68 FR 40187		68 FR 52703		68 FR 60865		68 FR 66532	
Latitude (North)	(west)	(east)	(west)	(east)	(west)	(east)	(west)	(east)
46°16' to Canada	200 fm	50 fm	**200 fm**	50 fm	**200 fm ** **	50 fm	**200 fm ** **	shoreline
40°10' to 46°16'	200 fm	50 fm	**200 fm**	50 fm	**200 fm ** **	50 fm	**200 fm ** **	shoreline

2004										
Actual Timeline	Jan 1-Feb 29		Mar 1-Apr 30		May 1-Jun 30		Jul 1-Sept 30		Oct 1-Dec 31	
FR Citation	69 FR 1322		69 FR 11064		69 FR 25013		69 FR 40805		69 FR 58916	
Latitude (North)	(west)	(east)	(west)	(east)	(west)	(east)	(west)	(east)	(west)	(east)
46°16' to Canada	200 fm **	75 fm	200 fm	60 fm	150 fm	60 fm	**150 fm**	**75 fm**	**250 fm**	shoreline
40°10' to 46°16'	200 fm **	75 fm	200 fm	60 fm	150 fm	60 fm	**150 fm**	**75 fm**	**250 fm**	shoreline

Note: ** = Modified for petrale fishing
FR = Federal Register

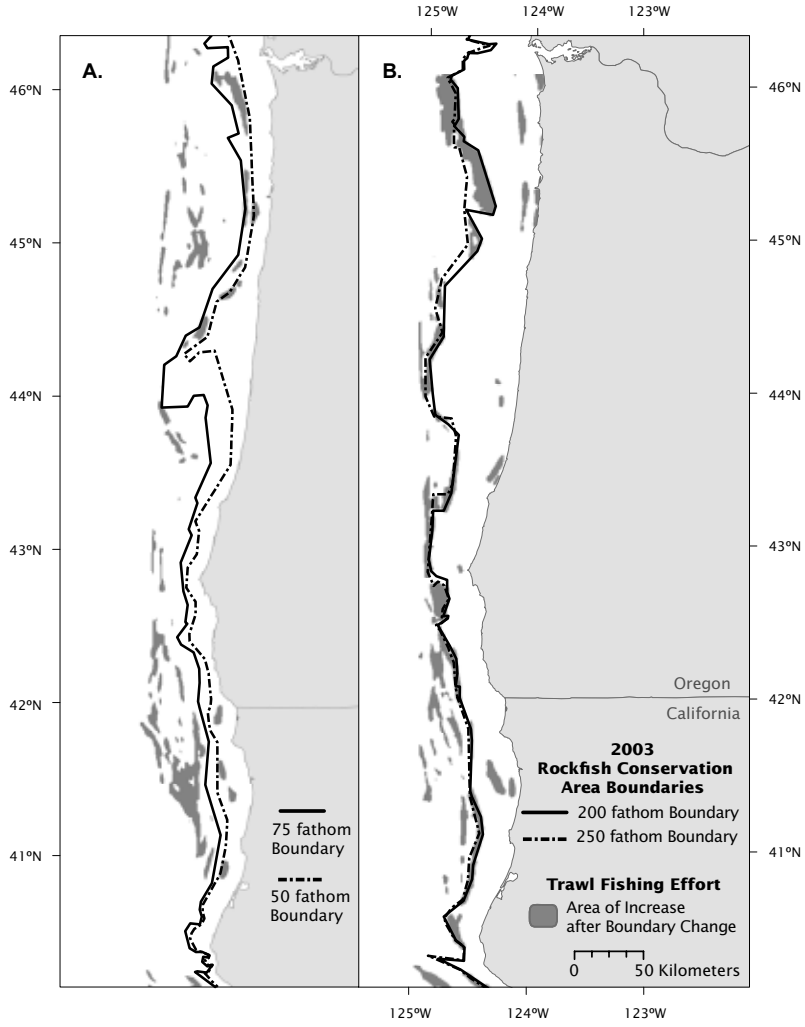


Figure 3. Trawl fishing effort of increased intensity in both patchy and consistent patterns when RCA boundary lines change; previous boundary (dashed line) and new boundary (solid line). Mapped trawl fishing effort is the aggregated result of a towline density analysis. A. RCA eastern boundary changed from 50 to 75 fathoms in July 2003; patchy increases within the newly opened area. B. RCA western boundary changed from 250 to 200 fathoms in May 2003; consistent area of increase within the newly opened area.

Shifts in fishing effort away from petrale sole fishing grounds were clearly seen when these areas closed between February and March. Fishing effort began increasing at this time east (shoreward) of the RCA boundary with many targeted fishing patterns along the eastern boundary line. When the eastern RCA boundary moved to the shoreline in May, fishing effort focused on the continental slope. When the western RCA boundary shifted at the end of May from 250 to 200 fathoms (457 to 366 meters), new areas of effort developed consistently along the western boundary line (Fig. 3B). A shift of the eastern RCA boundary from 50 to 75 fathoms (91 to 137 meters) in July resulted in only very small changes in targeted patterns along the eastern boundary area, but did not appear to substantially shift effort into the larger extent of area which had opened (Fig. 3A).

During the initial 2004 RCA closure from 200 to 75 fathoms (western boundary modified for the winter petrale sole fishery), trawl fishing effort was focused west of the closure. When the closure moved to 200-60 fathoms in March, patchy fishing effort along the boundary began east of the RCA. In May, the RCA changed to 150-60 fathoms and fishing effort increased significantly in the area between the previous western boundary and the new western boundary; from 200 to 150 fathoms. At that time, there was also a large increase in fishing effort east of the RCA, primarily off the coast of Washington and the northern tip of Oregon. The next RCA closure (150-75 fathoms) began in July and an increase in fishing effort was observed between the previous and new eastern boundary, from 75 to 60 fathoms, and also in large, broad patches off of Washington and in areas to the north and south of the Columbia River. Fishing patterns west of the RCA remained much the same. In October, trawl effort declined and was focused exclusively west of the RCA configuration (250 fathoms to the shoreline) for the remainder of the year.

Trawl fishing effort (km towed per day) observed during each RCA time period varied as to the amount of different geologic habitat types trawled (Table 3). During 2002 from July 1 to August 31 when small footropes were required for all LE trawling, trawl effort was at its annual highest over sand, rock, and boulder habitat, with a decrease in fishing effort over mud. In 2003, the highest fishing effort in rock and boulder habitat occurred during March and April when RCA boundaries were 250-100 fathoms. However, the highest effort in sand habitat occurred from May through August when RCA boundaries were 200-50 and 200-75 fathoms. In 2004, the highest annual effort in sand habitat occurred from May through September when RCA boundaries were 150-60 and 150-75 fathoms. From July through September (RCA 150-75 fathoms), the highest annual effort in rock and boulder habitat took place as well.

The percentage of each geologic habitat type (Washington and Oregon) enclosed within specific RCA closure boundaries is summarized

in Table 4. The largest spatial extent of RCA closure takes place when the eastern RCA boundary is moved completely to the shoreline. This results in significant coverage of seven of the eight geologic habitat types; over 87% of each habitat area is enclosed within its bounds. The exception is mud habitat, which is prevalent deeper than the western boundary of the RCA, with habitat area coverage at 30% maximum. Rock habitat within the closure area is greatly dependent on where the eastern RCA boundary is drawn. When the eastern boundary is set at 50 fathoms depth, 60% of the rock habitat is covered. When the eastern boundary is drawn at 60 fathoms, 51% of rock is covered, and when it is drawn at 75 fathoms depth, only 23% of rock habitat is included within the RCA. The RCA coverage of boulder habitat areas, located primarily off the state of Washington, is heavily dependent on interpretation of the coordinates and information published in the Federal Register. Areas found along the boundary of the Exclusive Economic Zone of the United States at the Canadian border are the most difficult to decipher in terms of where to draw actual RCA boundary lines from the published coordinates. The boundary interpretation in this study is believed to be legally accurate, but we also acknowledge that there is some spatial uncertainty as to which boundary interpretation the trawl fleet operates under.

Discussion

Both the spatial extent and intensity of fishing effort play important and separate roles in the study of fishing impacts to seafloor habitat (Jennings and Kaiser 1998, Auster and Langton 1999, Johnson 2002). The same fishing effort over a larger area will have a different impact from when it intensifies in a smaller area. Although there was an overall decline in trawl effort over the years of this study, the remaining effort changes in both spatial extent and intensity over time and in response to management measures. Trawl fishing effort (distance trawled) over the continental slope habitat did not change substantially between 2002 and 2003, yet the spatial distribution of 2003 fishing effort intensified in particular areas on the slope. One should exercise caution when comparing trawl fishing effort on the continental shelf between 2002 and 2003. The substantial increase in fishing effort on the shelf in July-August 2002 confounds the calculation of strictly interannual effort shifts, which display decreased areas of fishing effort on the shelf in 2003. These are clear indications that the review of spatial extent is an important step for consideration of fishing impacts, rather than solely quantifying a fishing effort metric.

When fishing effort is displaced, it can shift into otherwise lightly fished areas (Rijnsdorp et al. 2001, Holland 2003) or intensify effort within traditional fishing grounds (Larcombe et al. 2001). Overall, the influence of RCA closures resulted in trawl fishing effort patterns

Table 3. Trawl fishing effort over geologic habitat type exhibited in the context of depth-based spatial closure areas, the 2002 Darkblotched Rockfish Conservation Area (DBCA) and the 2003-2004 Rockfish Conservation Areas (RCA), by dividing towlines into time periods during which each closure configuration existed (duration of closure noted by number of days in parenthesis) and normalizing the results to fishing effort (km towed) per day.

In 2002, results are divided into management time frames, including before July 1, July 1 to August 31 when a small footrope was required for all LE trawling, September 1 to September 30 when trawling was closed shoreward of the eastern closure boundary, and October 1 to December 31. "P" indicates a closure boundary modified to allow for the winter petrale sole (*Eopsetta jordani*) fishery.

2002				
DBCA (fathoms)	Small Footrope		250-100	250-100
	Before July 1	Jul 1-Aug 31	Sep 1-Sep 30	Oct 1-Dec 31
Km towed	per day (181)	per day (62)	per day (30)	per day (92)
Mud	326.814	139.172	76.345	247.189
Sand	67.639	159.136	5.484	51.107
Sand/Mud	49.056	53.707	5.742	40.708
Rock	5.522	5.895	1.356	4.631
Boulder	2.318	9.367	1.293	2.862
Gravel	0.007	0.000	0.000	0.000
Mix Sand/Gravel	0.063	0.000	0.000	0.026
Rock/Sand	0.008	0.010	0.000	0.000

Table 3. (Continued.)

2003								
RCA (fathoms)	250P-100	250-100	250-Shoreline	200-50	200-75	200-50	200P-50	200P-Shoreline
	Jan 1-Feb 28	Mar 1-Apr 30	May 1-May 27	May 28-Jun 30	Jul 1-Aug 31	Sep 1-Oct 31	Nov 1-Nov 20	Nov 21-Dec 31
Km towed	per day (59)	per day (61)	per day (27)	per day (34)	per day (62)	per day (61)	per day (20)	per day (41)
Mud	300.027	362.184	336.244	328.242	272.601	242.601	259.698	63.121
Sand	27.160	46.311	29.384	68.189	73.636	49.818	28.153	13.792
Sand/Mud	8.741	75.348	9.693	23.630	45.255	10.597	5.336	0.500
Rock	2.890	5.730	2.322	2.317	3.380	2.491	3.402	0.005
Boulder	0.551	3.967	0.237	0.081	0.393	0.532	0.393	0.000
Gravel	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mix Sand/Gravel	0.025	0.000	0.000	0.000	0.008	0.000	0.025	0.000
Rock/Sand	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

2004					
RCA (fathoms)	200P-75	200-60	150-60	150-75	250-Shoreline
	Jan 1-Feb 29	Mar 1-Apr 30	May 1-Jun 30	Jul 1-Sep 30	Oct 1-Dec 31
Km towed	per day (60)	per day (61)	per day (61)	per day (92)	per day (92)
Mud	165.109	190.267	231.467	219.063	174.254
Sand	21.806	25.925	122.541	148.327	5.470
Sand/Mud	5.292	21.840	51.673	57.723	6.775
Rock	2.872	2.156	4.260	11.292	1.223
Boulder	0.030	1.093	2.023	3.563	0.000
Gravel	0.000	0.000	0.157	0.084	0.000
Mix Sand/Gravel	0.000	0.000	0.006	0.027	0.000
Rock/Sand	0.000	0.000	0.002	0.000	0.000

Table 4. The percentage of geologic habitat type off of Washington and Oregon that falls within the boundary of each Rockfish Conservation Area (RCA) trawl closure north of 40°10'N [(*RCA Habitat Area/Total Habitat Area*) × 100]. "P" indicates a closure boundary modified to allow for the winter petrale sole (*Eopsetta jordani*) fishery.

	2002	2003							
	Sep10-Dec31	Jan1-Feb28	Mar1-Apr30	May1-May27	May28-Jun30	Jul1-Aug31	Sep1-Oct31	Nov1-Nov20	Nov21-Dec31
West Boundary	W 250	W 250P	W 250	W 250	W 200	W 200	W 200	W 200P	W 200P
East Boundary	E 100	E 100	E 100	E Shoreline	E 50	E 75	E 50	E 50	E Shoreline
MUD	13.79	11.76	13.15	30.07	23.04	15.22	23.04	23.04	24.66
SAND	4.43	2.95	3.24	87.39	16.05	8.16	16.05	15.88	87.01
SAND/MUD	13.94	12.85	13.60	96.55	72.99	30.23	72.99	72.99	93.04
ROCK	6.64	6.28	6.65	98.17	60.77	22.85	60.77	60.77	97.70
BOULDER	51.37	59.12	58.86	99.93	98.43	79.93	98.43	98.43	99.93
GRAVEL	0.00	0.00	0.00	100.00	0.22	0.00	0.22	0.22	100.00
MIX SAND/GRAVEL	0.00	0.00	0.00	100.00	63.02	61.29	63.02	63.02	100.00
ROCK/SAND	0.00	0.00	0.00	100.00	96.38	0.00	96.38	96.38	100.00

	2004				
	Jan1-Feb29	Mar1-Apr30	May1-Jun30	Jul1-Sep30	Oct1-Dec31
West Boundary	W 200P	W 200	W 150	W 150	W 250
East Boundary	E 75	E 60	E 60	E 75	E Shoreline
MUD	14.46	19.47	16.19	11.45	30.07
SAND	6.47	11.02	10.71	6.10	87.38
SAND/MUD	28.14	58.16	55.83	25.88	96.55
ROCK	23.74	53.02	50.98	22.02	98.16
BOULDER	78.94	84.88	84.88	78.94	99.93
GRAVEL	0.00	0.22	0.22	0.00	99.95
MIX SAND/GRAVEL	61.30	63.02	63.02	61.30	99.98
ROCK/SAND	0.00	0.00	0.00	0.00	99.54

intensifying along RCA boundary lines, consistently in many areas along the western boundaries and often in a patchy manner along the eastern boundaries. Fishing effort did not necessarily change in proportion to the area opened or closed to trawling. Our results are in agreement with the outcomes of an outreach study conducted in fishing communities along the U.S. West Coast, where fishermen stated that vessels fishing shoreward of the RCA have experienced a compression of their historical fishing grounds and seen an increase in fishing effort along the eastern boundary areas of the RCA (Bloeser et al. 2005).

The proportion of coast-wide annual trawl fishing effort on the continental shelf has been rising in recent years. The highest trawl effort on the shelf normally occurs in the summer months. During this time frame, RCA closures have restricted fishing grounds on the shelf to shoreward of the eastern boundaries (75, 60, or 50 fathoms) and can greatly influence the intensity of potential fishing impacts. Increased trawl effort on the continental shelf is also reflected in higher efforts in sand habitat, which is found almost exclusively on the shelf. Interactions or conflicts with other fisheries (pot, trap, etc.) conducted on the shelf may also result from this trend.

It is a commonly held assumption that seafloor habitats are protected from fishing impacts through the establishment of areas closed to fishing, although fishery management did not have any stated objective for habitat conservation at the time the RCA closures were established. The changes to RCA boundaries have been used as an adaptive strategy for in-season management in an attempt to reduce catch of depleted species such as canary rockfish (*Sebastes pinniger*) north of 40º10'N and bocaccio (*S. paucispinis*) to the south, but this management strategy has not been evaluated in the context of EFH. Although large areas off the Pacific coast may be experiencing little or no impact from trawling, it does not necessarily mean that prime EFH for these and other depleted species is being protected through the RCA closures. Impacts from exempted fishing permit trawling within closure areas should be considered as well, and steps should be taken to ensure our ability to identify these tows in electronic databases.

In addition to any rock habitat protections afforded by gear restrictions, RCAs continue to offer protection for rock habitats from the impacts of trawling. This protection ranges from as little as 6% of total rock habitat up to 98%, depending on where the eastern boundary is set at any given time. Relatively small differences in depth-based boundaries can greatly influence this coverage, as demonstrated by the 200-75 fathom configuration covering 23% of total rock habitat versus the 200-50 fathom configuration covering 61% of total rock habitat. If these closure areas are considered in terms of habitat protection in future management decisions, careful consideration should be given to the selection of boundaries to ensure coverage of the desired EFH.

It is important to acknowledge that trawl fishing efforts are influenced by other concurrent factors, such as market conditions, weather, fuel prices, etc. A program to reduce excess capacity in the U.S. West Coast groundfish fleet, referred to as the buyback program, has played a role in further reducing fishing effort when accepted bidders' vessels permanently stopped fishing in December 2003. In the U.S. West Coast groundfish trawl fishery, it is very difficult to distinctly separate the impacts on trawl effort distribution of reduced trip limits, gear regulations, and large depth-based spatial closures due to the complexity of current groundfish management. Our results provide an initial overview of trawl fishing effort distribution in relation to seafloor habitat in the context of complex management measures.

As fishery management on the West Coast moves toward the use of spatial strategies, the importance of reviewing and evaluating management measures in a spatial context is increasing. Now that the importance of increased spatial resolution from trawl fishing effort data has been demonstrated, state management agencies have been able to adapt their policies and databases to incorporate tow end location data for future analyses. It is also important at this time to educate the fishery management community in the data requirements for spatial analyses, the methods used, and increase general understanding for interpreting and utilizing finished products. One such application has already been demonstrated, as these data were used for analyses to support consensus decision-making during the process of selecting preferred alternatives for the Groundfish Essential Fish Habitat Environmental Impact Statement (EFH-EIS) (NOAA Fisheries 2005). The outcomes of this study further the objectives of the EFH-EIS process by providing a better understanding of fishing effort in relation to seafloor habitat and can be used to formulate alternatives for minimizing fishing impacts to habitat. In addition, improved fishing effort information can now be used to identify areas of potential habitat recovery so that we may better understand the history of fishing impacts.

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A Share-Based Management Program for the Central Gulf of Alaska Rockfish Fishery

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Abstract

In 2005, the North Pacific Fishery Management Council adopted a pilot share-based program for management of the central Gulf of Alaska trawl rockfish fisheries. The program apportions the total allowable catch into exclusive shares that are allocated to cooperatives, based on the catch history of the members of those cooperatives. Allocating exclusive shares is expected to allow the harvest to be spread over a much longer season, allowing participants to schedule their activities and save on costs of fishing and processing. Historically, participants in the rockfish fishery have focused on maintaining quality of incidental catch species (such as sablefish and Pacific cod). The change in management should allow participants, particularly those in the catcher vessel/shore plant sector, to focus added efforts on producing higher valued, better quality products from targeted rockfish. Efforts are likely to be made to serve fresh fish markets with rockfish that could not be accessed under the existing management.

Introduction

In 2003, U.S. Congress directed the Secretary of Commerce to establish, in consultation with the North Pacific Fishery Management Council (the Council), a pilot program for management of the Pacific ocean perch (*Sebastes alutus*), northern rockfish (*Sebastes polyspinis*), and pelagic shelf rockfish (which includes dusky rockfish [*Sebastes variabilis*], yellowtail rockfish [*Sebastes flavidus*], and widow rockfish [*Sebastes entomelas*]) trawl fisheries in the central Gulf of Alaska (the Central Gulf). Following this directive, in 2005 the Council adopted a share-based management program under which the total allowable catch is appor-

tioned as exclusive shares to cooperatives based on the catch history of the members of those cooperatives.[1] The program is intended to address several concerns, including providing stability to both the fishing and processing sectors and to increase product value.

This study describes the current fishery and the pilot program and examines the potential for participants to benefit from the change in management. Typically, share-based management provides participants with the opportunity to spread their catch over a much longer season, schedule their activities, and save on costs of fishing and processing. Some unique aspects of the rockfish fisheries, such as the importance of valuable incidental catch, create additional opportunities for participants to benefit from the change in management to the pilot program.

The current fishery

Under current management, the rockfish fisheries are conducted under limited access management. The fisheries open to non-trawl participants on January 1. Non-trawl participants, however, have historically harvested a very small portion of the Central Gulf rockfish total allowable catch (TAC) (i.e., less than 1%). To accommodate growth of this sector, the program would allocate 2.5% of the aggregate TAC of rockfish to fixed gear vessels. Since this sector has limited participation in the fisheries the remainder of this paper is focused on practices of the trawl gear participants. The trawl season opens in early July and ongoing catch is monitored by managers with closings timed to coincide with harvest of the TAC.

Trawl participants are subject to an aggregate limit on the amount of Pacific halibut (*Hippoglossus stenolepis*) that can be caught, all of which must be discarded as prohibited species catch (PSC). Participation records show that between approximately 5 and 7 catcher processors (vessels that processor their catch on board) and approximately 30 and 35 catcher vessels (vessels that deliver their catch to shore plants for processing) participated in the fisheries annually in recent years. The limits on entry are not constraining as approximately half of the eligible catcher processors and less than one-third of the eligible catcher vessels typically participate in the fisheries.

Examination of openings and closings in the Central Gulf rockfish fisheries from 1996 to 2004 shows that all harvests are usually made in a few weeks each year (Table 1). A general progression of targeting is also apparent, as most participants target Pacific ocean perch first,

[1] This paper draws heavily on North Pacific Fishery Management Council and National Marine Fisheries Service, "Regulatory Impact Review, Environmental Assessment, and Initial Regulatory Flexibility Analysis for Amendment 68 to the Gulf of Alaska Fishery Management Plan, Central Gulf of Alaska Rockfish Demonstration Program," June 2005. The author of this paper is a primary author of that analysis.

Table 1. Openings and closures in the central Gulf of Alaska rockfish fisheries (1996-2004).

Year	Opening for species	Opening date	Closures			Reason for closure
			Pacific ocean perch	Northern rockfish	Pelagic shelf rockfish	
1996	All	July 1	July 11	July 20	none	TAC (POP, Nor)
1997	All	July 1	July 7	July 10	July 15	TAC
1998	All	July 1	July 6	July 14	July 19	TAC
1998 reopen	POP	July 12	July 14	—	—	TAC
1999	All	July 4	July 11	July 19	—	TAC(POP, Nor)
1999 reopen	POP, Nor	August 6	August 8	August 10	—	TAC(POP, Nor)
1999 closure	PSR	July 4	—	—	September 3	PSC
2000	All	July 4	July 15	July 26	July 26	TAC(POP, Nor)/PSC(PSR)
2001	All	July 1	July 12	July 23	July 23	TAC(POP)/PSC(Nor, PSR)
2001 reopen	Nor, PSR	October 1	n/a	October 21	October 21	PSC
2002	All	June 30	July 8	July 21	July 21	TAC
2003	All	June 29	July 8	July 31	July 29	TAC
2004	All	July 4	July 12	July 25	July 25	TAC(POP)/PSC(Nor, PSR)

TAC = Total Allowable Catch reached.
PSC = Prohibited Species Catch limit reached.
POP = Pacific ocean perch.
PSR = Pelagic Shelf rockfish.
Nor = Northern rockfish.
Source: NOAA Fisheries status reports and groundfish closure summaries.

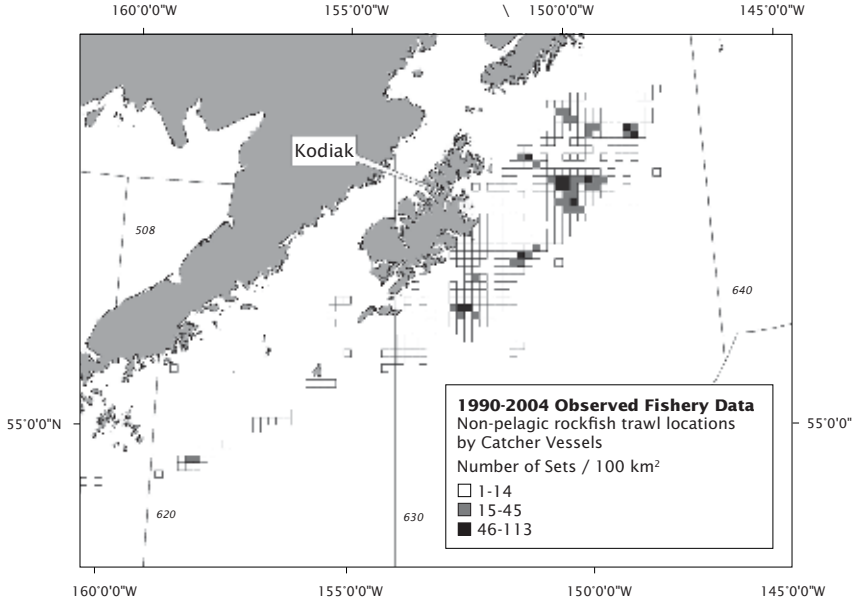


Figure 1. Locations of observed fishing effort for catcher vessels targeting rockfish with non-pelagic gear in the central Gulf of Alaska, 1990-2004 (hauls per 100 square kilometers). Source: NMFS Observer Data.

until the TAC of that species is fully harvested, after which most vessels move on to northern rockfish or pelagic shelf rockfish directed fisheries, while others move on to other fisheries in and outside of the Central Gulf. Typically, closures have resulted from the harvest of the rockfish TACs, although at times limits on catch of PSC, usually Pacific halibut, have closed the fisheries.

The short season has also contributed to the spatial concentration of catch in the fishery (Figs. 1 and 2). Catcher vessels make most harvests close to Kodiak, where a large majority of the catch is landed, because of the need to offload harvests and return to the fishing grounds to maximize total catch. In addition, processors have demanded that fishermen limit trips to less than 72 hours as a means of ensuring quality of catch. The limitation on fishing trip time effectively limits the spatial distribution of catch for catcher vessels. While catcher processors are also subject to the time limitation of the season, since they process their catch on board, their fishing activity is not spatially limited in the same manner as catcher vessels.

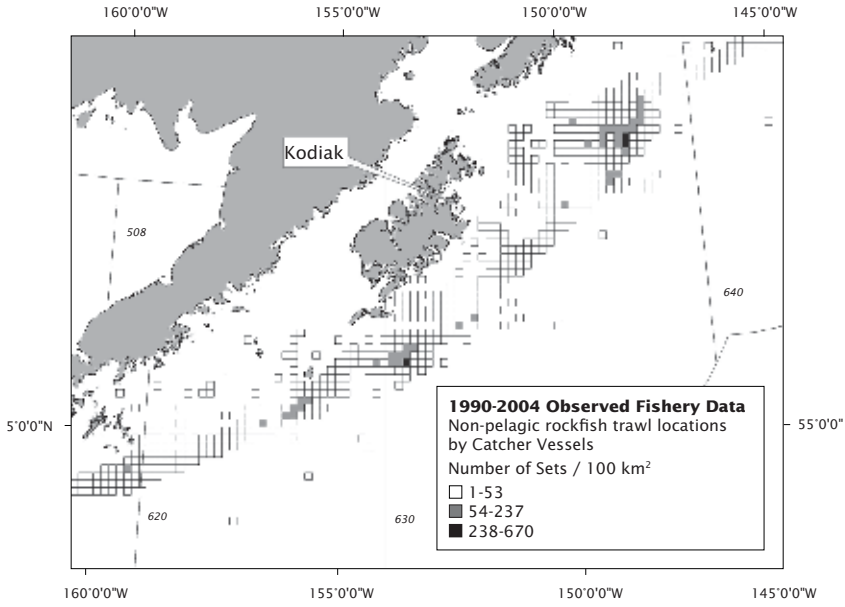


Figure 2. Locations of observed fishing effort for catcher processors targeting rockfish with non-pelagic gear in the central Gulf of Alaska, 1990-2004 (hauls per 100 square kilometers). Source: NMFS Observer Data.

Catch of Pacific ocean perch has dominated the rockfish fisheries in recent years, with harvests exceeding 6,000 t in the last 6 years of the period considered (Fig. 3). Combined catches of northern rockfish and pelagic shelf rockfish fluctuated with the lowest catch totaling approximately 4,000 t and the largest catch totaling approximately 6,500 t.

Participants catch a variety of other species during the directed Central Gulf rockfish fishery, most importantly sablefish (*Anoplopoma fimbria*), Pacific cod (*Gadus macrocephalus*), shortraker rockfish (*Sebastes borealis*), rougheye rockfish (*Sebastes aleutianus*), and shortspine thornyhead (*Sebastolobus alascanus*). Incidental catch rates on rockfish targeted tows, however, are generally quite low (Table 2). For example, from 1995 through 2004, none of the main incidental catch species in the rockfish fishery was observed in 50% of the tows. In the tow that is at the 75th percentile of rate of Pacific cod catch, Pacific cod was 3.2% of the target rockfish catch (or for each ton of rockfish approximately 0.032 t of Pacific cod was caught). Shortraker and rougheye were managed under a combined TAC until 2005. As a consequence, some of

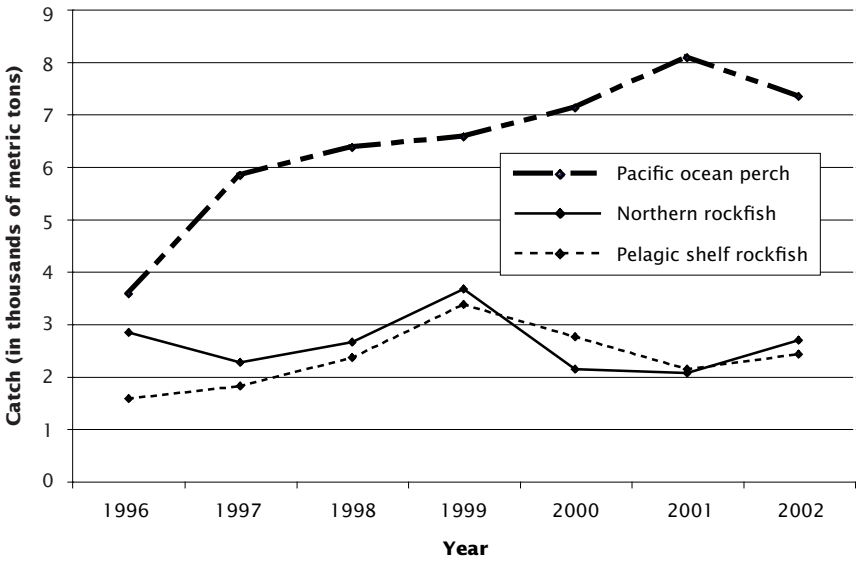


Figure 3. Catch of central Gulf of Alaska rockfish in thousands of metric tons (1996-2002). Source: NPFMC Rockfish Database, Version 1.

the data collected concerning these species fail to distinguish the two species.

Incidental catch species are currently managed under "bycatch status" with a maximum retainable allowance (MRA), which limits retention of these species to a percent of the retained target harvest (Tables 3 and 4). Comparing the low incidental catch rates from observed rockfish targeted tows (Table 2) and the overall catch rate in the fishery (in Tables 3 and 4) suggests that participants in the rockfish fishery often "top off" on these valuable incidental catch species, using single tows that target the incidental catch species during a directed rockfish trip. This conclusion is consistent with the findings of a study of "natural" bycatch rates (the rate at which bycatch occurs in targeted trawl tows in a fishery) by Ackley and Heifetz (2001), which concluded that participants in the Central Gulf of Alaska directed rockfish fisheries target sablefish to the extent permitted by MRAs. Catch of these incidental species is likely limited because of the race for the target rockfish as participants try to strike a balance of time harvesting target rockfish and valuable secondary species in an attempt to maximize their total revenues. Additional data show that overall incidental catch of Pacific cod and sablefish in the rockfish fishery are approximately 2.5% and 10% of the respective TACs of those species in the Central Gulf of Alaska. Incidental catch of short-

Table 2. Catch rates of various species in observed central Gulf of Alaska hauls targeting rockfish (1996-2003).

Species	Hauls with rockfish targets	Rockfish target hauls with species	Weight of catch of species (t)	Catch as percent of target rockfish	Catch of species as a percent of targeted rockfish in the					
					25th percentile	50th percentile	75th percentile	85th percentile	95th percentile	100th percentile
CGOA rockfish	2,756	2,756	18,833	100	100	100	100	100	100	100
Pacific cod	2,756	1,364	337	1.79	0	0	3.23	6.40	17.12	98.55
Sablefish	2,756	1,102	510	2.71	0	0	2.84	8.27	27.07	95.48
Thornyhead	2,756	638	141	0.75	0	0	0	0.66	5.21	87.70
Shortraker	2,756	232	153	0.81	0	0	0	0	2.59	92.53
Rougheye	2,756	371	177	0.94	0	0	0	0	3.13	88.11
Shortraker/ rougheye[a]	2,756	14	15	0.08	0	0	0	0	0	16.80

[a]where shortraker rockfish and rougheye rockfish were combined in the observer data.

Source: 1996-2003 GOA Observer data, with data calculations by NPFMC.
Central Gulf rockfish includes Pacific Ocean perch, northern rockfish and pelagic shelf rockfish.

Table 3. Catcher processor production, product revenues, average prices, maximum retainable allowance, and percent of target rockfish (1996-2002).

Species	Product	Number of vessels	Maximum retainable allowance (as percent of target rockfish)	Percent of target rockfish catch	Product weight (t)	Product revenues ($)	Average product price ($)
Pacific ocean perch	Whole	7	–	–	1,817.9	1,476,859	0.368
	Western cut	2	–	–	a	a	a
	Eastern cut	20	–	–	10,663.4	11,964,004	0.509
Northern rockfish	Whole	7	–	–	2,004.4	1,227,760	0.278
	Western cut	1	–	–	a	a	a
	Eastern cut	18	–	–	2,913.0	2,121,563	0.330
Pelagic shelf rockfish	Whole	4	–	–	434.3	399,409	0.417
	Western cut	1	–	–	a	a	a
	Eastern cut	18	–	–	4,310.9	4,469,553	0.470
Pacific cod		18	20	1.4	306.7	706,072	1.044
Sablefish		21	7	4.7	1,239.5	9,701,981	3.550
Shortraker/rougheye		19	15[b]	6.5	1,340.0	4,182,038	1.416
Thornyheads		21	15[b]	1.6	555.8	1,858,292	1.517

[a]Withheld for confidentiality.
[b]Retainable percentage is combined limit on shortraker/rougheye and thornyheads.
Source: NPFMC Rockfish Database, Version 1.

Table 4. Catcher vessel landings, average ex-vessel prices, maximum retainable allowance, and percent of target rockfish (1996-2002).

Species	Number of vessels	Maximum retainable allowance (as percent of target rockfish)	Percent of target rockfish catch	Landings (t)	Ex–vessel gross revenues ($)	Average ex–vessel price ($/lb)
Pacific ocean perch	50	–	–	21,350.0	2,810,256	0.060
Northern rockfish	49	–	–	10,270.1	1,301,287	0.057
Pelagic shelf rockfish	49	–	–	7,181.3	932,095	0.059
Pacific cod	47	20	11.1	4,293.9	2,499,464	0.264
Sablefish	49	7	6.3	2,455.6	8,175,541	1.510
Shortraker/rougheye	46	15[a]	0.6	231.9	60,677	0.119
Thornyhead	49	15[a]	0.7	290.7	309,481	0.483

[a]Retainable percentage is combined limit on shortraker/rougheye and thornyheads.
Source: NPFMC Rockfish Database, Version 1.

spine thornyheads by the rockfish fisheries during the qualifying years was approximately 25% of the Central Gulf total catch, while incidental catch of shortraker/rougheye (under a combined TAC) was over half of the total harvest from the Central Gulf (NPFMC/NMFS 2005).

Rockfish fishery participants gain substantial revenues from incidental catch species. In the catcher processor sector, all target rockfish production is whole and headed and gutted fish, as most vessels in the fishery are not equipped to produce more processed outputs (such as fillets). Most, if not all, of this product is delivered to Asia, where the whole fish are typically sold into the local market and the headed and gutted products are generally reprocessed into other products, including fillets. An increasing portion of this reprocessed product is returned to U.S. markets. Average product prices of the incidental catch species are all more than double the average product price of the different target rockfish products, while sablefish product prices average seven times the highest rockfish product price. In general, fish are processed by catcher processors soon after they are caught both to maintain high quality and to accommodate additional catch. Catcher vessels also receive substantial revenues from incidental catch species (Table 4). Catcher vessel revenues from sablefish exceed those from all three target rockfish species combined, and Pacific cod revenues are larger than revenues from northern rockfish and pelagic shelf rockfish combined, but slightly less than revenues from Pacific ocean perch.

Ex vessel prices are negotiated informally by the rockfish fleet in the preseason. Fishermen often contact processors in the preseason to inquire about pricing for the season and delivery scheduling. A processor typically offers a common price to all of its fleet members. Fishermen often communicate with each other concerning processor price offers, but most perceive that little negotiating leverage exists. Usually fishermen will remain with their primary processor throughout the season delivering on a rotation, keeping trips shorter than 72 hours, to maintain product quality. Fishermen typically do not receive payment for low quality fish that cannot be marketed (except as meal). At times, fishermen will move to another processor for a delivery midseason. These movements are typically made to avoid loss of quality because of a wait to offload, and at times are facilitated by the processors. Occasionally, post-season bonuses are paid by processors in response to good market prices for products or prices of competing processors.

Incidental catch species (particularly Pacific cod and sablefish) are an important part of pricing in the rockfish fisheries. Fishermen typically inquire about the price of these incidental catch species with processors in the preseason. Prices of Pacific cod are typically based on the price from the directed Pacific cod fishery earlier in the year, with a possible downward adjustment for the absence of milt and roe and the lower quality observed in the summer months, when the rockfish fishery

is prosecuted. Sablefish prices are based on prices in the hook-and-line IFQ fishery, with some downward adjustment for lower quality found in the rockfish trawl fishery. Rockfish fishermen typically separate incidental catch species from target rockfish, in particular, sablefish, which is often stored in iced totes to maintain quality.

Quality of target rockfish is difficult to maintain because of the race to harvest. Harvesters who try to maximize catch in a tow are likely to stuff their nets, which can reduce fish quality. In addition, rockfish are relatively difficult to handle because of scales, spines, and baratrauma (i.e., bloating that occurs from their air bladders exploding when they are brought to the surface quickly). Pacific cod are usually bled after they are caught. Sablefish are usually bled and sometimes are headed and gutted. Since both species bring a substantially higher price than the target rockfish and are priced based on quality, fishermen give extra attention to their care. Shortraker and rougheye rockfish and shortspine thornyheads also bring a premium price, but are caught in substantially lower quantities than Pacific cod and sablefish and therefore receive less attention.

Shore-based processors make a variety of products from rockfish (Table 5). Most of the catch is processed into whole and headed and gutted products, which sell for substantially less than fillets. A portion of the catch is processed into surimi. Since whole and headed and gutted products have substantially higher recovery rates (i.e., the amount of product recovered from the processing of a pound of round fish) than fillets, the return per pound of raw fish from fillet production is substantially higher than for whole and headed and gutted products (Crapo et al. 2004, for examples of standard recovery rates). The relatively high price for pelagic shelf rockfish is likely because of the contribution of the non-trawl fleet, which has some substantial catch of the nearshore pelagic shelf rockfish species (i.e., black rockfish [*Sebastes melanops*] and blue rockfish [*Sebastes mystinus*]) that are not included in this program, but cannot be separated in the production data.

Pilot program management

The pilot program will establish two related management programs for the two sectors participating in the rockfish fisheries (i.e., the catcher vessel sector and the catcher processor sector). The TACs of the target rockfish species will be split between the two sectors based on their respective historic catch. Two set-asides totaling 5% of the target rockfish TACs (mandated by Congress) will be made prior to splitting the rockfish TACs between the sectors. The first is intended to support incidental catch of rockfish in other fisheries; the second is intended to support a small entry level fishery for persons not eligible for the program. In addition, each sector is allocated the important incidental

Table 5. Production, revenues, and average prices of rockfish by shore-based processors in the central Gulf of Alaska rockfish fishery (1996-2002).

	Fillets				Surimi				Whole and head & gut			
Species	Number of processors	Pounds of product	First wholesale revenues ($)	Average price ($/lb)	Number of processors	Pounds of product	First wholesale revenues ($)	Average price	Number of processors	Pounds of product	First wholesale revenues ($)	Average price ($/lb)
Pacific ocean perch	8	4,997,971	7,823,210	1.565	4	3,525,587	2,310,370	0.655	10	7,670,954	2,437,360	0.318
Northern rockfish	7	2,049,212	3,132,966	1.529	2	a	a	a	7	3,184,011	920,369	0.289
Pelagic shelf rockfish	10	1,533,828	2,301,611	1.501	1	a	a	a	13	2,684,097	2,012,966	0.750

[a]Withheld for confidentiality.
Source: Commercial Operators Annual Reports.
Note: Includes all catch of these species in the central Gulf of Alaska. Production exclusively from target fishery is unavailable.

catch species (i.e., sablefish, Pacific cod, and shortraker and rougheye rockfish and shortspine thornyheads) based on the historic harvests of the sector. Each sector is also allocated Pacific halibut PSC based on historic catch of Pacific halibut in the target rockfish fisheries. Two exceptions are that Pacific cod will not be allocated to catcher processors and shortraker and rougheye rockfish will not be allocated to catcher vessels, but will instead by managed under MRAs. These species are not allocated in the different cases because the sector has limited catch of the species, which could lead to allocations inadequate to support catch of target rockfish.

Under the program, participants in each sector can either fish as part of a cooperative or in a competitive, limited access fishery. Each cooperative will receive allocations of target rockfish, incidental catch species, and Pacific halibut PSC from the sector's allocation based on the target rockfish catch histories of its members. The limited access fishery will receive an allocation based on the target rockfish catch histories of sector members that choose not to join a cooperative. Cooperatives are intended to manage and coordinate fishing of their allocations. Target rockfish and allocated incidental catch species would be subject to a full retention requirement to minimize discards. All allocations to a cooperative would be constraining, so a cooperative will need to manage and monitor members' catch of target rockfish, incidental catch species, and Pacific halibut PSC to ensure that it is able to fully harvest (but not overharvest) its allocation of retainable species. To protect processors, each catcher vessel would be eligible for a single cooperative, which must form an association with the processor that it delivered the most rockfish to historically. This cooperative/processor association is intended to ensure that a cooperative lands a substantial portion of its catch with its associated processor. The exact terms of the association will be subject to negotiation, but since the cooperative agreement requires the approval of the associated processor, it will likely bind the cooperative to land a substantial portion of its catch with the processor.

The fishing season for cooperatives would be extended substantially beyond the current season, opening of May 1 and extending until November 15. The limited access fishery would open at the beginning of July and would close when its participants have fully harvested the allocation in that fishery. The limited access fishery would be managed under rules similar to the current fishery, but MRAs for incidental catch species (sablefish, Pacific cod, and shortraker and rougheye rockfish, and shortspine thornyheads) would be reduced from current levels to maintain catch levels below the allocated amount.

Fishing practices under the pilot program

Historic harvests of Central Gulf rockfish are used to make allocations under the pilot program alternatives, so distribution of Central Gulf

rockfish allocations both to and within the different sectors will be similar to the historic distribution of harvests during the qualifying years. The number of persons receiving allocations is approximately twice the average annual participation in the catcher processor fleet, and approximately 50% greater than the average annual participation in the catcher vessel fleet, showing that some participants have moved in and out of the fisheries over time.

Most catcher vessel participants are likely to join a cooperative, since the opportunity in a cooperative is likely to be better than the opportunity in the limited access fishery. Each catcher vessel will be eligible for only one cooperative, which must associate with a particular processor. Given the required processor association, it is likely that each cooperative will have limited latitude to pursue markets for their landings beyond the single associated processor. This limitation could discourage some catcher vessels from joining the cooperative fishery, if the cooperative agreement or price offer from the processor is viewed as unfair. Cooperative membership, however, is likely to be favored because of the relatively poor opportunity in the limited access fishery, which is subject to a race for fish with reduced MRAs for the valuable incidental catch species to maintain historic catch rates of those species. While it is possible that some processors may choose to exploit the bargaining power that this structure provides, since the program is limited to two years, processors who wish to maintain long-term relationships and do not wish to lose political capital in development of future programs could see a long run benefit to offering harvesters reasonable terms.

Within each cooperative, it may be anticipated that each member would receive revenues based on the catch history (or allocation) that the person brings to the cooperative, with participants that fish shares that others have brought to the cooperative receiving additional compensation for their fishing effort. Fishing within a cooperative could be far more consolidated than the underlying allocations. To save on observer coverage and operational costs, it is likely that most cooperatives will consolidate harvests to some extent, removing some vessels from the rockfish fisheries. Participants in fisheries under shared-based management often consolidate to save on operating costs (NRC 1999, Sigler and Lunsford 2001). Since the rockfish fishery is a relatively small part of the fishing for which these vessels are used, few vessels are likely to be retired altogether. Instead, vessels will be used in other fisheries (to the extent permitted by limitations intended to protect participants in those other fisheries) or idled, possibly for maintenance, during the traditional rockfish season.

The two most pronounced differences in fishing practices that are likely under the pilot program are the spatial and temporal distribution of catch. Because the programs allocate cooperative fishing privi-

leges that may be fished during an extended season, participants in the program are likely to slow their rate of harvest and distribute that harvest over greater time and a larger area. Changes in activities across the two sectors are likely to differ somewhat because of operational requirements. Catcher vessels have typically been limited in the spatial range of fishing activity by processor demands for quality of product. Rockfish fishing trips usually last less than 72 hours. As participants in the pilot program alternatives strive to improve quality of landings, it is possible that fishing trip lengths could shorten slightly. To allow for short trips, catcher vessel fishing is still likely to be concentrated in areas in relatively close proximity to Kodiak, where all of the qualified processors are located. Catcher processors, on the other hand, are not constrained by shore-based processing, and may distribute their catch over larger areas of the grounds. The extent of this distribution of catch could be limited, if catcher processors perceive a cost reduction benefit from concentrating catch in one area. If catch is consolidated onto a few catcher processors, temporal concentration of catch is more likely.

Both sectors should distribute catch over extended time periods as allowed by the longer season. The extent to which catch is temporally distributed depends on potential revenues, operational needs of participants, and catch rates. For instance, catch may be distributed throughout the season (by catcher vessels particularly) to develop alternative markets for fresh fish. One of the primary benefits of introduction of an individual vessel quota in British Columbia Pacific halibut fishery and an IFQ program in Alaska's Pacific halibut fishery was the development of fresh markets for catch from those fisheries (Casey et al. 1995, NRC 1999). While a similar outcome could occur in the rockfish fisheries, development of fresh rockfish products could be more challenging, as most processing occurs in Kodiak, which is less accessible than most ports that produce fresh Pacific halibut.

Catcher processors may have less incentive to fish outside of the summer months than catcher vessels, as most produce only frozen headed and gutted and whole products and are less likely to attempt to serve fresh fish markets that are more accessible to the shore-based fleet. Operationally, most participants are likely to schedule rockfish fishing to avoid conflicts with their participation in other fisheries. At a minimum, one would expect substantial fishing to occur prior to or following the traditional July season to allow participants to fish in other July fisheries. "Sideboard" limitations are incorporated into the program to prevent participants from increasing effort beyond their historic levels in fisheries other than the Central Gulf rockfish fisheries. These sideboards will not prevent participants in the rockfish pilot program from maintaining their historic participation levels in those other fisheries.

Catch rates could also influence the temporal distribution of fishing for both sectors. Low catch rates of rockfish or high catch rates of incidental catch species or Pacific halibut could also lead a cooperative to change its timing of rockfish targeting. Some longtime participants in the fishery suggest that rockfish aggregations are at their greatest in the summer months. If participants observe relatively high rockfish aggregations (and catch rates) in summer months, it is likely that their harvests will be concentrated in the summer regardless of the extended season. Bycatch considerations could also affect the temporal distribution of fishing effort. Participating fishermen will be strictly limited by allocations of the target rockfish species, incidental species allocations, and Pacific halibut PSC. All of the allocations are based on historic catch that occurred in the traditional July season. Full harvest of these allocations could be challenging, if catch composition changes substantially outside of the traditional July season. One reason that the current limited access opening has been scheduled for early July is to avoid Pacific halibut bycatch. The extent to which participants will be able to harvest rockfish at other times and avoid Pacific halibut cannot be predicted. If participants find that Pacific halibut bycatch is relatively high outside of the traditional season, they are likely to restrict their fishing to times when Pacific halibut bycatch rates are low. Anticipating potential bycatch issues, some participants that use bottom trawl gear have suggested that they intend to experiment with pelagic gear and other gear modifications in an attempt to reduce Pacific halibut bycatch. If successful, these changes in effort could allow for greater distribution of catch across the extended season.

Production from the fisheries under the pilot program

The effects of the pilot program on fishery product outputs are likely to vary across the two sectors. Processing by catcher processors is likely to remain similar to the current processing by that sector. Most vessels in the sector are equipped for producing a few simple products (frozen whole and headed and gutted fish). Because of vessel size and regulatory limitations, few of these vessels are likely to change plant configurations to process higher-valued, more highly processed products. Quality could improve somewhat under the new program, as vessels are under less pressure to harvest fish rapidly to protect their share of the fishery. Instead, participants may slow their rate of harvest to reduce the time between when catch is brought on-board and when that catch is processed. Trends in the distribution of products are unlikely to change.

Processing of shore-based plants under the pilot program can be expected to change substantially, through several related factors. Catcher vessel cooperatives provide a structure for coordination of harvest activity and timing of landings similar to that observed under the American Fisheries Act (AFA) cooperatives in the Bering Sea pollock

fishery (see Matulich et al. 2001 for a discussion of AFA cooperatives and a discussion of some of these effects). Catcher vessels can use the cooperative structure to time landings to accommodate processing schedules and market demands, spreading landings over the longer season. While processing employment during the season peak may decline, employment should be more stable with the scheduling of landings. Coordination of landings could also be critical to maintaining quality, as product quality can decline if fish remain in the hold for extended periods of time. Most participants may be expected to choose to sacrifice some cost efficiencies (i.e., use more inputs such as fuel) to improve quality of deliveries and time those deliveries for specific markets. This trade-off may increase costs, but should result in improvements in overall returns.

Distribution of landings over a longer period should also contribute to improved quality of production, since processors are under less pressure to process large quantities in a short period of time to secure market share. A larger portion of the catch should be processed into fillets, rather than whole or headed and gutted products or surimi. Timing of landings could also be important to processors that attempt to serve time-sensitive markets. Processors participating in the program have expressed an interest in serving fresh markets in the United States that are currently experiencing a decline in rockfish products due to restrictions in fisheries off the West Coast of the contiguous United States. Distributing landings temporally will be critical to serving those fresh markets. These changes in landings should allow processor practices to evolve to serve higher value and higher quality markets.

Some processors may respond differently to the change in management. While product differentiation and pursuit of different markets can benefit both consumers and producers, the program structure may not compel some processors to aggressively pursue market opportunities. Since catcher vessels are eligible for a single cooperative associated with a specific processor, processors are likely to compete for landings only at the time of cooperative formation, which requires processor approval. This limit on the competition for landings from the fishery could reduce processor competition in output markets. For example, Anderson (2002) was critical of the less restrictive system of cooperative/processor associations created in the Bering Sea pollock fishery for its potential to decrease efficiency. While some processors may pursue any available markets, others may have less interest in extracting maximum revenues from rockfish landings, particularly if those landings interfere with their operations in other fisheries. So, while processing should expand to higher value and higher quality products, it is possible that some processors may be less aggressive in challenging high revenue markets.

Conclusion

In recent years, management of the Central Gulf rockfish fisheries with limited licensing has resulted in a race-for-fish. The race is evident in that the TAC is usually caught in the fishery over the span of a few weeks by license holders competing for a share of the catch. Some predictable (and typical) effects of this management are that participants' costs of harvesting and processing are increased as effort choices that increase catch and processing rates. Quality and value of products from the fishery also suffer (less so in the catcher processor sector where catch is typically processed shortly after it is brought on-board). In addition to these expected effects, a few less predictable effects are evident. Participants in the rockfish fisheries have typically derived a substantial share of their revenues from the harvest of valuable incidental catch species (most importantly sablefish, Pacific cod, and shortraker and rougheye rockfish and shortspine thornyheads). The current management limits retention of these species to a percentage of the target catch. In response, rockfish fishermen focus efforts on increasing quantities of rockfish catch giving minimal attention to quality. "Top off" harvests of the permitted incidental catch species are usually subject to greater care in handling to maintain higher quality.

The exclusive allocations in the pilot program, together with an extended 6.5 month season, will allow participants to refocus their efforts to maximize returns from the fishery, by making production choices that improve revenues and minimize harvest and processing costs. Allocations of directed rockfish and most of the valuable incidental catch species are included in the program. Full retention of allocated species is required, with all allocations binding to reduce discards. For catcher processors, most improvement will from reduced costs of catching and processing fish. Most vessels in the sector produce relatively high quality products and are limited by vessel and regulatory constraints from changing product forms. The catcher vessel/inshore processing sector, however, should have opportunities to change product forms while minimizing harvest and production costs. While some improvements in production from incidental catch species are possible, a large change can be expected in production of target rockfish species. Some participants have expressed interest in providing target rockfish to fresh fillet markets, previously inaccessible because of the short season and relatively unreliable quality. The program should provide additional experience and information to both regulators and participants in the fishing and processing sectors concerning the potential improvements in returns from fisheries under share-based management.

Acknowledgments

Much of the description of fishing activities in this paper is derived from conversations with participants in the subject fisheries. Several industry members and their representatives were consulted including Doug Hodel, Jay Stinson, Al Burch, Matt Moir, Joe Plesha, Tim Blott, Julie Bonney, Lori Swanson, Teresa Kandianis, Susan Robinson, and several others. Special thanks to Elaine Dinneford, Cathy Coon, and Jim Richardson, staff of the North Pacific Fishery Management Council, for assistance. Comments by Jon Heifetz and two anonymous reviewers are gratefully appreciated. Any errors, and the opinions, in this paper are those of the author.

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Past, Current, and Future Management of Commercial Fisheries for Black Rockfish in the Kodiak Management Area

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Abstract

Commercial harvest of black rockfish, *Sebastes melanops*, in the Kodiak Management Area located in the central Gulf of Alaska began in the early 1990s. Prior to 1997, the National Marine Fisheries Service (NMFS) managed black rockfish within the Exclusive Economic Zone (EEZ) as part of the pelagic shelf rockfish group that included dusky rockfish *S. variabilis*, yellowtail rockfish *S. flavidus*, and widow rockfish *S. entomelas*. Biomass of the pelagic shelf rockfish group was estimated by the annual NMFS survey, and annual quotas were set for the entire group. The majority of the biomass for the group was composed of dusky rockfish. When a directed commercial fishery developed for black rockfish, a large portion of the harvest of the pelagic shelf rockfish group became composed of black rockfish, and the Alaska Department of Fish and Game (ADFG) was concerned with harvest levels. While black rockfish predominately occur inside state waters of Alaska, misreporting of harvest from adjacent federal waters was common. In 1997, as a protective measure, the North Pacific Fishery Management Council (NPFMC) separated black rockfish from the pelagic shelf rockfish group within its Gulf of Alaska groundfish fishery management plan (GOA FMP). In 1998, the NPFMC removed black rockfish from the GOA FMP and ADFG's management authority was extended from 3 miles to the offshore boundary of the EEZ.

In order to distribute effort, ADFG established guideline harvest levels for seven districts in the Kodiak Management Area. Quotas within management districts were monitored through landings reported by statistical areas. Black rockfish populations appear stable; however, due

to the sensitivity of this species to overexploitation and lack of population assessment, ADFG proposed a mandatory logbook requirement that was adopted during the January 2005 Alaska Board of Fisheries meeting. Logbook data provide more resolution on fishing locations than from statistical areas. Possible future management based on logbook data is discussed.

Introduction

The primary focus of this paper is the black rockfish *Sebastes melanops* commercial fishery in the Kodiak Management Area. Black rockfish (sometimes called black bass) have been commercially and sport harvested off the West Coast of the United States since the 1940s (Parker et al. 2000). A directed black rockfish commercial fishery on a relatively unexploited population has occurred in the Gulf of Alaska since 1990 (Mattes and Failor-Rounds 2005). Substantial declines in many rockfish populations have been observed off the coast of California, Oregon, and Washington (Ralston 1998, Parker et al. 2000). In particular, black rockfish populations in Oregon and Washington have been in a general state of decline since 1970 (Ralston 1998).

The American Fisheries Society (AFS), in response to concerns over rockfish management, developed a policy statement for the management of Pacific rockfishes in 2000 (Parker et al. 2000). This policy statement stressed the importance of conservative rockfish management because of the low population rebound potential of Pacific rockfish. The Alaska Department of Fish and Game (ADFG) is attempting to be proactive in the management of black rockfish in the Kodiak Management Area, by managing smaller areas (e.g., seven separate management units around Kodiak Island) and collecting detailed information from the fishing fleet. We review black rockfish biology, development of the Kodiak black rockfish fishery, current management of the Kodiak fishery, and ideas for the future management in the Gulf of Alaska.

Black rockfish biology

Black rockfish are common from Southeast Alaska to northern California; however, they can occur from Amchitka Island in the central Aleutian Islands to Baja California (Kramer and O'Connell 2003, Love et al. 2002, Mecklenburg et al. 2002). Black rockfish occur at depths 0-366 m, but they are most common in shallower waters, less than 55 m (Kramer and O'Connell 2003).

Black rockfish are long-lived, and moderately fecund with a long reproductive lifespan (Love et al. 2002). Black rockfish can live to 50 years of age (Meyer 2000), and grow to 690 mm in length and 5 kg in weight; females grow larger than males (Love et al. 2002). In a study off

of the Oregon coast, Bobko and Berkeley (2004) found that the smallest mature female was 345 mm, and all females were mature by 450 mm. This study estimated the age at maturity for females to be 7.5 years of age. Off of Alaska, black rockfish have been reported to be 50% mature at 380-420 mm and 6-8 years of age (Love et al. 2002). The rate of growth during their first few years is quite variable depending on oceanographic conditions and food availability. Therefore, young fish can be as large as or larger than much older fish (Bobko and Berkeley 2004).

The longevity and late age at maturity are presumed to be adaptations to allow successful reproduction over the lifespan despite long periods between favorable environmental conditions (Leaman and Beamish 1984, Berkeley et al. 2004, Bobko and Berkeley 2004). These factors make black rockfish more susceptible to overexploitation from fisheries that selectively remove older, more fecund individuals from the population (Berkeley et al. 2004, Bobko and Berkeley 2004). For example, Ralston (1998) found that the total biomass of age 4+ black rockfish in Oregon and Washington had declined to 68% of its apex between 1970 and 1994 as a result of commercial and sport harvest. During that time period, reproductive output had fallen even more, to 48% of the maximum. Absolute and relative fecundity increased with age for female black rockfish in Oregon waters; although, there was a great deal of variation not accounted for by age (Bobko and Berkeley 2004).

After maturity, energy is used more for reproduction than growth. Black rockfish, like all rockfish, have internal fertilization and bear live young. Females retain the embryos for 4-5 weeks until hatching (Boehlert and Yoklavich 1984). Parturition generally occurs in spring or summer off of Alaska (O'Connell 1987). Females release larvae with an oil globule attached. Older female black rockfish provide larvae with significantly larger oil globules than younger females, and the size of the oil globule appears to strongly affect larval growth and survival (Berkeley et al. 2004). Larvae are pelagic, usually found offshore in the upper-mixed zone, and capable of feeding immediately after birth (Larson et al. 1994). Juveniles remain pelagic and move inshore to intertidal and estuarine areas at age 4-6 months (Love et al. 2002). Love et al. (2002) found that juveniles and subadults in Southeast Alaska were abundant in shallow water during the summer and retreated to deeper water later in the year. Black rockfish inhabit deeper water as they grow and form mixed-age schools near bottom structure, high- and low-relief rocky terrain, often along steep dropoffs, and in high current areas (Love et al. 2002, Johnson et al. 2003). Black rockfish have been known to school with other midwater rockfish species, such as yellowtail *S. flavidus*, widow *S. entomelas,* and dark rockfish *S. ciliatus* (Johnson et al. 2003).

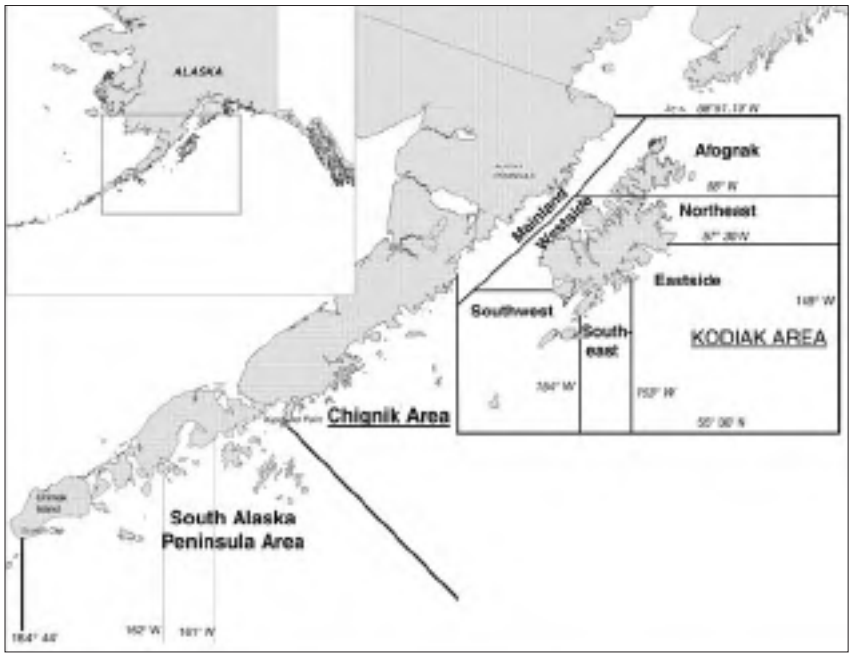


Figure 1. The Alaska Department of Fish and Game manages black rockfish fisheries in three areas of the Westward Region: Kodiak, Chignik, and the South Alaska Peninsula Area-Eastern District.

Tagging studies have shown that black rockfish have small home ranges. Ayers (1988) and Culver (1987) found that most tagged fish did not move more than 10 miles. Some fish moved among and within rock outcroppings, usually during the day, retreating to cover at night. During at least part of the year, females may be more abundant than males in offshore areas. However, it is unknown whether a large number of black rockfish make spawning migrations (Love et al. 2002).

Black rockfish feed opportunistically, primarily in the water column on a variety of fish and zooplankton (Love et al. 2002). Occasionally, they feed on various benthic crustaceans and octopus (Love et al. 2002). Black rockfish engage in feeding frenzies at or near the surface, usually near kelp beds. They appear to feed on small fishes such as herring *Clupea pallasii* and sandlance *Ammodytes hexapterus*, or concentrations of Dungeness crab *Cancer magister* larvae (Love et al. 2002, Mecklenburg et al. 2002, Johnson et al. 2003). Known predators on black rockfish include king salmon *Oncorhynchus tshawytscha,* lingcod *Ophiodon elongata*, and pigeon guillemots *Cepphus columba*, especially on young rockfish (Hobson et al. 2001).

Table 1. Catch and effort in the Kodiak Management Area black rockfish fisheries, 1990-2004.

Year	Vessels	Landings	Directed GHL (t)	Total harvest (t)	Price per kg
1990	12	na	na	30.3	$0.10
1991	58	na	na	394.0	$0.13
1992	45	na	na	221.0	$0.11
1993	18	na	na	48.9	$0.10
1994	19	na	na	58.3	$0.11
1995	41	na	na	143.2	$0.16
1996	52	na	na	141.5	$0.15
1997	65	na	na	101.6	$0.12
1998	74	277	86	90.8	$0.15
1999	92	320	84	61.5	$0.18
2000	95	346	84	116.2	$0.19
2001	55	236	84	102.5	$0.18
2002	26	121	84	92.8	$0.20
2003	50	108	79	38.7	$0.16
2004	45	166	79	56.1	$0.15

na = not available

Study area

ADFG manages black rockfish fisheries in three areas of the Westward Region: Kodiak, Chignik, and the South Alaska Peninsula Area-Eastern District (Fig. 1). The Kodiak Management Area consists of all waters of Alaska south of a line extending east from Cape Douglas (58º51.10'N), west of 149ºW, north of 55º30.00'N, and east of a line extending south from the southern entrance of Imuya Bay near Kilokak Rocks (156º20.22'W).

Directed commercial fishery

Black rockfish were of low market interest and generally not harvested in the Kodiak Management Area until 1990. The catch jumped from 30 t in 1990 to 394 t in 1991 as fishermen targeted populations that had only been lightly exploited (Table 1). Fishermen primarily used jig gear to target black rockfish but some bycatch occurred in longline and trawl gear in other directed fisheries. Production was concentrated in areas easily accessible to the city of Kodiak. Harvest fell sharply in 1992 and 1993 in areas that had been previously exploited (Fig. 2). Harvests increased again in 1995-1996 (Table 1 and Fig. 2).

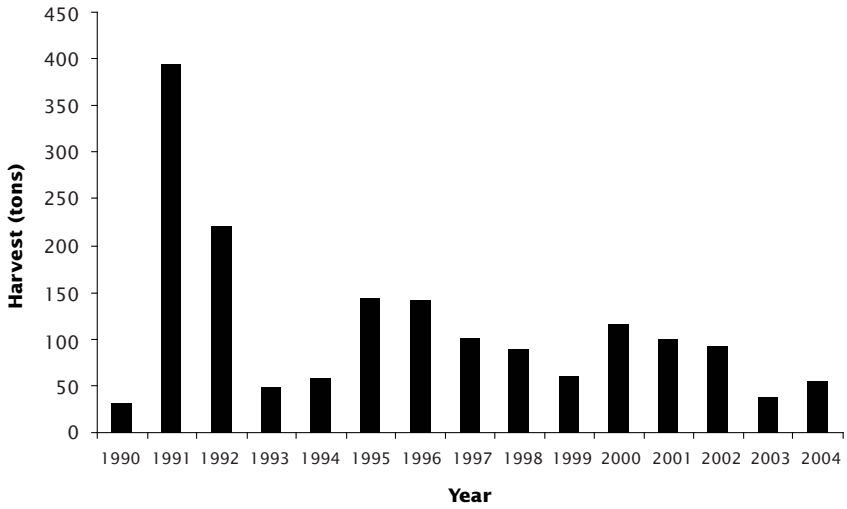


Figure 2. Black rockfish commercial harvest from the Kodiak Management Area, 1990-2004.

Commercial fishery management

Prior to 1997 black rockfish were managed by ADFG within state waters (0-3 miles) and by the National Marine Fisheries Service (NMFS) in the Exclusive Economic Zone (EEZ). Because there was only minor commercial harvest in state waters, ADFG adopted the same management measures in state waters that NMFS employed in federal waters. NMFS managed black rockfish as part of the pelagic shelf rockfish (PSR) group that included dusky rockfish *S. variabilis*, yellowtail rockfish *S. flavidus*, and widow rockfish *S. entomelas*. However, the majority of the PSR biomass was dusky rockfish. As markets developed for black rockfish, effort increased rapidly. In the mid-1990s a large percentage of the PSR total harvest was composed of black rockfish despite quotas being based on the larger biomass of dusky rockfish. ADFG implemented guideline harvest levels (GHLs) for state waters, but frequent misreporting of harvest from adjacent federal waters made management difficult. As an interim measure, the NPFMC separated black rockfish from the PSR group in 1997. This action enabled federal fishery managers to place a separate 260 t acceptable biological catch (ABC) on black rockfish in the central Gulf of Alaska. This ABC was based on 75% of the average production from 1978 to 1995, using the council's Tier 6 guideline, which applies to fisheries with little stock assessment information (Clausen and Heifetz 1997, DiCosimo et al. 2005). ADFG requested the

North Pacific Fishery Management Council (NPFMC) to amend its Gulf of Alaska groundfish fishery management plan (GOA FMP) to relinquish black rockfish management in the EEZ in the Gulf of Alaska to the State of Alaska. The FMP amendment to relinquish authority to the State of Alaska was effective April 5, 1998, giving full management authority of black rockfish from 3 to 200 miles to the State of Alaska.

After the State of Alaska gained full management authority of the black rockfish resource, ADFG developed management plans that included GHLs and vessel registration. GHLs for Kodiak and Chignik management areas were based on NMFS Tier 6 guidelines. The difference between the NMFS and ADFG guidelines was that NMFS had established an ABC for the entire Gulf of Alaska whereas ADFG separated the harvest guidelines among areas within the Gulf of Alaska. Assigning GHLs to state management areas was aimed at distributing the fishing effort and avoiding localized fishing pressure that could cause long-term harm to the stocks (Jackson and Ruccio 1998). In 1997, the total directed harvest GHL for the Kodiak Management Area was set at 77 t. The GHL was further divided among four districts: three that encompassed the areas of historic harvest and one additional district for the remainder of the Kodiak Management Area with a low GHL to allow for exploration.

Recent fishery and management

In 1998, the Kodiak Management Area was further subdivided into seven districts with separate GHLs (Fig. 1) in an effort to disperse harvest and effort. The fleet was small, but highly effective at fishing black rockfish. Individual vessels were capable of harvesting over 4 t of black rockfish in 2-3 days of fishing. Despite distributing fishing effort, the Kodiak Management Area-wide GHL during 1998 to 2002 was exceeded in four out of five years and district GHLs were exceeded up to 38%. Compounding the difficulty in managing the fishery, vessels were allowed by regulation to simultaneously target Pacific cod or rockfish, making it difficult to estimate directed effort in-season.

In 2001, several ADFG proposals were adopted by the Alaska Board of Fisheries[1] (BOF) to help rectify this situation: black rockfish registration and trip limits. The black rockfish registration required vessel operators to specifically register for black rockfish in the Kodiak Management Area. In addition, vessel operators could not simultaneously hold another groundfish registration. Vessel maximum trip limits of 2.27 t (5,000 pounds) per vessel in a five day period were also imposed to slow the harvest rate. Both of these measures greatly slowed

[1]The Alaska Board of Fisheries (BOF) is composed of seven members appointed by the Governor for the purposes of conservation and development of fishery resources. The BOF has the power to adopt regulations affecting the utilization of fishery resources in accordance with AS 44.62 (Administrative Procedures Act).

Table 2. GHLs, harvest, and closure dates for the Kodiak Management Area by district, 2001-2004.

	GHL (t)	Total harvest (t)	Closure date	GHL (t)	Total harvest (t)	Closure date
	2001			2002		
Afognak	15.9	15.0	20-Mar	15.9	24.4	16-Apr
Northeast	9.1	10.8	23-Feb	9.1	17.2	2-Apr
Eastside	13.6	19.5	6-Mar	13.6	15.8	21-Mar
Southeast	13.6	25.5	19-Mar	13.6	13.2	2-Apr
Southwest	9.1	5.4	29-Mar	9.1	9.8	7-Jun
Westside	13.6	12.9	30-Jul	13.6	9.3	31-Dec
Mainland	9.1	13.2	22-May	9.1	2.2	31-Dec
Total	83.9	102.5		83.9	91.9	
	2003			2004		
Afognak	15.9	11.1	31-Dec	15.9	17.2	24-Jun
Northeast	9.1	11.2	16-May	9.1	10.3	29-Jun
Eastside	13.6	9.7	31-Dec	13.6	14.1	10-Jul
Southeast	13.6	6.7	31-Dec	13.6	14.5	31-Aug
Southwest	9.1	0.0[a]	31-Dec	9.1	0.3	31-Dec
Westside	9.1	0.0[a]	31-Dec	9.1	0.0	31-Dec
Mainland	9.1	0.0[a]	31-Dec	9.1	0.0[a]	31-Dec
Total	79.4	38.7		79.4	56.5	

[a]Less than 1 kg was harvested in these sections, but harvest is included in the total.

the fishery and maintained black rockfish harvests below GHLs (Table 2). ADFG adopted a voluntary logbook program in 2004 that was made mandatory by the BOF in 2005. Logbooks allow ADFG to gather harvest data on a finer scale than afforded by statistical reporting areas (Fig. 3).

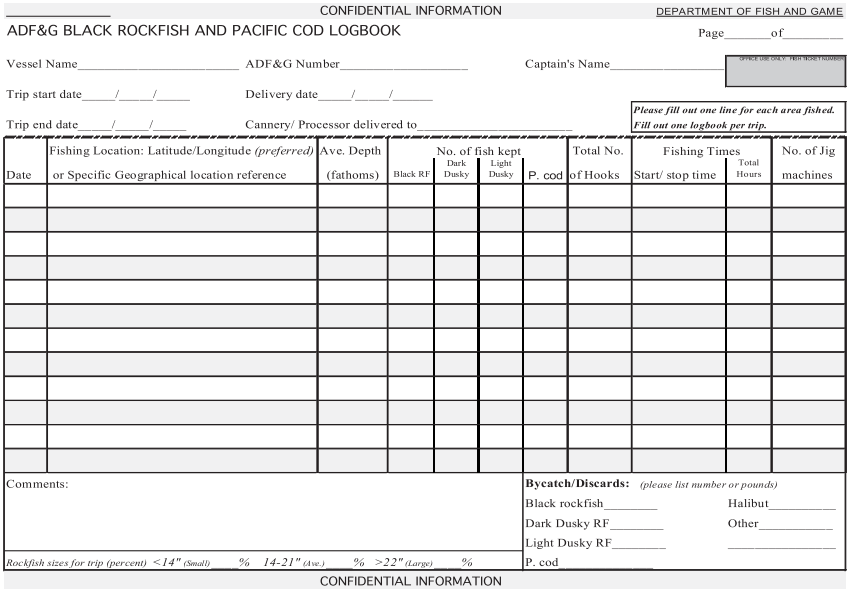
New approaches to black rockfish management in the Kodiak Management Area

The standard management scheme for black rockfish off the U.S. West Coast has been to manage for a fishing mortality of *F40%*, as a rate that will approach the maximum sustainable yield (Parker et al. 2000). This rate is defined as the fishing mortality that reduces the spawning potential per recruit to 40% of the unfished population (Clark 1993). Even with low harvest rates, rockfish require a spatial component to prevent localized depletion (Parker et al. 2000, O'Connell et al. 1999). Due to the small home range of black rockfish, localized depletions make it difficult for rockfish to replenish fished areas. In extreme cases,

this may eliminate some spawning populations (DiCosimo et al. 2005). Management should consider the magnitude of fishing mortality, and how the fishing mortality is distributed spatially and demographically (Parker et al. 2000). If stocks are managed on a geographic scale larger than that of their stock structure, loss of productivity can occur (DiCosimo et al. 2005). The American Fisheries Society policy statement on the management of Pacific rockfish (Parker et al. 2000) suggests a number of changes to current rockfish fisheries management. One recommendation was to collect species-specific information on age, maturity, fecundity, location, and conditions of capture. Parker et al. (2000) further stated, "baseline data collection on unexploited species should begin before major fisheries develop."

ADFG is beginning this process via dockside sampling, confidential vessel skipper interview forms, logbooks, fish tickets (landing receipts), and a nearshore marine research program. Dockside sampling provides age, length, maturity, and species composition data from harvested rockfish. These data are used to help evaluate population age structure and age and length at maturity. Skipper interviews provide data on effort at fishing location. While fishing locations are also recorded on fishtickets, information from interviews is considered more reliable because they are treated confidentially. Fishtickets provide harvest by statistical area, which are then corroborated with the skipper interviews. ADFG statistical areas are large (~900 square nautical miles), covering several bays, inlets, reefs, and rock pinnacles (Fig. 4). The logbook program was implemented, in part, to collect finer-scale spatial data on harvest location. Logbook information provides the latitude and longitude of harvest and includes information on depth, number of hooks used, and associated bycatch. These data are evaluated to determine whether fishing locations remain consistent within a season, whether fishing locations remain consistent among years, and whether fishing locations are consistent among fishermen.

The goal of these objectives is to determine whether fishing locations are geographically isolated and whether fishers are targeting specific locations and then moving when catch per unit effort declines. In addition, logbook data are evaluated to determine whether harvested black rockfish age classes are similar among fishing locations and whether ages of harvested black rockfish are similar among fishermen within a fishing location. More data is needed in order to investigate these objectives. However, preliminary analysis of the logbook data has shown spatial patterns in fishing locations of the fleet, and fishing locations among fishermen. Targeted fishing locations included rocky pinnacles and rocky exposed shorelines. Additionally, some areas are targeted by multiple fishermen, but other areas have only been targeted by a single person.



CONFIDENTIAL INFORMATION DEPARTMENT OF FISH AND GAME

ADF&G BLACK ROCKFISH AND PACIFIC COD LOGBOOK Page_____of_____

Vessel Name_____ ADF&G Number_____ Captain's Name_____ OFFICE USE ONLY: PATH ROSET NUMBER

Trip start date_____/_____/_____ Delivery date_____/_____/_____

Trip end date_____/_____/_____ Cannery/ Processor delivered to_____

Please fill out one line for each area fished. Fill out one logbook per trip.

Date	Fishing Location: Latitude/Longitude *(preferred)* or Specific Geographical location reference	Ave. Depth (fathoms)	No. of fish kept				Total No. of Hooks	Fishing Times		No. of Jig machines
			Black RF	Dark Dusky	Light Dusky	P. cod		Start/ stop time	Total Hours	

Comments:

Bycatch/Discards: *(please list number or pounds)*

Black rockfish_____ Halibut_____

Dark Dusky RF_____ Other_____

Light Dusky RF_____ _____

Rockfish sizes for trip (percent) <14" (Small)____% 14-21" (Ave.)____% >22" (Large)____%

P. cod_____

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Figure 3. Example of an ADFG black rockfish logbook.

Age and location information will allow better resolution of whether marine protected areas (MPA), a popular management element for many different species in areas along the West Coast of the United States, are useful for black rockfish in the Kodiak Management Area.

Nearshore marine research has focused on determining age at maturity for black rockfish in the Gulf of Alaska (Worton and Rosenkranz 2003) and developing hydroacoustic methods to assess population size (D. Urban, Alaska Department of Fish and Game, Kodiak, pers. comm.). Population assessment in conjunction with spatial harvest and effort data will provide better information on localized black rockfish populations.

Over time, these data will allow managers to track fishing patterns by individual fishermen and the fleet as a whole on a scale smaller than district or even statistical area, potentially to the bay, pinnacle, or rock outcropping. If specific bays, pinnacles or rock outcroppings are continually targeted by fishermen, managers will then have the necessary data to make decisions regarding the closure of specific locations to commercial fishing on a temporary, long-term, or rotating basis in an effort to distribute harvest and prevent localized temporal and spatial depletions of black rockfish. Conversely, data could show that fishing pressure and current guideline harvest levels might be lower than necessary, and restrictions or guidelines could be liberalized.



Figure 4. Statistical area chart of the Kodiak Management Area.

Acknowledgments

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A Management Strategy Evaluation of Rebuilding Revision Rules for Overfished Rockfish Stocks

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Abstract

Under the U.S. Sustainable Fisheries Act, Rebuilding Plans must be developed for overfished stocks. Rebuilding Plans typically include analyses to determine the minimum time to recover to B_{MSY} and the fishing mortality that is consistent with stock recovery within the required timeframe and with specified probability P_{MAX}. Seven rockfish stocks are currently under Rebuilding Plans adopted by the Pacific Fishery Management Council (PFMC). Progress toward meeting rebuilding objectives must be evaluated at least every second year, which could lead to changes to how these stocks are managed. Although a harvest control rule has been adopted by the PFMC for healthy stocks, and methods for conducting the initial analyses needed to develop Rebuilding Plans for overfished stocks are well established, there are presently no agreed upon methods ("Rebuilding Revision Rules") for (1) assessing adequacy of progress toward rebuilding and (2) altering Rebuilding Plans, given a change in stock status. To assist decision-making, we conducted a management strategy evaluation (MSE) to compare alternative Rebuilding Revision Rules using a suite of performance measures selected to quantify likely PFMC goals for rebuilding. The results of the MSE show that (1) adjustments to harvest rates occur often, (2) a policy that attempts to maintain the original P_{MAX} tends to be overly responsive to noise, and (3) setting P_{MAX} to a high value provides a buffer against uncertainty.

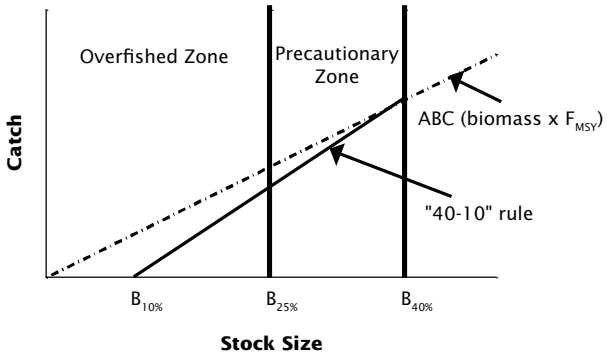


Figure 1. The 40-10 control rule used by the Pacific Fishery Management Council (PFMC).

Introduction

The Pacific Fishery Management Council (PFMC) Groundfish Management Plan (PFMC 2004) includes 82 species of roundfish, rockfish, and sharks, of which 62 are rockfish (*Sebastes* and *Sebastolobus* spp.). Under the U.S. Sustainable Fisheries Act, "Conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the OY [optimum yield] from each fishery for the U.S. fishing industry," while the Groundfish Fishery Management Plan includes the goal to "prevent overfishing and rebuild overfished stocks by managing for appropriate harvest levels and prevent, to the extent practicable, any net loss of habitat of living marine resources." In this paper "overfishing" means that the current fishing mortality rate exceeds that associated with obtaining maximum sustainable yield (MSY) and "being in an overfished state" means that the current spawning output is less than a minimum stock size threshold (MSST).

The scientific component of the management system for West Coast groundfish species involves conducting quantitative assessments to estimate stock status and fishing impacts relative to specified reference points and applying a control rule to determine harvest guidelines. The control rule (Fig. 1) involves calculating an allowable biological catch based on an estimate of F_{MSY}, the fishing mortality at which maximum sustainable yield is achieved, and reducing this catch if the stock size is estimated to be below the proxy for B_{MSY} (40% of the unfished spawning output, B_0). In practice, F_{MSY} for rockfish species is not estimated based on fitting a stock-recruitment relationship, but is instead set to a proxy fishing mortality rate equivalent to a spawning potential ratio (SPR) of 50% (Ralston 2002, PFMC 2004). Fishing mortality rate, F, is expressed

in terms of its effect on SPR (spawning output-per-recruit relative to that in an unfished state), because this standardizes for differences in growth, maturity, fecundity, natural mortality, and fishery selectivity patterns to some extent.

The MSST for groundfish species managed by the PFMC is $0.25B_0$. Stocks estimated to be below $0.25B_0$ have been designated by NOAA Fisheries to be "overfished," requiring the development of a Rebuilding Plan. The period for rebuilding is to be as short as practicable, taking into consideration the biology of the stock and the needs of the fishing community, and is not to exceed 10 years, unless the biology, environmental conditions, or other factors dictate otherwise. The technical requirements for a rebuilding analysis involve a sequence of calculations (Jacobson and Cadrin 2002). First, the minimum time for an overfished population to have a 50% probability of recovery to the proxy for B_{MSY} if there was no fishing in the future, T_{MIN}, is calculated. If T_{MIN} is greater than 10 years, as is the case for most rockfish, the technical guidance provided by NOAA Fisheries is that the rebuilding period should not exceed T_{MAX}, defined as T_{MIN} plus one mean generation time (i.e., the average age of the maternity function). Analysts then conduct projections based on a range of fishing mortality levels to determine the relationship between the probability of recovery to the proxy for B_{MSY} by T_{MAX} and the impact of rebuilding on catches and fishing mortality. Based on these, and other, considerations, the PFMC selects its intended probability of recovery to the proxy for B_{MSY} by T_{MAX} (P_{MAX}) and hence a target fishing mortality level (or SPR) and a target year for recovery. This year, referred to as T_{TARGET}, must lie between T_{MIN} and $T_{MAX,}$ and corresponds to the year in which recovery to 0.4 B_0 is predicted to occur with 50% probability

Seven rockfish species off the U.S. West Coast (bocaccio *Sebastes paucispinis*, cowcod *S. levis*, canary rockfish *S. pinniger*, darkblotched rockfish *S. crameri*, Pacific ocean perch *S. alutus*, widow rockfish *S. entomelas*, and yelloweye rockfish *S. ruberrimus*) are currently designated as overfished (see Table 1 for rebuilding parameter values). T_{TARGET} for these species ranges from 2023 (bocaccio) to 2090 (cowcod). The differences in T_{TARGET} among species reflects the PFMC's selected trade-off between the rate at which recovery occurs and the short- to medium-term impact of rebuilding on fishing communities. In general, the PFMC selected higher T_{TARGET}s for species for which management measures would have a larger impact on the catches of species that are not overfished, but are caught together with overfished species.

The need to satisfy the requirements for Rebuilding Plans leads to a substantial increase in the demands for technical analyses (Restrepo et al. 1999) and the results of rebuilding analyses, although considered to be the best available science, are nevertheless subject to considerable uncertainty (e.g., Punt 2003, Punt and Methot 2005). For example,

Table 1. Rebuilding parameter values for the seven overfished rockfish species.

Species	T_{MIN}	T_{MAX}	P_{MAX}	T_{TARGET}
Darkblotched rockfish	2014	2047	0.8	2030
Pacific ocean perch	2012	2042	0.7	2027
Canary rockfish	2057	2076	0.6	2074
Bocaccio	2018	2032	0.7	2023
Cowcod	2062	2099	0.6	2090
Widow rockfish	2026	2042	0.6	2038
Yelloweye rockfish	2027	2071	0.8	2058

forecasts of the future size of the darkblotched rockfish stock under the current Rebuilding Plan became markedly more optimistic following a change to the assumed value for the natural mortality rate (Rogers 2005).

It should be expected therefore that the results of rebuilding analyses in the future will not conform exactly with the expectations based on the original rebuilding analysis. The question that arises, then, is whether the fishing mortality rate used to set harvest guidelines specified as part of a Rebuilding Plan should be changed, and if so how? A further consideration is that data now available may show that the original basis for the Rebuilding Plan is no longer valid (e.g., because the values assumed for natural mortality or stock recruitment steepness have changed markedly). A second consideration is that councils are required to decide whether progress toward rebuilding is adequate no less frequently than every second year, although there is no formal definition of "adequate" at present, which precludes an objective evaluation of whether progress is acceptable.

This paper introduces the idea of "Rebuilding Revision Rules," i.e., extensions to the current control rules that measure progress toward rebuilding and make appropriate adjustments to Rebuilding Plans as needed. The study evaluates several candidate Rebuilding Revision Rules using an MSE framework (Smith 1994). The focus of our work is on the consequences of changes to assessments resulting from the analysis of new data; it being taken for granted that major changes to the stock assessment (e.g., a change to the stock structure assumption underlying the assessment) will lead to the need for revision to the Rebuilding Plan.

This paper is based on the guidelines for rebuilding in force when the analyses were conducted; these guidelines may have been revised somewhat since. Specifically, the analyses of this paper were conducted

before a court decision (Natural Resources Defense Council [NRDC] v. NMFS, 421 F.3d 872 [9th Cir. 2005]) based on a lawsuit originally filed in opposition to management measures for darkblotched rockfish was handed down. It seems likely that the way Rebuilding Plans are developed for overfished groundfish species will change in response to this court decision, but at present, what these changes will be is unknown. It seems likely, however, that the need for Rebuilding Plans, measuring progress toward rebuilding, and adjusting Rebuilding Plans in the light of new information will remain.

Methods

The MSE approach uses Monte Carlo simulation techniques to evaluate management strategies. In context of this paper, a management strategy includes how the data are collected, how stock assessments are conducted using the data, and how the results of the assessments are used to determine management actions for overfished species (the control rules, and the Rebuilding Revision Rules that are applied to evaluate whether progress is adequate and, if needed, to adjust fishing mortality). Although account could have been taken of implementation uncertainty (Rosenberg and Brault 1993, Francis and Shotton 1997) due to actual removals differing from those that were intended, this compliance aspect is not considered here.

The MSE approach involves the following steps to evaluate a set of candidate management strategies (Punt et al. 2001, Punt 2003).

1. Identification of the objectives that the candidate management strategies are aiming to satisfy, and quantification of these objectives using a small set of performance measures.

2. Specification of the set of alternative management strategies (in this case, specifications for how assessments and rebuilding analyses are conducted and the Rebuilding Revision Rules).

3. Development and parameterization of a set of alternative operating models that represent different states of the "true" system being managed.

4. Simulation of the future using each management strategy. For each step of the projection period, the simulations involve the following steps.

    a. generation of the data available to the stock assessment;

    b. application of the stock assessment method to the data to determine inputs to rebuilding analyses and Rebuilding Revision Rules;

c. determination of the harvest guideline for the next year, either based on a rebuilding analysis (if this is the first year that the stock is identified to be overfished) or using the Rebuilding Revision Rules (if the stock is already overfished); and

d. determination of the biological implications of this harvest guideline by setting the catch for the "true" population represented in the operating model to the estimated harvest guideline.

The harvest guideline is not updated every year in the simulations of this paper, but rather every fourth year. This reflects the frequency with which regular assessments for West Coast groundfish species are likely to be conducted. Each simulation trial (i.e., an operating model variant combined with a candidate management strategy) involves 20-100 simulations of an 80-year period. Although 100 (or more) simulations for each simulated scenario would have been ideal, the computational requirements of the calculations (in particular the need to conduct assessments and rebuilding analyses every fourth year) restricted the number of simulations. Twenty simulations are, however, adequate to capture the qualitative impact of the factors that underlie a simulated scenario.

The operating model

The operating model used here is essentially identical to that used by Punt (2003). It includes an age-structured population dynamics model in which recruitment is governed by a Beverton-Holt stock-recruitment relationship with lognormal deviations (σ_R=0.6), natural mortality that is independent of age and equal to 0.15 yr^{-1}, and a single fishery, the selectivity of which is time-invariant and dome-shaped. The values for the biological and technological parameters of the operating model are based somewhat loosely on those for widow rockfish off the U.S. West Coast (Williams et al. 2000). The stock is fished down to below the overfished level of 0.25 B_0 (to either 0.1 B_0 or 0.15 B_0) after 26 years of catches when a Rebuilding Plan is first implemented. The simulations are based on a status when a Rebuilding Plan is first implemented of 0.1 B_0 or 0.15 B_0 so that there is a reasonable probability that a stock assessment would have detected that the stock was depleted to below 0.25 B_0.

The data available to the assessment are catches, weight- and fecundity-at-age and natural mortality (all known exactly), catch-rate-based indices of abundance, survey indices of abundance, catch age-composition data, and survey age-composition data. The survey is assumed to be conducted tri-annually from 28 years before the stock is declared overfished (survey CV = 0.5; effective sample size for the survey age-composition data = 100) while the catch-rate indices and

Table 2. The specifications that define the alternative "true" scenarios considered in the simulations.

Scenario	True initial biomass	Steepness	Autocorrelation in recruitment	Natural mortality (yr^{-1})	σ_R
A – Base case	0.1 SB_0	0.4	0	0.15	0.6
B – Depletion = 0.15	0.15 SB_0	0.4	0	0.15	0.6
C – Steepness = 0.7	0.1 SB_0	0.7	0	0.15	0.6
D – With autocorrelation	0.1 SB_0	0.4	0.707	0.15	0.6
E – M = 0.1 yr^{-1}	0.1 SB_0	0.4	0	0.1	0.6
F – M = 0.2yr^{-1}	0.1 SB_0	0.4	0	0.2	0.6
G – σ_R= 1	0.1 SB_0	0.4	0	0.15	1

the catch age-composition data are assumed to be available in all years when the catch is non-zero. The CV for the catch-rate indices is set to 0.4 and the effective sample size of the catch age-composition data is set to 100. On the U.S. West Coast, these specifications correspond to a data rich stock.

Table 2 summarizes the parameters of the seven operating model scenarios we considered. These are based on specifying the depletion when the management strategy is first applied (either 0.1 B_0 or 0.15 B_0), the steepness of the stock-recruitment relationship (h = 0.4 or h = 0.7), whether recruitment is temporally autocorrelated, the true value of M (0.1 yr^{-1}, 0.15yr^{-1}, or 0.2 yr^{-1}), and the extent of variation in recruitment, σ_R (0.6 or 1).

The stock assessment

The method of stock assessment is a statistical catch-at-age analysis (e.g., Fournier and Archibald 1982), which mimics the common use of the stock synthesis framework (Methot 2000) when conducting assessments of rockfish species off the U.S. West Coast. The population dynamics model underlying the assessment is essentially identical to the operating model. The estimable parameters of the stock assessment model are the annual recruitments and the parameters of the selectivity function. Parameter values are estimated by minimizing an objective function in which the catch rate data and the survey indices of abundance are assumed to be lognormally distributed and the catch and survey age-composition data are assumed to be multinomially distributed. For simplicity, the stock assessment assumes the correct effective sample sizes and coefficients of variation for the data. The outcomes from the assessment model are (a) an estimate of spawning output at the start of year n + 1 divided by the pre-fishery spawning

output, where year n is the last year for which catch data are available, and (b) estimates of the spawning output and recruitment time-series. In reality, there is a time-lag between the last year for which data are available and the year for which a harvest guideline is set, but this complication is ignored here.

Rebuilding analyses

There are many ways that a rebuilding analysis can be conducted (e.g., PFMC 2001, Punt and Methot 2005). The following steps, which have formed the basis for several recent rebuilding analyses for rockfish species off the U.S. West Coast (e.g., Methot and Rogers 2001, He et al. 2003), are followed when conducting simulated rebuilding analyses.

1. B_0 is calculated by multiplying the spawning output-per-recruit in the absence of exploitation by the arithmetic average recruitment for the first 10 years of the assessment period.

2. The method for generating future recruitment is selected. Recruitment for some future year y is either generated by (1) randomly sampling a recruitment from the most-recent 20-year time series of estimated recruitments or (2) by multiplying the spawning output for year y by a recruits-per-spawning output ratio selected at random from the most-recent 20 years. The choice between these two approaches depends on whether recruits or recruits-per-spawning output is more stable (Punt and Methot 2005).

3. T_{MIN}, the time to rebuild to $0.4B_0$ with 50% probability in the absence of fishing, is calculated by projecting the population forward from the estimated age-structure at the start of the year when the stock was declared overfished (which may differ from that for the current year) 1,000 times in which fishing mortality is set equal to zero and recruitment is stochastic; T_{MIN} is then the median of the distribution for the year in which the spawning output exceeds $0.4\ B_0$.

4. T_{MAX}, the maximum time allowable for rebuilding is then calculated. In this paper T_{MAX} is set equal to T_{MIN} plus one mean generation time because the biology of the simulated populations implies that recovery to $0.4B_0$ cannot occur within 10 years.

5. Given values for T_{MAX} and P_{MAX}, the appropriate rebuilding SPR is determined by projecting the population forward 1,000 times with stochastic recruitment for a range of levels of fishing mortality (and hence SPRs) from the age-structure of the population at the start of the current year.

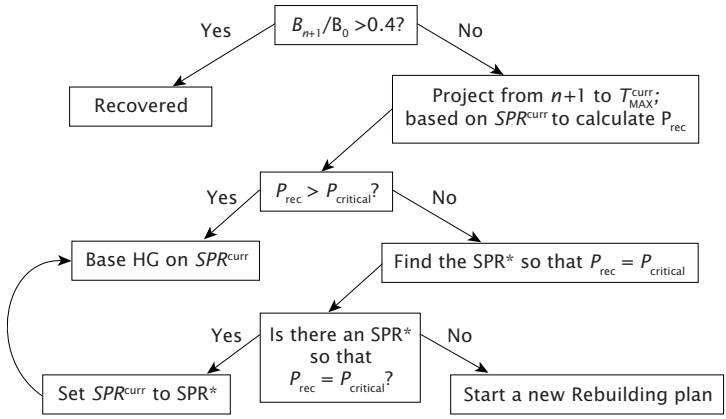


Figure 2. Flowchart of the reference Rebuilding Revision Rule.

Rebuilding Revision Rules

Several candidate Rebuilding Revision Rules are considered. All of these are based on a pre-specified and fixed value for P_{MAX}. A rebuilding analysis is assumed to have been conducted when the stock was first declared overfished (year 41), which led to values for T_{MIN}, T_{MAX}, and the rebuilding SPR that corresponds to an estimated probability of recovery of P_{MAX} by T_{MAX}. These values define the initial values for T^{curr}_{MIN}, T^{curr}_{MAX}, and SPR^{curr}, the "current" values for T_{MIN}, T_{MAX} and the SPR used to determine future harvest guidelines (HGs). The Rebuilding Revision Rules are applied after a stock assessment is conducted which provides updated estimates of the status of the stock as well as the probability of recovery if fishing mortality (i.e., SPR) remains at its current level. The alternative Rebuilding Revision Rules are all variants of a "reference" rebuilding rule. The reference rule is based on the idea that (1) performance is adequate as long as the estimated probability of rebuilding by T_{MAX} remains above 0.5 (allowing the probability of recovery to fall below 0.5 would be inconsistent with the guidance provided by NOAA Fisheries that the rebuilding period should not exceed T_{MAX}) and (2) that the entire Rebuilding Plan must be redefined if there is no SPR for which the estimated probability of rebuilding to T_{MAX} is at least 0.5. The reference rule therefore does not modify the SPR if progress is adequate; increases the SPR (reduces fishing mortality) if progress is inadequate, but recovery by T_{MAX} with 50% probability is still possible; and only changes T_{MAX} if it is impossible to recover by T_{MAX} with at least 50% probability. The base case value of P_{MAX} is 0.6 for the reference rule, which operates as follows if a stock assessment has been conducted in year n (Fig. 2).

a. If $B_{n+1} / B_0 > 0.4$, rebuilding is completed. Note, however, that the actual resource may or may not have rebuilt to 0.4 B_0 even though this is assessed to be the case because the assessment is based on data subject to sampling error.

b. Project the population from year $n + 1$ until T_{MAX}^{curr} using SPR^{curr} to determine future harvest guidelines and to compute the probability, P_{rec}, that the stock will rebuild to $0.4B_0$ at least once by T_{MAX}^{curr}.

c. If P_{rec} is larger than a critical value, $P_{critical} = 0.5$, progress is considered to be adequate and the harvest guidelines for the next four years are based on SPR^{curr}.

d. If P_{rec} is less than $P_{critical}$, progress is deemed to be inadequate and some measures need to be taken to reduce fishing mortality to improve the probability of recovery, i.e.,

    1. Determine if there is an SPR (and hence fishing mortality) such that the probability of rebuilding by T_{MAX}^{curr} from the current state of the stock is $P_{critical}$ (this SPR is denoted SPR^*).

    2. If $SPR^* < 1$ (i.e., recovery with probability $P_{critical}$ is possible by T_{MAX}^{curr}) then set SPR^{curr} to SPR^* and base the harvest guidelines for the next four years on SPR^*.

    3. If there is no SPR such that the probability of recovery from the current state of the stock to $0.4B_0$ by T_{MAX}^{curr} is at least $P_{critical}$, a new Rebuilding Plan is needed. This involves redefining T_{MIN} and T_{MAX} and hence SPR^{curr} is based on starting the new Rebuilding Plan from the stock size in year n+1. However, only T_{MAX} is changed if the new SPR is lower than the old (i.e., the new fishing mortality rate is higher).

We identified five alternatives to the reference rule:

1. "No change." This alternative maintains the initial SPR throughout the rebuilding period. While not necessarily a viable Rebuilding Revision Rule, it sets a standard against which the other alternatives can be compared.

2. "At least P_{MAX}." This alternative involves setting $P_{critical}$ equal to P_{MAX}, i.e., the SPR on which future harvest guidelines are based is increased if the probability of rebuilding drops below P_{MAX} (rather than 0.5).

3. "Attain P_{MAX}." This alternative involves adjusting the SPR every time a new assessment is conducted so that the probability of rebuilding is always estimated to be P_{MAX}. This option differs from the "At least

P_{MAX}" option because the SPR can be decreased (fishing mortality increased) if the probability of rebuilding exceeds P_{MAX}.

4. "$P_{MAX} = 0.8$." This alternative is identical to the reference rule, except that $P_{MAX} = 0.8$.

5. "With phase." This option involves not revising a Rebuilding Plan between years $T_{MAX}^{curr} - 5$ and T_{MAX}^{curr} to avoid making large changes to SPR (and hence catches) when a stock is believed to be close to the target level.

The five alternatives are only a small subset of those that might be constructed by varying the features of the reference rule. They were chosen to capture a range of alternatives from nonadaptive ("No change") to highly adaptive ("Attain P_{MAX}") and to consider a more conservative alternative ("$P_{MAX} = 0.8$"). The "With phase" option avoids making large changes to SPR (and hence catches) when a stock is believed to be close to the target level and would be expected to reduce the number of times there is a need to redefine the Rebuilding Plan.

Performance measures

There are many statistics that could be used to summarize the performance of a management strategy. This study focuses on five principal management goals: (a) a high probability of the stock recovering by the T_{MAX} selected when the Rebuilding Plan was originally developed, (b) high catches during rebuilding, (c) low interannual variation in catches, (d) stability in the Rebuilding Plan (i.e., minimizing changes to the value of T_{MAX}), and (e) simplicity. The first three of these five goals are typical of those commonly selected when conducting an MSE. The fourth goal is included because it measures the "administrative cost" of a management strategy; changing the SPR used to set the harvest guideline and changing harvest guidelines themselves is relatively straightforward administratively. In contrast, changing T_{MAX} may require an amendment to the Fishery Management Plan. The importance of the goal of simplicity cannot be overstated. It is likely that the PFMC would select a simple set of Rebuilding Revision Rules over a more complicated set even if the performance of the more complicated set was marginally better than that of the simple set, purely because of the need for the public to know how decisions are made regarding the management of overfished stocks.

The performance measures used to quantify these five goals are

1. The "rebuilding ratio," the ratio of the number of years before the stock was assessed to be rebuilt divided by the number of years that it was expected that rebuilding would take based on the

original Rebuilding Plan, i.e., if the rebuilding ratio exceeds unity then rebuilding is perceived to have taken longer than originally expected.

2. A measure of the variability of the catches (abbreviation AAV), defined as:

$$AAV = 100 \frac{\sum_y \left| C_y - C_{y+1} \right|}{\sum_y C_y} \qquad (1)$$

where C_y is the catch during year y.

3. The average catch during the years when the resource was under a rebuilding plan.

4. The average catch during the first ten years of the rebuilding period.

5. The number of times it was necessary to change the value of T_{MAX}.

Note that the rebuilding ratio is based on the perception that the stock has recovered, rather than the stock having actually recovered. This is because this performance measure relates to what the decision makers would actually see. Also, the simulated use of the management strategy stops once it is perceived by the stock assessment that recovery to $0.4B_0$ has occurred. The performance measures include both short- and long-term catches because the short-term catch reflects the likely immediate impact on the fishery.

Results and discussion

Results for a single operating model and management strategy

It is illustrative to examine detailed results for a few individual simulations before attempting to interpret the values for the performance measures (which integrate performance over years and simulations). Figure 3 shows detailed results for two realizations based on the reference management strategy and the "base case" operating model. As noted above, P_{MAX} is 0.6 for the reference management strategy, and the SPR used to set harvest guidelines is increased (fishing mortality reduced) if the probability of recovery by the current T_{MAX} drops below 0.5. The length of the x-axes in the panels in Fig. 3 is defined by the number of years until the stock assessment indicates that recovery to the proxy for B_{MSY} of 0.4 B_0 has occurred.

The left panels of Fig. 3 summarize the decisions arising from the reference management strategy; the solid line indicates SPR^{curr} (the

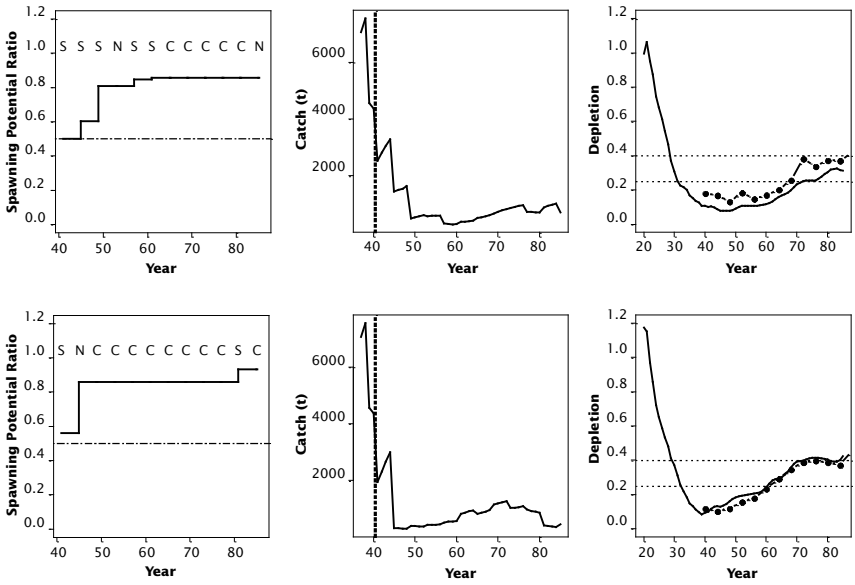


Figure 3. Results of two illustrative simulations for the reference management strategy and the "base case" operating model. The left panels summarize the decisions arising from the reference management strategy: the solid line indicates SPR^{curr} and dashed horizontal line is the spawning potential ratio (SPR) proxy for F_{MSY}. The letters in the upper parts of the left panels indicate whether SPR is increased ("S"), whether the SPR is unchanged from its previous value ("C"), or whether it is necessary to implement a new Rebuilding Plan ("N"). The center panels show the time-trajectories of catch. The vertical lines in these panels indicate the first year in which the management strategy is used to set the harvest guideline. The right panels show the true (solid lines) and assessment model-based estimates of depletion (solid dots) along with the thresholds that define the proxy for B_{MSY} and the minimum stock size threshold (MSST).

SPR used to determine the harvest guideline) each year (the dashed horizontal line is the SPR proxy for F_{MSY}; harvest guidelines cannot be based on a SPR lower than this) while the letters in the upper part of the panel indicate whether SPR^{curr} is increased so that the probability of rebuilding remains at least 0.5 ("S"), whether the SPR is unchanged from its previous value ("C"), or whether it is necessary to implement a new Rebuilding Plan (which would involve changing T_{MAX} and well as SPR^{curr}) ("N").

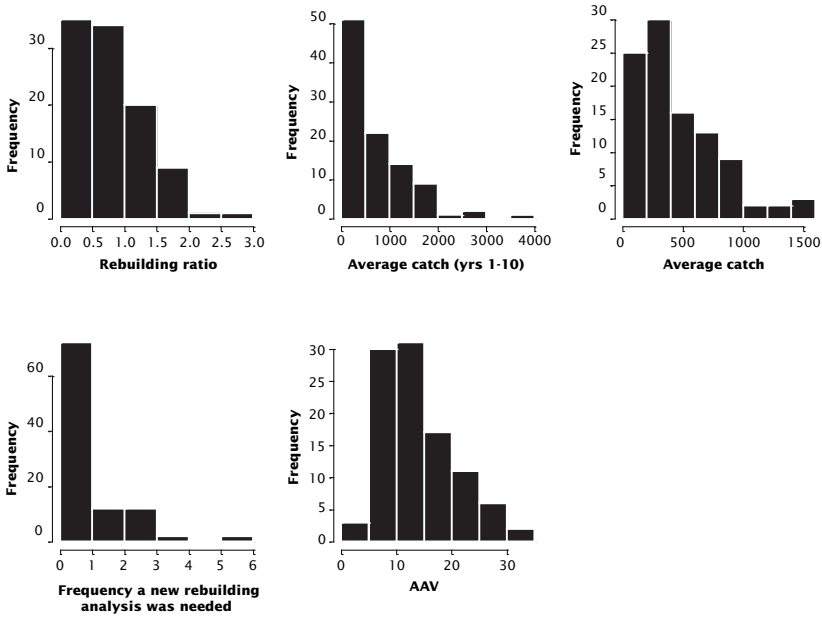


Figure 4. Summary of the five performance measures for 100 simulations for the reference management strategy and the "base case" operating model.

An ideal management strategy would lead to an "S" in year 41 (the year in which the management strategy is first applied) and "C"s for all years thereafter because this would imply that there was no need to adjust the plan during the rebuild period. In contrast to the ideal, it is frequently necessary to both revise SPR^{curr} and implement a new Rebuilding Plan. It is particularly noteworthy that new Rebuilding Plans can be required early during the rebuild period (12 and 4 years after the Rebuilding Plan is first implemented in Fig. 3) and right at the end of rebuild period (the simulation in the upper panel).

The center panels of Fig. 3 show the time-trajectories of catch. The vertical line indicates the first year in which the management strategy is used to set the harvest guideline. In both simulations, the catch is not reduced sufficiently during the first few years of the rebuild period, which is one reason for the marked reductions thereafter. Interannual catch variability, as quantified by the AAV statistic, is 14% and 15% for the two simulations in Fig. 3. The right panels in Fig. 3 show the true (solid lines) and assessment model-based estimates of depletion along with the thresholds that define the proxy for B_{MSY} ($0.4B_0$) and the mini-

mum stock size threshold (MSST) ($0.25B_0$). The stock assessment tends to overestimate relative stock size for the simulation in the upper panel, and consequently indicates that recovery has occurred even though the true stock size is still appreciably below the $0.4B_0$.

The method used to generate future recruitments when conducting rebuilding analyses is one cause for the need to redefine a Rebuilding Plan. For example, if recent recruits-per-spawning output ratios are used as the basis for projections, the rate of recovery will tend to be overestimated because this method assumes that there is no change in the distribution of recruits-per-spawning output ratios as the stock recovers. However, if the recruits-per-spawning output ratios are based on a period when the stock is low (and density-dependence is high), the central tendency of the distribution of recruits-per-spawning output ratios would be expected to drop over time.

Figure 4 summarizes the results of 100 simulations for the five performance measures for the "base case" operating model and the reference management strategy. The data in this figure were selected from a slightly larger sample because cases in which the stock was incorrectly assessed not to be overfished at the start of year 41 were excluded. In general, the stock assessment indicates that recovery occurs regularly before the initial T_{MAX} selected (62 of the 100 simulations have a rebuilding ratio of 1 or less), although there are cases in which recovery occurs well after that. Given that P_{MAX} is 0.6 for the reference management strategy, it would be expected that recovery should occur before T_{MAX} more often than not. Note also that the range for the average catch over years 1-10 is much wider than that of the average catch over the entire rebuild period, primarily because the feedback nature of the management strategy corrects for large initial catches by lowering catches as the stock assessment detects that recovery is proceeding too slowly. The interannual variation in catches ranges between 5 and 30% per annum. There is no need to replace the Rebuilding Plan in 33 of the 100 simulations, but the incidence of simulations wherein two or more revisions are required is not small.

Implications of different management strategies

Figure 5 summarizes the results of the six management strategies (the reference strategy and the five alternatives) in terms of plots of the rebuilding ratio versus the average catch, the number of times the Rebuilding Plan is redefined versus the average catch, and the AAV versus the average catch. The results in Fig. 5 are based on 20 simulations using the "base case" operating model.

The results for the reference management strategy are essentially identical to those for the "With phase" strategy, suggesting that the impact of not modifying the Rebuilding Plan at the end of the rebuild period has little adverse effect on the performance measures, but little

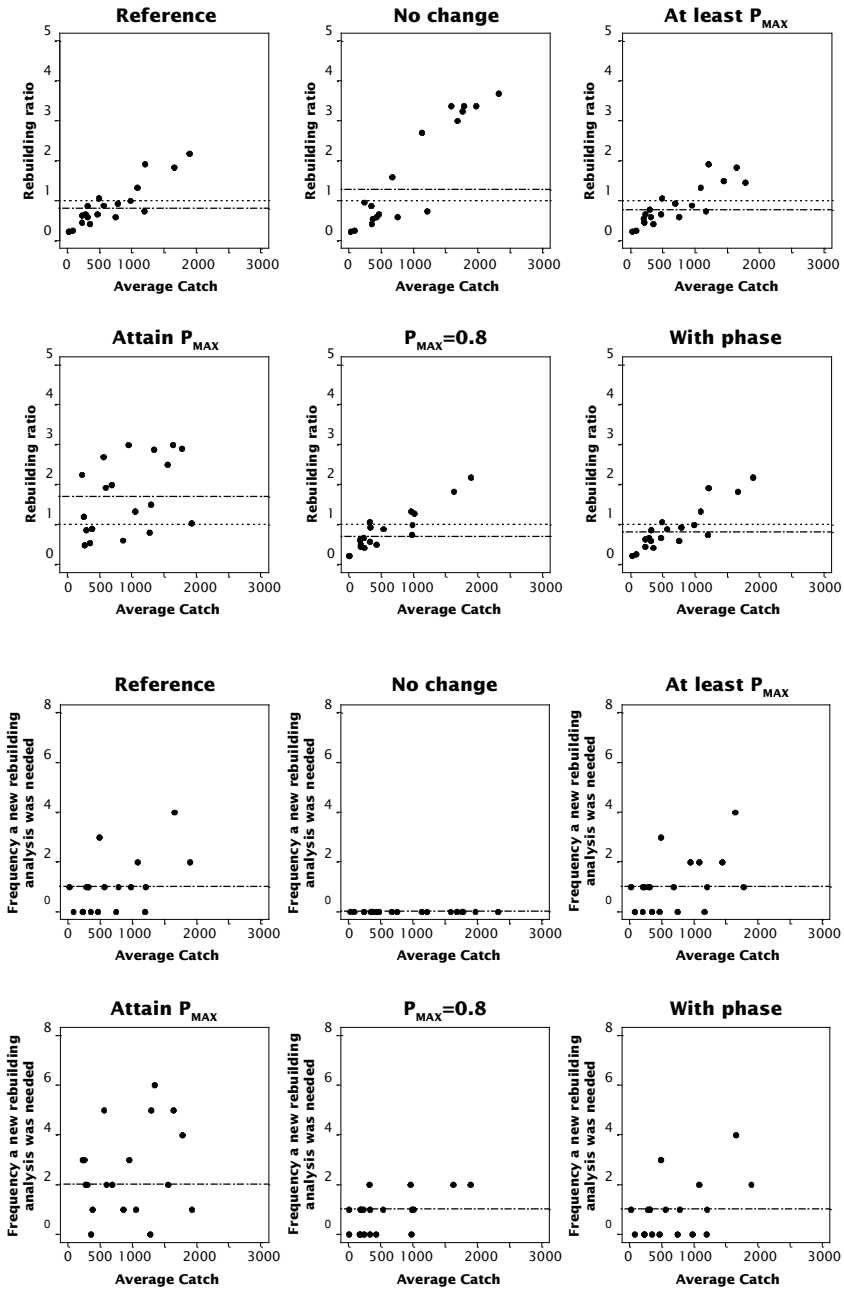


Figure 5. Performance measures (see text for details) for six management strategies for the "base case" operating model. The horizontal dashed line in each panel indicates the median of the performance measure represented on the y-axis.

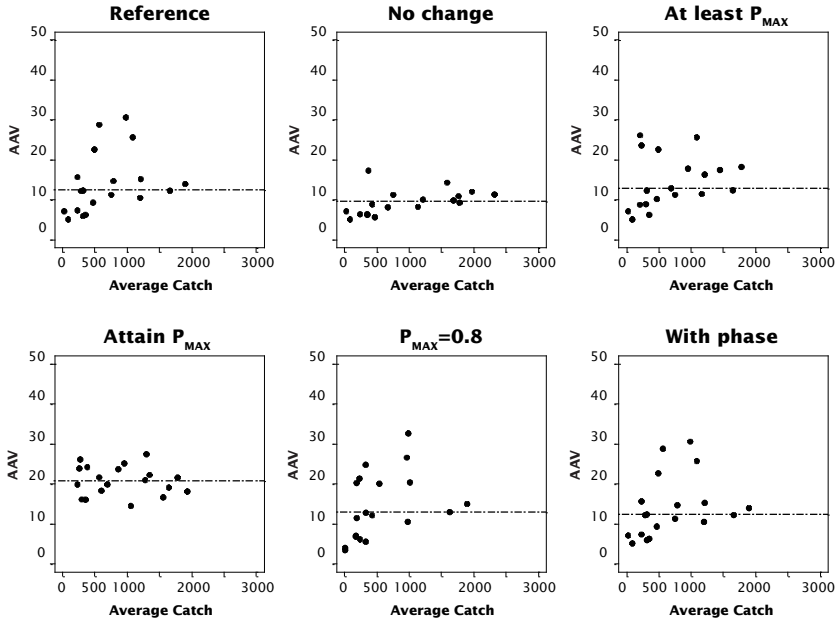


Figure 5. (Continued.)

beneficial effect either. The "No change" strategy, wherein the initial SPR selected when the stock was declared overfished is maintained, leads to much longer times to recovery in some instances. One consequence of not updating SPR^{curr} every fourth year is a lesser chance of high interannual variation in catches and a higher probability of larger average catches during the rebuild period.

The "At least P_{MAX}" management strategy leads to slightly shorter recovery times, but consequently to a slightly higher chance of needing to redefine T_{MAX} during the rebuild period. There is an obvious (and expected) relationship between the rebuilding ratio and the average catch in Fig. 5, except for the "Attain P_{MAX}" strategy because this strategy increases fishing mortality when progress is faster than anticipated and vice versa. Apart from longer times to recover, the "Attain P_{MAX}" management strategy also leads to frequent redefinitions of Rebuilding Plans and to increased interannual variation in catches (see Fig. 6, which shows detailed results for the simulations illustrated in Fig. 5). One reason for the latter result is that this strategy permits a decrease in SPR^{curr} if progress is faster than expected, unlike the reference strategy. Increasing P_{MAX} from 0.6 to 0.8 increases the buffer between P_{MAX} and $P_{critical}$. Consequently, not only are rebuilding times shorter for $P_{MAX} = 0.8$,

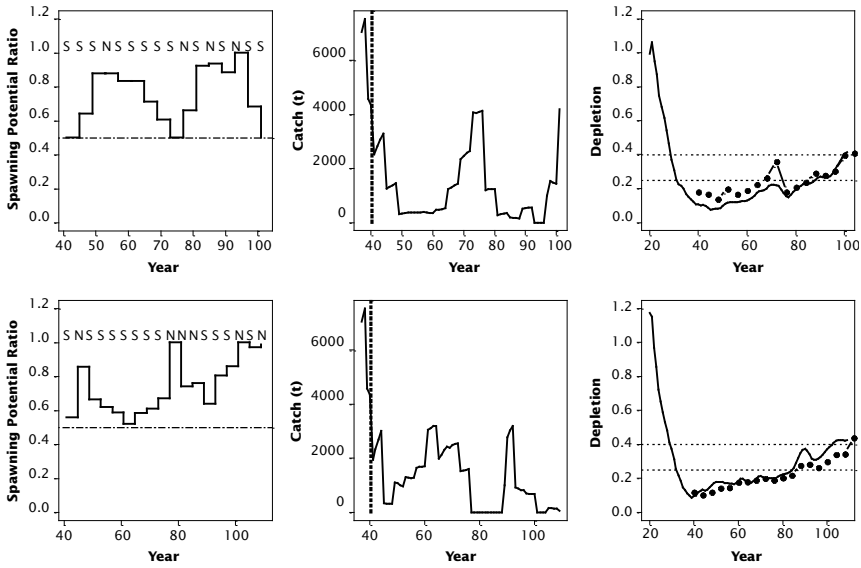


Figure 6. Results of two illustrative simulations for the "Attain P_{MAX}" management strategy and the "base case" operating model. The left panels summarize the decisions arising from the management strategy: the solid line indicates SPR^{curr} and dashed horizontal line is the spawning potential ratio (SPR) proxy for F_{MSY}. The letters in the upper parts of the left panels indicate whether SPR is increased ("S"), whether the SPR is unchanged from its previous value ("C"), or whether it is necessary to implement a new Rebuilding Plan ("N"). The center panels show the time-trajectories of catch. The vertical lines in these panels indicate the first year in which the management strategy is used to set the harvest guideline. The right panels show the true (solid lines) and assessment model-based estimates of depletion (solid dots) along with the thresholds that define the proxy for B_{MSY} and the MSST.

but there is also a lower likelihood of needing to redefine T_{MAX}, which are both desirable features from a conservation perspective.

In summary then, the "No change" and "Attain P_{MAX}" management strategies lead to the highest average catches, but also to the longest recovery times and, for "Attain P_{MAX}," to frequent redefinitions of the Rebuilding Plan. In contrast, the "$P_{MAX} = 0.8$" management strategy leads to the lowest average catches, the shortest rebuilding times, and the lowest probability of needing to redefine the Rebuilding Plan.

Implications of changes to the operating model

Figure 7 summarizes the results of the reference management strategy for the six alternative operating models outlined in Table 2. Results are presented using the same format as Fig. 5. The patterns in Fig. 7 are quite similar to those in Fig. 5, although there are some noteworthy differences. For example, average catches are higher and the rebuilding ratio lower if the stock is initially less depleted or if steepness is higher than in the "base case." Neither of these findings is unexpected. Somewhat surprisingly perhaps, the rebuilding ratio is not much higher when recruitment is temporally autocorrelated. This is probably because the reference management strategy makes more frequent changes to the Rebuilding Plan in this case, i.e., its feedback nature allows the reference management strategy to correct for sequences of poorer-than-average recruitment by decreasing the SPR used to determine the harvest guidelines. Also, interannual variation in catch is increased if recruitment variation is increased, but there is relatively little impact on the rebuilding ratio and the frequency of the need to construct a new rebuilding plan.

Conclusions

The results of the simulations of this paper only consider a limited set of possible Rebuilding Revision Rules and a narrow range of operating models. However, it is possible to draw some general conclusions from our findings that are likely to be robust to a broader set of Rebuilding Revision Rules and operating models.

- There is clearly a need for Rebuilding Revision Rules; the "No change" management strategy, which fixes the SPR equal to that when the stock was declared overfished, leads to occasional very long rebuilding times compared to those expected when the stock was declared overfished.
- It should be expected that there will be both frequent revisions to the SPR and occasionally to T_{MAX}.
- The management strategies considered in this paper tend to allow recovery to occur before T_{MAX}; the extent to which this occurs depends on P_{MAX}.

The PFMC has not adopted any set of Rebuilding Revision Rules. However, past practice is most similar to the "Attain P_{MAX}" management strategy. Unfortunately, this management strategy leads to high interannual variation in catches and frequent changes to the Rebuilding Plan (e.g., Fig. 6). This management strategy adjusts the SPR every time new data become available and is very susceptible to following noise rather than signal. For these reasons we recommend that this particular strategy be given less consideration when alternative policies are evaluated.

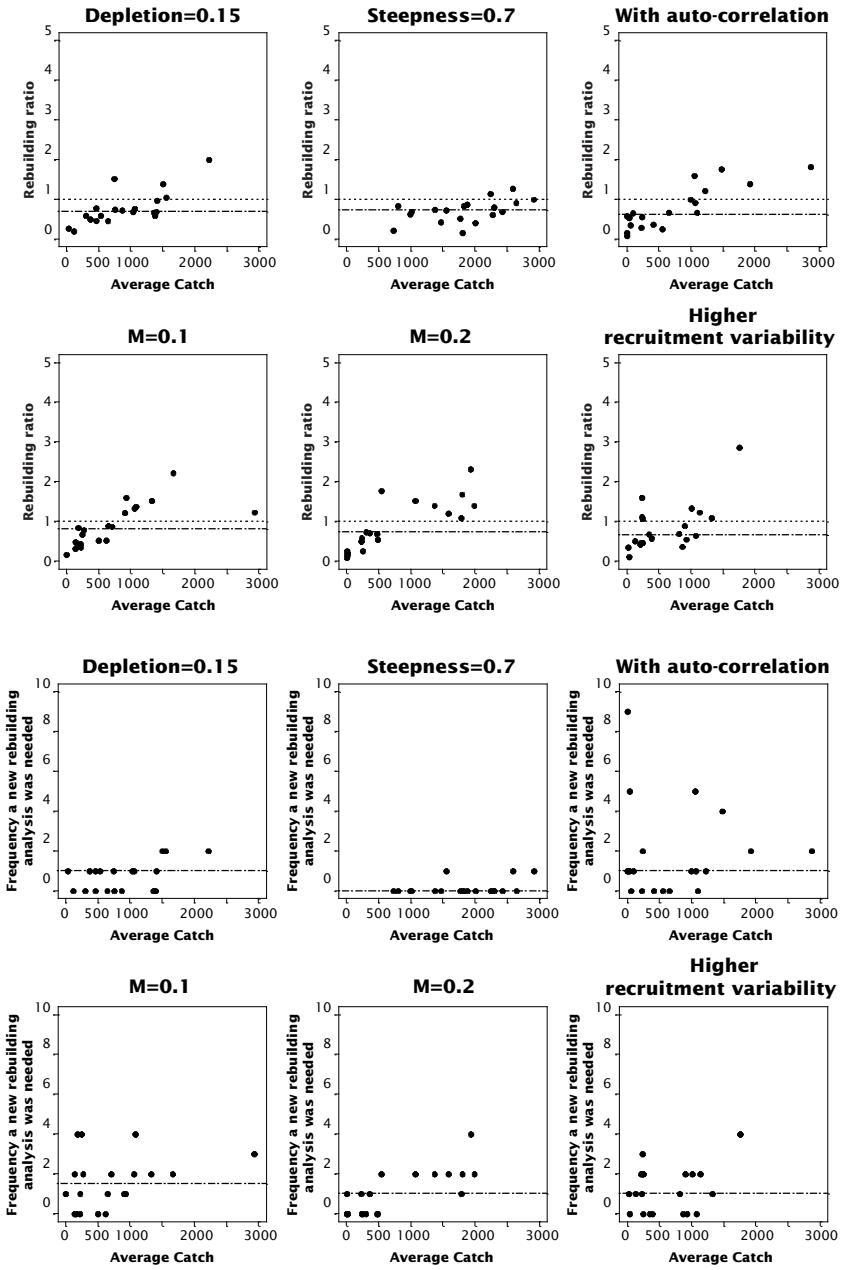


Figure 7. Performance measures (see text for details) for the reference management strategy for six alternative operating models. The horizontal dashed line in each panel indicates the median of the performance measure represented on the y-axis.

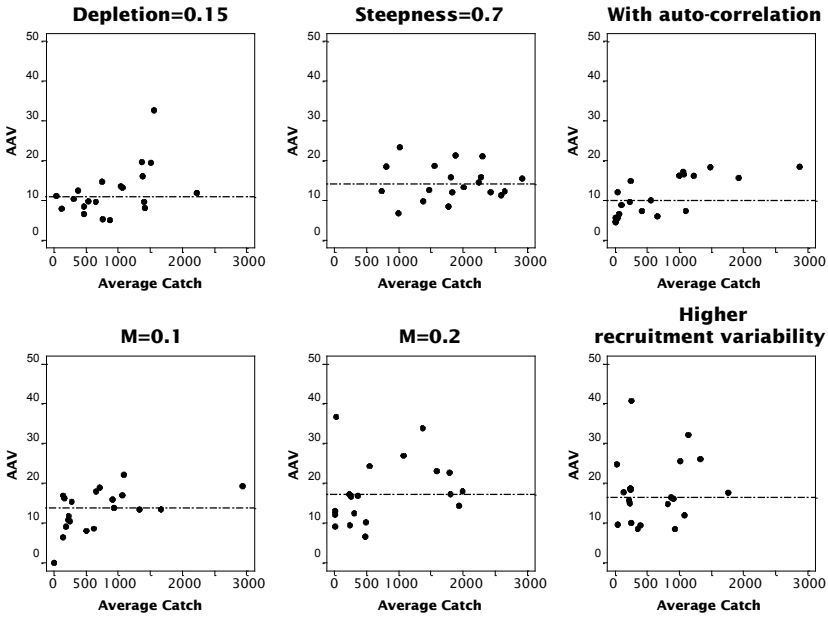


Figure 7. (Continued.)

The analyses of this paper only consider a subset of the possible sources of uncertainty. In particular, the only reasons for failing to recover with the intended probability relate to unforeseeable events such as a random occurrence of a string of poor recruitments and changes in assessment results due to additional data. There are several other reasons why failure to recover with the intended probability could occur, such as catches exceeding harvest guidelines and low-frequency changes in ocean productivity. Future analyses along the lines developed in this paper could explore the consequences of such effects.

The analyses of this paper are based on changes to assessments owing primarily to the acquisition of new data. However, there are other, more philosophical, reasons why the results of assessments may change over time. For example, the assessment scientists who conduct the assessments and rebuilding analyses for overfished species are apt to change over time. Different assessment authors have different backgrounds and attitudes to modeling; for example, whether all possible, or just the best, data sources should be included in an assessment. Thus, it may be that one assessment scientist will use commercial catch rate data in an assessment, but the next would not. Such decisions could strongly impact estimates of stock status and productivity. Similarly,

there are philosophical differences among assessment scientists in how uncertainty should be quantified. For example, Punt et al. (2003) conducted rebuilding analyses for Pacific ocean perch starting from the best estimates of current stock size and taking account of uncertainty through a Bayesian posterior. Notably, they found major differences in the resulting harvest guidelines.

The analyses of this paper assume that assessment methods and P_{MAX} do not change over time, primarily because of computational constraints. In contrast, it seems likely that rebuilding analyses will eventually be based on the results of fitted stock-recruitment relationships rather than by sampling recruitments or recruits-per-spawner ratios (this approach is already being used for some stocks). Also, P_{MAX} for overfished species may increase with time as management moves to a more ecosystem-orientated approach to management.

Finally, the analyses of this paper focus only on management strategies during the rebuilding period and do not consider the implications of what happens after rebuilding is perceived to have occurred. Future MSE analyses need to consider not just rebuilding considerations, but the entire harvest policy and management system.

Acknowledgments

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Developing an Integrated Commercial Groundfish Strategy for British Columbia: Insights Gained about Participatory Management

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Abstract

The British Columbia fishing industry with the provincial and federal governments formed the Commercial Groundfish Integrated Advisory Committee (CGIAC) in 2003 to establish a strategic approach toward integrating the groundfish fisheries. The process was initiated largely because of the difficulty of managing many species and stocks of rockfish across many gear sectors and user groups. In spite of a difficult birth, this initiative has progressed even beyond the expectations of some of the participants. In March 2005, a subcommittee of CGIAC, the Commercial Industry Caucus, submitted a Pilot Integration Proposal for discussion among industry and recreational interests and the federal, provincial, local and First Nations governments. The present report, authored by industry and government participants, summarizes the context and main elements of the proposal. It then focuses on four of the main ingredients of the negotiations that were critical for moving the project forward.

Table 1. Commercial Industry Caucus (CIC) membership.

Member	Number	Number of alternates
Processors (1 Trawl/1 hook-and-line)	2	2
Industry advisory committees		
Trawl (T-license)	2	1
Halibut (L-license)	2	1
ZN Inside (ZN-A license)	2	1
ZN Outside (ZN-B,C,D-license)	2	1
Schedule II Dogfish	2	1
Schedule II Lingcod	2	1

Introduction

In November 2003, the governments of British Columbia and Canada formed the Commercial Groundfish Integrated Advisory Committee (CGIAC). Membership includes the governments, commercial fisheries, coastal communities, Marine Conservation Caucus (representing environmental nongovernmental organizations [ENGOs]), Sports Fish Advisory Board, and the B.C. Aboriginal Fisheries Commission. CGIAC's task is to develop a strategic approach to management that integrates all groundfish fisheries (all of which capture rockfish) and satisfies five initial criteria:

1. The fishery must account for all rockfish catches.
2. Rockfish catches will be managed according to rockfish management areas.
3. Fishermen will be individually accountable for their catch.
4. Monitoring standards will be established to meet the above three objectives.
5. Species of concern will be closely examined and actions such as reduction of TACs and other catch limitations will be considered and implemented to be consistent with the precautionary approach for management.

The Commercial Industry Caucus (CIC) was formed as an industry-only Subcommittee of the CGIAC to coordinate planning within the commercial fisheries (Table 1). The CIC was specifically tasked to explore and recommend action on reducing rockfish bycatch, more progressive fisheries management, security of access, at-sea monitoring, and other emerging issues facing the commercial groundfish industry during its transition toward an integrated model.

The CIC deliberations have been difficult and time-consuming but they continue to progress and have resulted in preparation of the "Commercial Industry Caucus Pilot Integration Proposal March 2005" (Diamond Management Consulting, www.diamondmc.com) which is currently under review. The present report, authored by government and industry participants, summarizes the context and the proposal, and focuses on four key ingredients that have helped the process move forward. In summarizing activities at the CIC level and not those of the CGIAC, this paper focuses only on the work and progress within the commercial sectors, although the process is being closely monitored by the First Nations and recreational groups.

Groundfish fisheries

The groundfish fisheries are operationally and spatially complex with numerous licenses/sectors operating in overlapping areas, under different management regimes, using different arrays of management tools such as limited entry and/or individual vessel quotas (IVQs), trip limits, and partial or 100% at-sea monitoring (Fig. 1, Table 2). This complexity led to significant inefficiencies and wastage. Foremost among these was the result that as each of the sectors was retaining their target or directed species, they were discarding, often dead, the directed species of other sectors. Furthermore, the lack of monitoring made it problematic to attempt stock assessments let alone quota management, since total harvest was largely unknown for many important species. Harvesters complained that reported harvests grossly underestimated the true harvest, thus assessments based on these data underestimated the productivity of the populations. Researchers responded that as long as harvesters did not report discards, and partial coverage observer programs were known to be biased because "observed" skippers would alter their behavior, there was little choice. Complete coverage observer programs were deemed too costly to implement by the harvesters.

In spite of the complexity and inefficiencies, however, the groundfish fisheries remained viable and reasonably manageable for many years. However, by the mid 1990s, all parties began to recognize that the increasing pressures for precautionary management, "responsible" fishing, the Canadian Species at Risk Act (SARA), and the federal government's decision to move to "user-pay" fisheries required a radically new way of doing business. In addition to a long list of operational problems that needed fixing, including suspected quota overruns and poorly monitored bycatch, there were strong positive incentives for change such as the perception of benefits that might accrue with introduction of individual transferable quotas (ITQs) as part of the package.

The seminal moment occurred in May 2001 with the presentation of a discussion paper by the commercial hook-and-line sectors. This

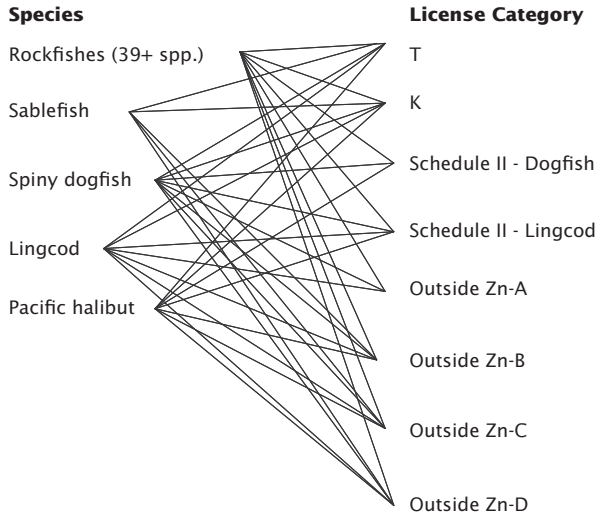


Figure 1. Schematic to illustrate the overlap (many-to-many relationship) between some of the species that are captured (directed and nondirected) by commercial groundfish fishers and the license categories that capture them (see Table 1 for license definitions).

Table 2. Existing groundfish licenses in British Columbia.

License/ sector	Gear[a]	Landed value ($CDN)	Active licenses	Target
L	LL, jig, HL, troll	$40 million	215	Halibut
Schedule II/C	LL	$5 million	200-300	Lingcod, dogfish
Inside ZN	LL and HL	$1 million	55-60	Live rockfish, lingcod
Outside Zn-A	LL and HL	$4 million	85	Live rockfish, lingcod
Outside Zn-B	LL and HL			Yelloweye rockfish
Outside Zn-C	LL and HL			Slope rockfishes
Outside Zn-D	LL and HL			Halibut, rockfishes
K	Trap and LL	$20 million	27	Sablefish
T option A	Trawl	$75 million	60	Most groundfish species
T option B	Trawl		14	Most groundfish species

[a]LL = longline; HL = hook-and-line.

document suggested moving toward an integrated fishery by combining fishing privileges in order to "reduce bycatch . . . rationalize fishing capacity and allow for more efficient, effective and rational fishing practices." This was presented to DFO management in the Pacific Region who encouraged the industry to work toward integration.

The report was followed by three DFO-convened meetings in 2003 which included representatives from the commercial fishing industry, the Sierra Club of British Columbia, First Nations' and Provincial governments. These groups, with funding from the Provincial Government, commissioned two more discussion papers. These documents further refined the statement of the problem:

". . . the groundfish resource is a complex web of varied and overlapping species and stocks susceptible to different gear types. Sustainable management of the groundfish resources is similarly complex, requiring a web of interdependent harvesting and management measures. The closer you look at this complex web, the more it becomes obvious that significant change is going to be necessary." (Bruce Turris, Canadian Groundfish Research and Conservation Society, pers. comm.).

They also expanded the objectives to include

- Conservation with improved research and assessments.
- Improved catch utilization.
- Sector and individual accountability.
- Increased industry responsibility and cost recovery.
- Security of access and a "year-round" fishery.
- Economic viability and efficiency.
- Improved social benefits.
- Comprehensive management with administrative and operational simplicity.

The documents evolved from a "fix-it" perspective to an attempt to develop a lasting structure that could respond and therefore persist. They also recognized that the problems were not limited to rockfishes and began to address many more groundfish species. The documents also proposed an advisory and coordinating structure and membership. The CGIAC, co-chaired by DFO and the groundfish industry, is the overarching committee that addresses policy matters. Advice on matters specific to individual groundfish sectors will remain the role of the existing sector advisory committees. For example, the CGIAC and its CIC subcommittee may recommend ITQs in the ZN-license rockfish fishery, but specifics on the implementation should come from the

ZN-DFO advisory committee, the Groundfish Hook-and-Line Advisory Committee (GHLAC).

CGIAC hired a facilitator for the CIC meetings in December 2003 and the CIC was tasked by DFO to develop an integration plan. Meetings continued through 2004, culminating in April 2005 with delivery of a first draft of the proposal. This report has since been endorsed in general principle by DFO, although DFO noted that the proposal represented a "Major Fishery Reform" and would require extensive consultation. The proposal has substantial implications with respect to allocation that go beyond the commercial sectors and include the sport fishing sector and First Nations. At that time, DFO requested that the finished plan be in place by 2005, later modified to 2006. The CIC is currently overseeing the expenditure of $CDN 1 million (~ $US 0.8 million) in industry funds plus some DFO funds to develop and implement 100% electronic monitoring by April 2006, as well as develop the companion data systems.

The plan

Transferable quotas

The driving operational elements of the integration proposal are the introduction of ITQs in conjunction with accurate monitoring. These two elements are seen as the major tools/incentives to provide accurate catch accounting, prevention of TAC overruns, reduction of discards, and improvement of research and assessment. Each sector will be allocated by DFO the specific amounts of "nondirected" species (bycatch). A nondirected catch cap, calculated as a percentage of individual directed license holdings, will be transferable among licenses. Sectors will target only their primary, or "directed" species; they may not target nondirected species.

At the beginning of the fishing season, each sector will make two calculations:

- What percentage of the TAC of their directed species will it temporarily re-allocate to other sectors to provide nondirected catch in those sectors?
- What amount of nondirected species, according to estimated catch history, do fishermen in its sector require to prosecute their fisheries?

The sectors will then negotiate within the CIC the percentages of each TAC that will be temporarily allocated to each commercial groundfish sector. While ITQs are generally viewed within the CIC as a key to the integration, and already implemented in the trawl (T-license), sablefish (K-license) and halibut (L-license) fisheries, the proposed integration can still be implemented if quotas are assigned to only the sector level

in the remaining, and non-IVQ, sectors. CIC deliberations will have to consider that while IVQs provide obvious operational benefits, the broader social and economic impacts cannot be ignored. It will be up to each sector to determine how its license holders will utilize the quota. Nondirected species will be transferable from one license to another, both within and among sectors. All temporary transfers of quota will return to their sector of origin at season's end.

100% monitoring

The dockside monitoring programs (DMP) are already established for all commercial sectors and provide accurate credible landings records. Automated vessel monitoring systems (VMS) have already demonstrated the capacity for cost-effective tracking of vessel fishing activity in space, but the estimation of discards, especially for species that suffer high post-release mortality, remains problematic. The cost and logistical difficulties of taking an observer in single-operator, small-vessel fisheries, such as the live rockfish fishery, are prohibitive. Similarly, the cost of 100% review of videotape from electronic monitoring (EM) is prohibitive since it takes almost one hour to review one hour of fishing.

The path around this issue became clearer at one meeting of the EM Working Group of the CIC in early 2005. It was noted that 100% observer coverage or tape review would cost about 10 times the expense that could be tolerated by some of the sectors on top of all other user-pay expenses. The question was restated as what could be attained with 100% capture of video footage but only 10% review. In this scenario the "threat" of video review would be used to ensure that fishers would keep accurate logbooks of retained and discarded catch. The onus would be on the fishers to provide an accurate record but the fisher would know that about 10% of his/her fishing effort would be selected at random and then reviewed and compared with the logbook. While designed for cost-cutting, the scenario was also valued by fishers since it put them in charge of the accountability rather than an observer or a "black box." During discussions, some fishers commented that keeping track would be a major imposition, but other fishers commented that many present-day activities in fisheries that are taken for granted (such as counting steelhead trout during salmon seining) were once thought to be onerous changes.

While the solution to accurate monitoring appears to be in sight, participants realize many operational issues remain to be managed, including:

1. What are the acceptable tolerances when matching logbooks to the EM 10% sampling?

2. What are the repercussions if fisher logs do not match the EM records?

3. How well can EM video distinguish similar species?
4. How to create an overall governance system of the monitoring to resolve issues like (1) and (2) above.

The plan has also yet to accommodate the problem of discarding undersized specimens. To this point, DFO catch restrictions in hook-and-line, and trap fisheries relate to legal-sized specimens. Fishers can therefore circumvent personal quotas by discarding at the rail and claiming the fish were too small.

Other requirements of the plan

While the allocation and monitoring issues are the most problematic, other operational issues to resolve include development of a database management system that provides a 24-hour catch update for each fisher, after blending data from logbooks, DMP, VMS, and video review. Integration also requires a quota trading system, although a template was already developed for the trawl fishery.

It has also been noted that the integrated system will create a large demand for stock assessment advice on all species affected by the groundfish fisheries. Science advice will also be sought in deriving post-capture mortality rates to be used to adjust estimates of discards. Implementation will also place large demands on managers in coping with mismatches between nondirected catch needs of some sectors (see below under "The Spreadsheet"). Since discarding has not been recorded in some of the sectors, fishers have argued that historical productivity of these populations is being underestimated. While fishers agree it is not possible to recreate this "harvesting" in historical catch records, they can be expected to ask managers for some quota latitude given the unknown historical harvest.

Key elements that aided progress in the CIC discussions

While the integration plan is far from being fully implemented, the progress to date has been a surprise to even the participants. Much of the progress obviously stems from the energy generated from the collective desire to "avoid a mutual disaster" (Hanna 2003a); however, a variety of tactical and strategic choices during negotiations have been essential to the process. Below, we have summarized four of the decisions or tactics that participants have suggested were key elements of the negotiations.

Initialization-facilitation

The CIC recognized from the outset that they needed professional facilitation but now view that they underestimated the benefits. Not only would it have been impossible for a person from within the industry to have filled this role when there was so much distrust, but it took two months to find an acceptable facilitator who could be assumed by all sectors to be "untainted."

While participants noted that progress past the table-thumping and finger-pointing phase could not have been achieved without a good facilitator, they also now view these months of initialization as being essential for developing and consolidating the organizing principles of the CIC (see Jentoft et al. 2003). Quoting from the integration plan: "Development of the consensus building process that led to the ten principles of participation [shown below] was a notable achievement in its own right."

1. Fishery participation.
2. Respectful involvement.
3. Inclusive and constructive process.
4. Individual accountability.
5. Fair treatment.
6. Equitable treatment.
7. Voluntary reallocation (i.e., DFO cannot unilaterally re-allocate among the sectors).
8. Allocation restorations (i.e., should the TACs increase, the additional catch goes back to the original sectors).
9. The presence of nondirected catch will not be used as an excuse to disenfranchise a sector. The sector will be allowed to address the issue.
10. Existing allocations to the sectors will be respected and allocations for previously non-allocated species will respect the catch history.

Once these elements were established progress was more rapid, but on numerous occasions the facilitator had to ask the group to "re-affirm the principles" and remind participants that "those to be affected should be heard." Wilson (2003) noted that "Action Research" in the 1970s and 1980s showed that heterogeneity and conflict among stakeholders must be addressed openly and not hidden or buried during comanagement efforts. Also, during this phase, the group learned that the participants had to move forward together in their understanding. Each time a mem-

Table 3. Projected totals (lb) for nondirected catch for two example sectors (halibut and trawl) and 10 selected species and the estimated nondirected catch for all sectors combined.

Species	1. Halibut fishery (L)	2. Trawl fishery (T)	3. TACs (all sectors: (L) + (T) plus other sectors)	4. Proposed nondirected catch (all sectors: (L) + (T) plus other sectors)	5. TAC utilized (%) by nondirected catch
Yellowtail rockfish	60,705	–	8,877,483	154,018	2%
Canary rockfish	364,230	–	2,381,850	488,132	20%
Rougheye rockfish	1,821,150	–	1,977,526	2,707,154	137%
Shortraker rockfish	1,214,100	–	402,340	1,656,579	412%
Yelloweye rockfish	1,214,100	20,258	482,930	1,378,596	285%
China/quillback rockfish	182,115	5,065	324,076	273,578	84%
Spiny dogfish	3,642,300	–	25,476,358	4,934,656	19%
Sablefish	2,428,200	506,458	9,569,595	3,444,648	36%
Big skate	2,428,200	–	1,125,007	2,748,460	244%
Halibut		–	12,141,000	3,189,809	26%
Actual total all species	20,156,488	531,781		30,918,783	
License quota (“target”)	12,141,000	202,583,118			

Note: Columns 3 and 4 represent the sum of columns 1 and 2 plus other sectors, such as sablefish. License quota (bottom line) is the directed quota for the sectors. For example the halibut fishery has a halibut quota of 12,141,000 lb.

ber could anticipate the direction of the talks and attempt to “jump a step,” talks would not only stall but sometimes take a step backward as other participants would become suspicious of their motives.

The Spreadsheet

One of the difficult elements in the process was exploration of the inter-connectedness of each sector’s and individual’s fishing plans with respect to the catches of the large number of directed and nondirected species. At the beginning of the discussions, some sectors argued that there was so little overlap with their fishery that they did not really need to participate. Conversely, participants that could foresee the degree of overlap were reluctant to engage in discussion because they could not predict how their sector, or they as individuals, would be positioned once the traditional allocations were compared with the estimated nondirected needs of each sector.

The CIC-generated tool for exploring this issue came to be known as "The Spreadsheet." The intent was to examine for each sector the projected catch of nondirected (or bycatch) species that those sectors would require to prosecute their directed fisheries. For example, it was used to project how much dogfish an L-license halibut fisher would catch while directing effort on halibut, or how much halibut would be captured by a Schedule II/Dogfish-license while fishing for dogfish. The summary table from The Spreadsheet (excerpted in Table 3) was used to show how much nondirected species allocations would be required across the entire commercial groundfish fishery, sector-by-sector and in total. For example, column 1 of Table 3 shows examples of the projected nondirected catch for the "Halibut fishery" (L-license). The L-license holders project that while they are capturing their directed catch of halibut (12,141,000 lb) they will "accidentally" capture 60,705 lb of yellowtail rockfish. In fact, they project that they will harvest over 20,000,000 lb of non-halibut species incidental to their fishery. (Note: only some nondirected species are shown, so the bottom total does not match the sum.)

The second author of this paper populated various worksheets of The Spreadsheet one cell at a time while meeting with each sector separately and asking them to project catches of the 68 highest priority species/populations. They did this by imagining typical trips by individual vessels then expanding by the number of active licenses. The Spreadsheet manager worked through each sector and then provided a summary table (excerpted in Table 3). This process was repeated five times to allow each sector to explore the impact of varying their projections on the summary results and to ensure they were comfortable with the projections.

As can be seen even in the condensed version of the summary table (Table 3), The Spreadsheet revealed some major problems. Reading the table vertically, it is clear that some sectors that have been treated as "single-species" fisheries, by their own projections, have significant catches of nondirected species. For example, the halibut (L-license) fishery may require 20,000,000 lb of nondirected species in order to capture their typical quota of about 12,000,000 lb of halibut, even though this fishery currently does not have sufficient allocation for these nondirected species.

Reading the table horizontally indicates the species or populations for which there is not currently enough TAC to satisfy the needs of the fishery. For example, ignoring the directed fishery for rougheye rockfish (*Sebastes aleutianus*) by trawlers (T-license) and rockfish hook-and-line fishers (ZN-license), there is not enough TAC to satisfy the nondirected requirements for this species by the remaining licenses. The TAC is already oversubscribed by 37%. The situation is even worse for shortraker rockfish (*S. borealis*).

While The Spreadsheet created anxiety by revealing the scope of the allocation issues, it was essential to solve the problem. It was the summary page that really got everyone talking because now they could now see which species/population "belonged" to which sector, and therefore who were the sellers if you needed to intercept it. This was the point where the dialogue began in earnest. Initially the room went quiet while each fisher scanned the other sectors' allocations, and then either "agenda" or fear set in. It even switched between fear and agenda from one day to the next. No trading rules had yet been discussed but it was assumed that the rules would be restrictive. Even worse, there was not enough fish to go around. It was many months before all sectors were up to a similar level of understanding, but the problems were now visible and the overall group had not only taken ownership of The Spreadsheet but had taken responsibility for deriving the solution rather than blaming the messenger.

While a similar product could have been derived by DFO staff using observer programs, it was important that it be developed within the CIC. It was more a modeling or gaming process than an analytical one. During the different iterations, fishers were able to explore various strategies. Second, DFO data or even DFO participation would have been viewed with suspicion. The Spreadsheet had to be constructed by the CIC so that the participants could take ownership of the projections and the implications. Finally, the catch projections developed at a pace that allowed all representatives to fully understand the mechanics of the tables and thus the projections, and they were able to adjust to the resulting implications as they became obvious in the summary tables.

Stepwise progress

In retrospect, the participants emphasized that the early decision to work on all issues concurrently, rather than solve one issue at a time, was essential. Once they settled on the objectives, they only had to focus on moving closer to achieving these objectives while making a conscious effort to ensure that initiatives designed to satisfy one set of objectives were not undermining others. Furthermore, many of the objectives and issues overlapped and could not be considered exclusively. For example, they commented that such issues as increased cost recovery (user-pay), individual accountability, and economic viability cannot be addressed one issue at a time.

A good example of how significant progress could be achieved on one issue while working on another was development of The Spreadsheet. Given the cost, 100% observer or 100% video review was rejected by some sectors at the beginning of negotiations and therefore put aside. Had discussions started with an ultimatum, these sectors would have immediately withdrawn from discussion. But while subsequently working on The Spreadsheet it gradually became obvious

to everyone that the entire strategy hinged on credible accounting for each fisher's landings and discards. Each sector and individual realized that their allocations only had trade value if the other sectors could not circumvent catch restrictions by secretly discarding. It soon became obvious that if everyone else had to be monitored then so must "I."

Leadership

Although the requirement for effective leadership in cooperative management is well documented (Pinkerton 1989), the key roles played by specific individuals in the B.C. process is worth noting. Certain leaders were obviously valued as reliable brokers of discussion and trusted to represent and communicate the collective needs regardless of their individual situation. Members of the leadership group were also valued because of their experience and success in earlier integrating activities, such as with the trawl fishers who, during the mid-1990s, had met weekly for six months to plan their transition to a transferable IVQ system. Thus, unlike discussions decades earlier, when the fishers who caught the most fish seemed to dominate joint discussions, leadership in the CIC meetings appeared to be derived from reputations for integrity, business skills, and creativity.

In addition to characteristics of integrity and experience, the leaders also used their existing personal skill sets to facilitate discussion. One individual commented that his previous experience with lifestyle counseling and therapy, first as a receiver and then provider, was essential to his contribution during CIC meetings, not to mention when interacting with DFO.

Finally, the need for "Generous Persistence" (Hanna 2003b) was obvious. The process required that the leaders not only had the capacity but the commitment. One participant, when asked how much of his personal funds had gone toward the process, without chance of reimbursement, stated that he had stopped adding one night when the total passed $50,000. It can be argued that self-interest can explain the commitment but the benefits will accrue to the entire industry so, at the end of the process, these leaders will still be over $50,000 in the red in comparison with the constituents they represent.

Summary

We suggest that the proposed integration strategy now under consultation provides a plausible basis for developing a sustainable and viable groundfish fishery in British Columbia, and that it will help meet an obviously complex and evolving set of needs. While the work has just begun and the process may even fail, we are encouraged and surprised at the progress to date. We have written this paper to illustrate some key "hands-on" ingredients which we think have been essential to the

progress of this initiative as well as leading to the overall self-empowerment by a commercial fishing industry group (Jentoft 2005).

While these ingredients, in generic form, are well known (see Pomeroy et. al. 2001), we hope that providing specific concrete examples will emphasize their importance and assist other projects. Finally, while the challenge of creating healthy fishing communities and responsible fishing is typically viewed as an engineering process of aligning the correct suite of management tools and tactics, not to be ignored is Jentoft's (2005) suggestion that a healthy and effective fishery community is required to provide the underlying context in which the engineering tactics can work.

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Nearshore Habitat Associations of Young-of-Year Copper (*Sebastes caurinus*) and Quillback (*S. maliger*) Rockfish in the San Juan Channel, Washington

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Abstract

We established scuba survey methods for young-of-year (YOY) copper (*Sebastes caurinus*) and quillback (*S. maliger*) rockfishes and used these to conduct density and habitat assessments in the San Juan Channel in 2004 and 2005. Results for both years indicated that YOY copper and quillback rockfishes occur primarily in areas with a high percent coverage (60-100%) of understory kelp at shallow depths (1.5-4.5 m). YOY copper and quillback rockfishes were patchily distributed in these areas, and predator densities did not seem to be a factor in determining which areas were utilized. Preserving shallow-water understory kelp habitats is a critical part of the conservation and management of copper and quillback rockfishes in the San Juan Archipelago.

Introduction

Copper and quillback rockfish populations in the San Juan Archipelago have declined sharply in recent years (PSAT 2002). These declines may be attributed to fishing pressures, because these species are frequently targeted by recreational fishermen in Puget Sound (Stout et al. 2001) and dominate the recreational catch in the San Juan Archipelago. Rockfish are also incidentally taken in the recreational salmon fishery.

In response to these declines, bag limits in the San Juan Archipelago were reduced from ten rockfish per person per day to five in 1994. In 2000, bag limits were further reduced to the current bag limit of one rockfish per person per day. Over approximately the same period, twelve marine protected areas (MPAs) were created in the San Juan Archipelago, all of which are no-take zones for rockfishes. Copper rockfish and lingcod were found to be larger and more abundant inside some reserves in the San Juan Channel, compared to nearby non-reserve sites (Eisenhardt 2001). Despite these protective measures, results from PSAT (2002) show that copper and quillback rockfish populations in the area continue to decline.

A remotely operated vehicle (ROV) survey of subtidal habitats (3 to 150 m) within the San Juan Channel conducted in 2004 showed that copper and quillback rockfishes dominated the adult rockfish fauna, with other species of rockfish being relatively uncommon (Robert Pacunski, Washington Department of Fish and Wildlife, 2006, pers. comm.). While it is known that adult copper and quillback rockfishes prefer high relief, rocky reef habitat (Pacunski and Palsson 2002), much less is known about the habitat associations of YOY (young-of-year or 0+) in the San Juan Archipelago (Buckley 1997). Knowledge of YOY copper and quillback rockfish habitat associations will help us determine which habitats need protection in order to manage and conserve rockfish populations in the San Juan Archipelago.

Carr (1991) found that YOY copper rockfish recruit to canopy kelp and drift algae off the central coast of California. In the Strait of Georgia, Haldorson and Richards (1986) found that copper rockfish recruit to kelp beds in August, and then move to eelgrass and *Agarum* beds in September and October. Buckley (1997) reported YOY quillback rockfish on shallow (<20 m) rocks in artificial reefs in Puget Sound, and hypothesized that they might initially settle on drift algae on sandy bottom and then drift into areas with canopy and understory kelp. Thus, previous work gave us an idea of where to start looking for YOY copper and quillback rockfishes. The present study is the first to use quantitative surveys to examine YOY copper and quillback habitat associations over time in natural habitats within the San Juan Archipelago.

Methods

In 2003 and 2004 we surveyed several areas using a towed video camera, and used habitat information from these video surveys to choose six sites throughout the San Juan Channel for further study: Tift Rocks, Shady Cove, Pt. George, North Bay, Shark Reef, and Cattle Pt. (Fig. 1). We chose these sites because each included a variety of habitat types including understory kelp, eelgrass, and ulvoids, and because these sites are distributed throughout much of the Channel. Each site was

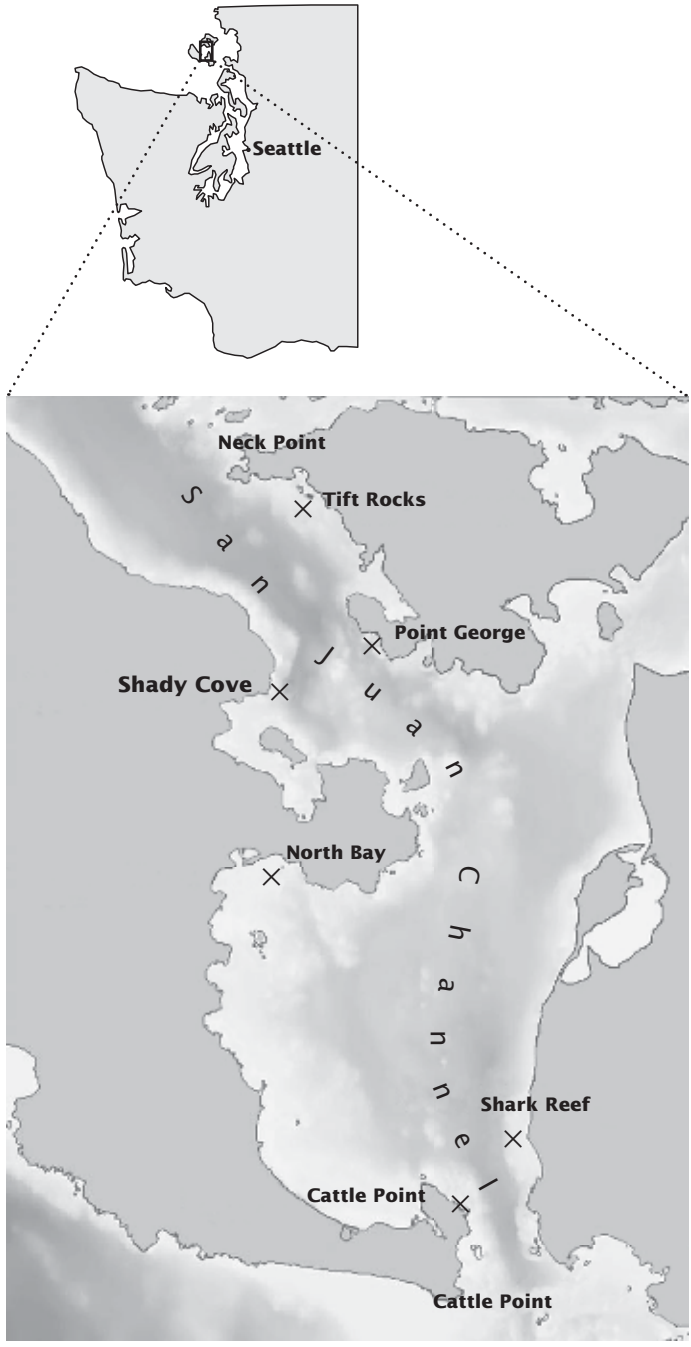


Figure 1. Study sites (indicated by ×) within the San Juan Channel.

defined as a 100-300 meter length of shoreline. Site length varied in order to include the greatest variety of habitat types possible at each site. During July 2004 we performed weekly snorkel surveys to monitor rockfishes within the kelp canopy, based on previous findings that YOY rockfish move from the pelagic zone to kelp canopy in early summer, before finally settling into nearshore habitats shortly thereafter (Buckley 1997). We began seeing YOY rockfish in the kelp canopy in late July 2004 and initiated the scuba surveys immediately. Surveys were conducted July 28–September 15, 2004 and July 18–September 20, 2005.

For scuba surveys, each site was subdivided into sampling points approximately ten meters apart along a line parallel to the shoreline. From a randomly selected sampling point, we moved perpendicular to the shoreline until we reached one of four randomly selected seafloor depths (3, 6, 9, or 12 meters). This location and depth was the starting point for each dive. From this starting point we then swam consecutive 5-meter transects along the depth contour. We swam in a direction so as to maintain constant depth and reasonably constant sampling speed relative to the current. Each dive consisted of 7-25 consecutive 5-meter transects. Over the course of the study we dove each site 9-13 times from multiple randomly selected sampling points and depths. We did not go deeper than 12 meters because YOY copper and quillback rockfish are found in relatively shallow waters in the summer (Buckley 1997). In order to eliminate tidal height as a potentially confounding variable we dove each site at high and low tide before moving on to the next site. We conducted 39 dives in 2004 and 22 in 2005.

The transect line was defined by a 5 meter, collapsible PVC pole placed along the depth contour. Diver #1 then swam the length of the pole, pressing down any vegetation in an attempt to flush out YOY. This diver searched for fish two meters or less from the bottom and one meter to either side of the pole, and counted individuals of all species of rockfish (copper, quillback, and Puget Sound: *Sebastes emphaeus*), lingcod (*Ophiodon elongatus*) and greenling (Hexagrammidae spp.) using the approximate size categories in Table 1. Diver #2 followed several meters behind diver #1 and conducted point-contact habitat surveys (Murray et al. 2006) by noting all vegetation types present (Table 2) at each 1 meter increment, from 0 to 5 meters along the pole (6 observations). During each dive we swam as many 5 meter transects as possible, depending on limitations such as water temperature, current speed, and air consumption. We averaged 19 transects per dive in 2004 and 14 transects per dive in 2005.

It was not possible to visually differentiate YOY rockfish species (particularly copper and quillback) in the field or in the laboratory at the time surveys were conducted. In an effort to confirm species composition we collected 26 YOY rockfish from sites near our study area. Twenty of these YOY were raised in tanks until they were large enough

Table 1. Species and abundance of all fish counted in 2004 and 2005.

Species	Number of fish		Approximate size (cm)
	2004	2005	
YOY copper/quillback	59	202	3-7
Juvenile quillback	0	3	8-20
Adult quillback	5	3	21-40
Juvenile copper	13	35	8-30
Adult copper	32	26	31-45
Juvenile greenling	7	0	10-20
Adult greenling	31	25	21-50
Adult Puget Sound	4	15	8-18
Adult lingcod	21	9	50-100

Table 2. Vegetation types quantified by diver #2.

Vegetation types noted	Example
Sea lettuce	*Ulva* spp.
Eelgrass	*Zostera marina*
Canopy kelp	*Nereocystis luetkeana*
Understory kelp	*Laminaria* spp.
Stipitate kelp	*Pterygophora* spp.
Desmarestia (filamentous)	*Desmarestia viridis*
Sargassum	*Sargassum muticum*
Fucus	*Fucus gardneri*
Green filamentous algae	*Acrosiphonia* spp.
Red branched algae	*Callophyllis* spp.
Red bladed algae	*Chondracanthus* spp.

to visually identify, while six were genetically analyzed. Of the 20 YOY maintained in the lab, 12 proved to be quillback rockfish. The remaining eight were either quillback or copper. Mitochondrial and satellite DNA analyses are still in progress, but of the six fish processed, four were quillback, one was a copper, and one was identified as either a copper, quillback, or a hybrid of the two (Piper Schwenke, NOAA, 2006, pers. comm.).

We converted the point-contact observations into percentages by summing the number of contact points for each vegetation type (including "no algae") and dividing this by the total number of observations. More than one vegetation type could be present at each contact point. For example, if understory kelp was present at 5/6 contact points along a particular transect, the transect was considered 83.33% understory kelp. However, if red branched algae was present at 3/6 contact points, this transect was also 50% red branched algae. The total vegetative cover for this transect would be 133.33%.

Several brief behavioral studies were conducted to observe YOY rockfish reaction (neutral, attraction, or avoidance) to the pole. In these studies, we chose an area where YOY rockfish had previously been sighted. Once a YOY rockfish was located, we placed a 1 meter PVC pole on the seafloor immediately adjacent to it and observed any reaction to the pole. We conducted 13 trials on 14 individuals. Typically (73% of observations) the YOY rockfish moved less than 0.5 meters, and then remained stationary, even when a diver was present. Twenty-seven percent of the time the YOY rockfish showed no reaction at all. The behavioral studies support our assumptions that YOY rockfish are not significantly affected by the PVC pole used to indicate each transect, nor by the diver holding the pole. Because our transect width was 1 meter, results are not affected by fish avoidance and suggest that there is little potential for double-counting or undercounting because fish moved away from the counting area.

Results

During 2004, we surveyed a total of 7,160 m^2, and found 59 YOY copper and quillback rockfish. In 2005, we surveyed a total of 4,440 m^2 and found 202 YOY copper and quillback rockfish. In both 2004 and 2005, all YOY rockfish (261 out of 261) were found in transects containing some amount of understory kelp (Fig. 2).

We analyzed the percentage of YOY rockfish observed in each habitat type, compared with the total percent of each habitat type that was available. Note that the total percentage of YOY rockfish sums to more than 100 because it is possible for a YOY to be associated with more than one habitat type in a given transect. In 2004 100% of the YOY rockfish were found in understory kelp, yet this habitat type made up

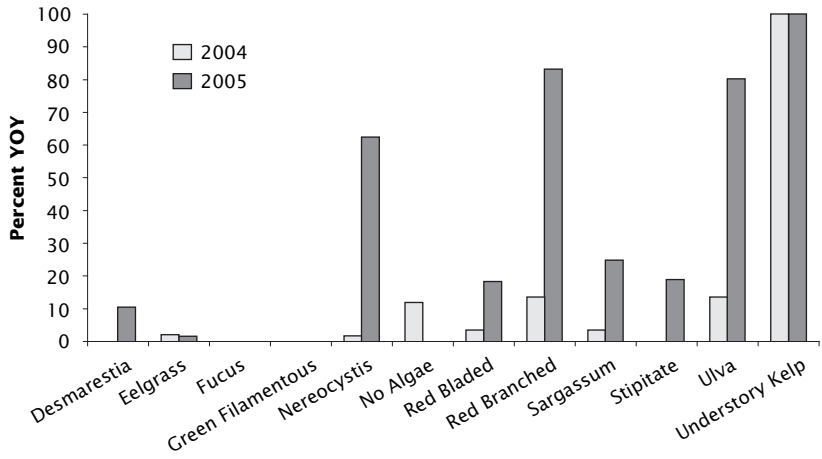


Figure 2. Percentage of young-of-year rockfish (YOY) found in each vegetation type, by year. Note that a given transect could have more than one vegetation type. Therefore, percentages total to more than 100%.

only 52% of the total area surveyed (Fig. 3). In 2005, 100% of the YOY rockfish were again found in understory kelp, yet this habitat type made up only 43% of the total habitat surveyed (Fig. 3). In 2005, YOY rockfish were found in a greater variety of habitat types than in 2004, in that disproportionately high densities of YOY rockfish were also found in *Ulva*, *Nereocystis*, and red branched algae, as well as understory kelp.

We found that YOY copper and quillback rockfishes not only prefer areas with understory kelp, but they prefer areas with a high percent coverage of understory kelp. In both 2004 and 2005, a disproportionately high fraction of YOY rockfish were observed in transects with a large amount of understory kelp (Fig. 4), and these differences were highly significant statistically (chi square test, $p < 0.001$). In 2004, 88% of YOY rockfish were present in transects composed of 80-100% understory kelp even though this high percentage of understory kelp coverage represented only 35% of all available habitats (Fig. 4). Although a greater percentage of YOY were observed in transects containing 60-80% understory kelp in 2005, the overall pattern remains the same: all of the YOY were found in areas with a high percent cover of understory kelp (60% cover or more) (Fig. 4).

In 2004, YOY rockfish were observed at tide-corrected depths of 0.6-9.8 m with the majority (83%) between 1.5-4.5 m (Fig. 5). In 2005, YOY

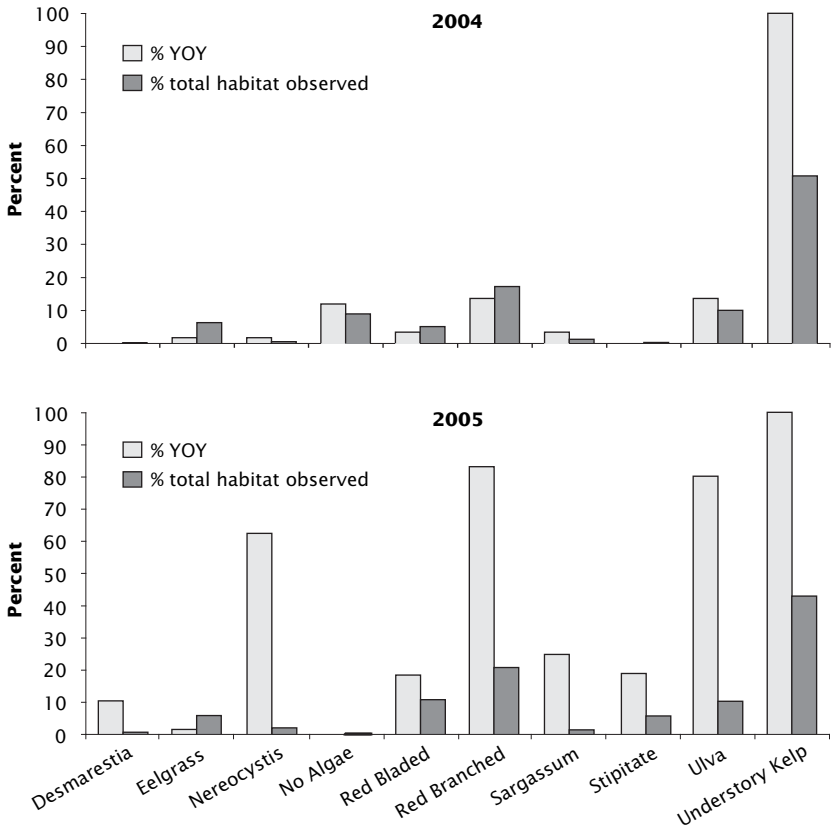


Figure 3. Percentage of young-of-year rockfish (YOY) observed in each vegetation type (light gray bars), compared to percentage of each habitat type available (dark gray bars), by year.

rockfish were observed at tide-corrected depths of 0.7-6.8 meters, with the majority (93%) between 1.5 and 4.5 meters (Fig. 5).

We found that YOY copper and quillback rockfishes require a combination of both relatively shallow depths and high percent cover of understory kelp. In 2004, 81% of YOY rockfishes were found at shallow depths (<4.5 meters) and high percent coverage (>60%) kelp, whereas only 5% of YOY rockfishes were found in shallow depths and low understory kelp cover, and only 12% were found at deeper depths with high understory kelp cover (Table 3) . In 2005, we observed a similar pattern: no YOY rockfish were found in shallow depths and low understory kelp cover, 5% were found at deeper depths with high understory kelp cover,

Table 3. Percentage of young-of-year rockfish (YOY) found at shallow vs. deep depths and high vs. low kelp coverage, 2004-2005.

	Low (<50%) kelp coverage	High (>50%) kelp coverage
2004		
Shallow (<4.5 meters)	5	81
Deep (>4.5 meters)	2	12
2005		
Shallow (<4.5 meters)	0	95
Deep (>4.5 meters)	0	5

with 95% of YOY found at shallow depths and in areas with a high cover of understory kelp (Table 3).

Although YOY rockfish prefer areas with a high percent cover of understory kelp at depths of 1.5-4.5 meters, habitats that fit this description do not always contain YOY copper and quillback rockfish. In 2004, YOY rockfish were found in only 10% of transects composed of at least 60% understory kelp at 1.5-4.5 meters, and in 2005 YOY rockfish were found in only 17% of transects fitting this description.

Of the six sites we surveyed in 2004, we measured the highest densities of YOY rockfish at Shady Cove and Point George (Fig. 6). Both of these sites are within MPAs, where both size and density of adult rockfish and lingcod are higher than in comparable unprotected sites (Eisenhardt 2001; Fig. 7). In 2005, YOY densities at Shady Cove and Pt. George were higher than in 2004, and there were also high densities of YOY rockfish in North Bay and at Shark Reef (Fig. 6). North Bay and Shark Reef are not within or adjacent to MPAs.

Although we saw numerous other fishes while conducting surveys (Table 1, Fig. 8), only two fish were seen in transects containing YOY rockfish: one adult greenling in the same transect as three YOY rockfish, and one adult lingcod in the same transect as one YOY rockfish.

Discussion

Our results indicate that understory kelp beds are important habitats for YOY rockfishes. All YOY rockfishes in this study were sighted in transects that contained understory kelp, while understory kelp represented only 52% of the total available habitat surveyed in 2004, and 43% of the total available habitat surveyed in 2005. The density of understory kelp was also important: 88.15% of YOYs were found in transects composed

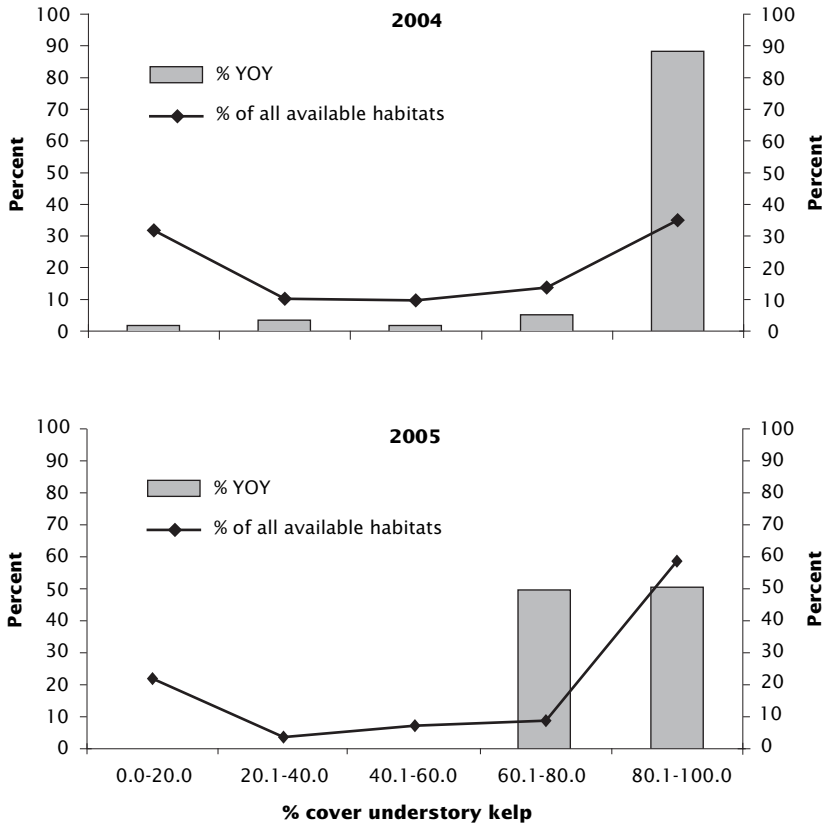


Figure 4. Percentage of young-of-year rockfish (YOY) observed (bars), and percentage of all available habitats (line) for five levels of understory kelp coverage, by year.

of 80-100% understory kelp in 2004, and 100% of YOYs were found in transects composed of 60-100% understory kelp in 2005 (Fig. 4).

Depth distributions of YOY rockfishes were clearly defined in this study, with highest occurrence in relatively shallow depths (1.5-4.5 m) (Fig. 5). We conducted 643 transects outside of this depth range, and 313 of these transects (49%) were composed of 60-100% understory kelp, so the depth range occupied by YOY rockfish represents only a minor fraction of understory kelp habitat available.

YOY rockfishes require a combination of both relatively shallow depths and a high percent cover of understory kelp. In both 2004 and 2005, areas with high percent coverage (>50%) of understory kelp at depths greater than 4.5 meters, and areas with a low percent cover of

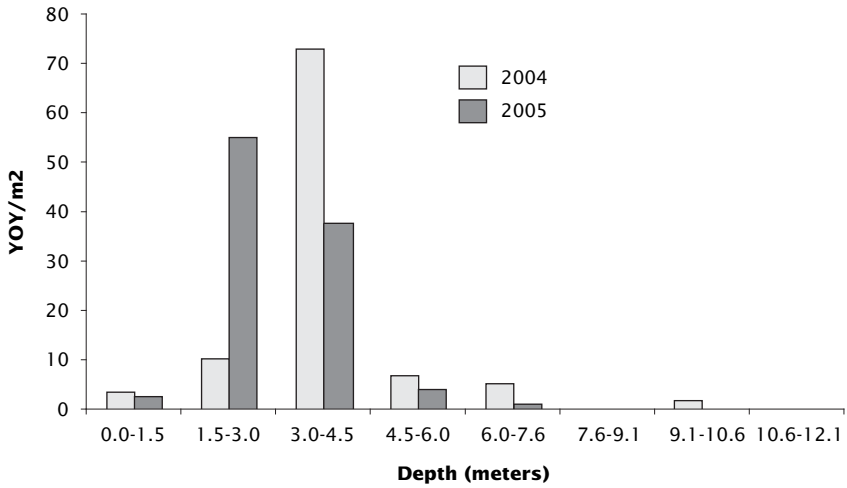


Figure 5. Density of young-of-year rockfish (YOY per m^2) observed, by depth and year.

understory kelp at depths shallower than 4.5 meters contained very few YOY rockfish (Table 3).

YOY copper and quillback rockfishes are patchily distributed in that a high percent cover of understory kelp at depths of 1.5-4.5 meters does not necessarily indicate the presence of YOY. Although most of the YOY we saw were found in areas with a high percent cover of understory kelp at depth of 1.5-4.5 meters, YOY are not present in all areas fitting this description. In other words, a high percent cover of understory kelp at depths less than 4.5 meters are necessary but not sufficient habitat requirements for YOY copper and quillback rockfish.

One possible explanation for this patchy distribution is predator avoidance. Adult rockfish, lingcod, and kelp greenling are all potential predators of YOY rockfish (Miller and Geibel 1973, Simenstad et al. 1979, Hobson et al. 2001), and although these species were observed in areas with a high percent cover of understory kelp at depths of 1.5-4.5 meters (Fig. 8), we rarely sighted any fish in the same transect as YOY rockfish. This could indicate that YOY rockfish are avoiding predators on a small spatial scale. Another explanation is that even in optimal habitat both YOY rockfish and their predators occur in low densities, so we might not be seeing them in the same transect because there is a low probability of two rare events occurring in a single 5-meter transect.

Although YOY may be avoiding predators at a small-scale, predator avoidance does not explain the difference in YOY rockfish densities at

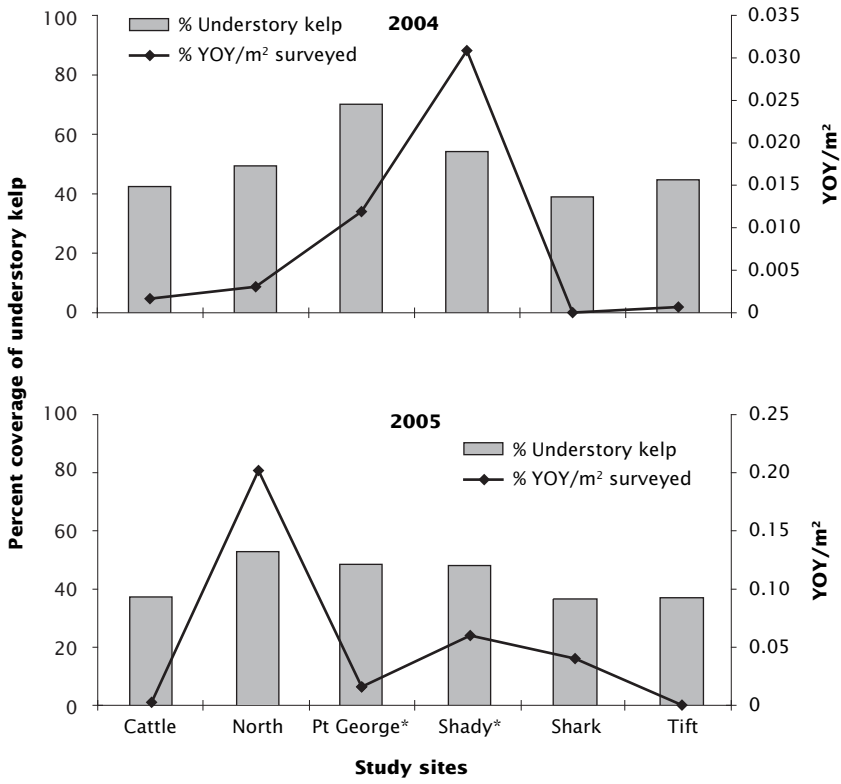


Figure 6. Density of young-of-year rockfish (YOY per m²) at each study site, by year. Asterisks signify marine protected areas (MPAs), where YOY predators are larger and more abundant.

a larger scale, between study sites. In 2004 we found relatively high densities of YOY rockfishes at the two study sites within MPAs. This was unexpected because YOY rockfish predators such as lingcod are larger and more abundant within MPAs (Eisenhardt 2001; Fig. 7). In 2005, although higher densities of YOY were found at some sites outside of MPAs, YOY densities at sites within MPAs remained high. Our results indicate that differences in YOY densities between sites can not be attributed to predator avoidance (Fig. 7). Understory kelp coverage was relatively uniform across sites (Fig. 6) and did not explain the difference in YOY densities between sites either.

YOY were found in a greater variety of habitat types in 2005 than in 2004. Higher densities of YOY in 2005 may have resulted in spillover from the optimum habitat (areas with a high percent coverage of under-

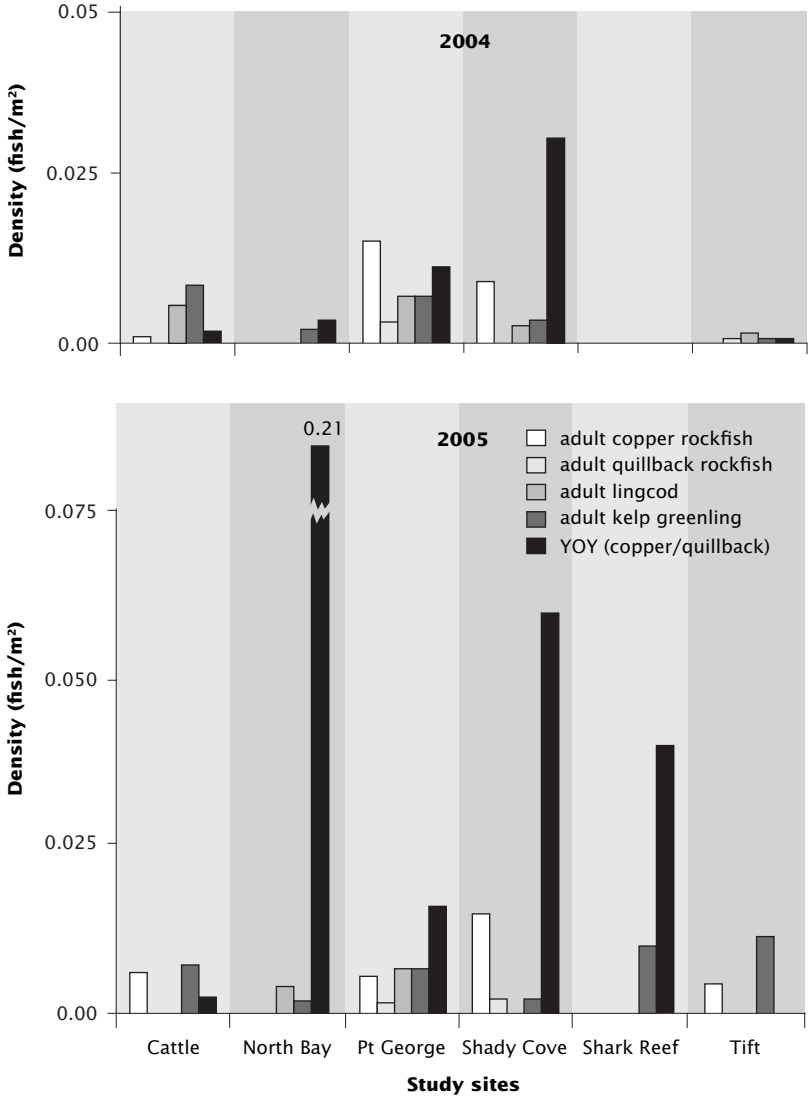


Figure 7. Density of young-of-year rockfish (YOY) predators and YOY at each study site, by year.

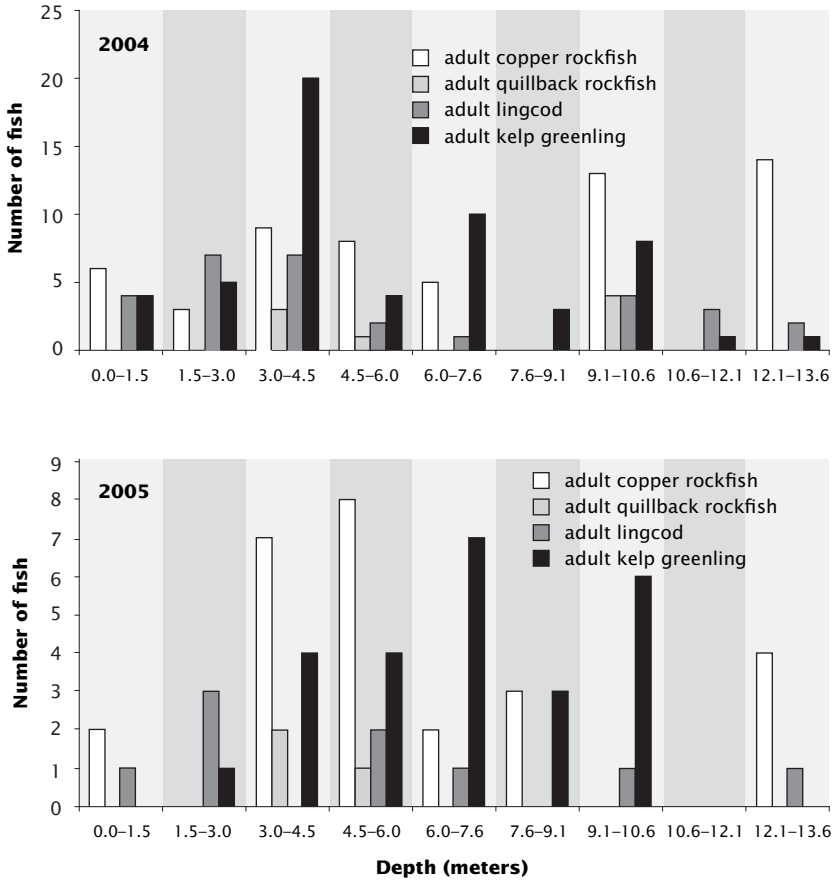


Figure 8. Depth distribution of young-of-year rockfish (YOY) predators, by year.

story kelp) into less ideal habitat types such as *Ulva, Nereocystis,* and red-branched algae. Although understory kelp is not a limiting habitat type overall, it could be locally limiting in specific areas where YOY are found. Another explanation is that YOY prefer areas with a high percent cover of understory kelp, and in 2005 these transects also had a high percent cover of *Ulva, Nereocystis*, or red branched algae, either by random chance or because of interannual differences in algal abundance.

YOY rockfish were not found in association with other common algae such as *Desmarestia*, *Fucus*, or filamentous green algae in the San Juan Channel, and they were rarely found in eelgrass beds. These results differ from Haldorson and Richards (1986), who found that YOY copper

rockfish made extensive use of eelgrass beds in the Strait of Georgia. One possible explanation for this difference is that eelgrass was not as common as alternative vegetation types in our study areas (Fig. 3).

It is clear that YOY copper and quillback rockfishes in the San Juan Channel prefer areas with a high percent coverage of understory kelp, at depths of 1.5-4.5 meters, and preservation of these habitats should be an important component of the conservation and management of these species. Nevertheless, YOY rockfishes are patchily distributed across areas that fit this description. There were differences in YOY rockfishes density between sites, but these differences could not be readily explained by predator abundance or kelp coverage. Future studies should examine the influence of factors such as small-scale eddies and convergence of currents on habitat utilization by YOY rockfishes.

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Characterizing Aspects of Rockfish (*Sebastes* spp.) Assemblages in the Aleutian Islands, Alaska

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Abstract

Understanding the spatial and temporal persistence of rockfish (*Sebastes* spp.) communities in the Aleutian Islands would help define their essential habitat as well as aid in the management of their fisheries. It is known that some *Sebastes* spp. can be distributed non-uniformly or uniformly within discrete depth zones throughout the North Pacific, but it is not known whether these patterns are consistent within assemblages of *Sebastes* species. In this study, five years of data from surveys conducted between 1991 and 2002 were used to analyze rockfish species associations in the Aleutian Islands. Agglomerative hierarchical cluster methods were used to create small-scale haul-groups (groups defined by hauls with similar species composition) and large-scale species-groups (defined for the entire Aleutian Islands area) using rockfish species and three primarily benthic species that make up the main fisheries in the Aleutian Islands (Atka mackerel [*Pleurogrammus monopterygius*], Pacific cod [*Gadus macrocephalus*], and sablefish [*Anoplopoma fimbria*]). Six haul groups were found, three of which were persistent throughout the five-year study period. The dominant species within these groups were Pacific cod, Pacific ocean perch (*Sebastes alutus*), and a group with a combination of rougheye rockfish (*Sebastes aleutianus*), shortraker rockfish (*S. borealis*), and shortspine thornyhead (*Sebastolobus alascanus*). Depth and longitude were found to be important environmental parameters in describing a haul group. For example the rougheye rockfish, shortraker rockfish, and shortspine thornyhead group was a deepwater slope haul group, whereas the Pacific ocean perch group occurred mainly in the lower shelf depth zone. The three main haul groups were located in consistent geographical areas suggesting spatial persistence:

locations such as the north side of Amlia Island and near Little Sitkin Island were found to be areas where the rougheye rockfish, shortraker rockfish, and shortspine thornyhead haul group was persistent. The identification of areas where rockfish aggregations consistently occur may assist in defining logical areas for spatial management strategies such as marine protected areas.

Introduction

In Alaska, the number of rockfish species ranges from about 35 in Southeast Alaska to less than 10 species in the outer Aleutian Islands and northern Bering Sea (Orr et al. 1998, Love et al. 2002). In the Bering Sea/Aleutian Islands groundfish fishery management plan, 12 species of rockfish are managed in five stock assessments (four single species, one "other rockfish" complex), using a harvest strategy based on the maximum sustainable yield (MSY) of the species or complex (NMFS 2006). The four single species assessments are Pacific ocean perch (*Sebastes alutus*), northern rockfish (*S. polyspinis*), shortraker rockfish (*S. borealis*), and rougheye rockfish (*S. aleutianus*). Eight other species of rockfish are currently managed in a complex called "other rockfish" (*S. babcocki*, *S. ciliatus*, *S. proriger, S. ruberrimus*, *S. variabilis*, *S. variegatus*, *S. zacentrus*, and *Sebastolobus alascanus*). Pacific ocean perch (POP) is the only rockfish species that is commercially targeted in the Aleutian Islands (AI) region. The remaining rockfish species are caught as incidental catch by the commercial fisheries of Atka mackerel (*Pleurogrammus monopterygius*), Pacific cod (*Gadus macrocephalus*), and sablefish (*Anoplopoma fimbria*) (Reuter and Spencer 2003, Spencer and Reuter 2003).

The incidental catch of rockfish in the Aleutian Islands fisheries may negatively impact rockfish populations if the catch is high and limited to a particular area. Rockfish may be vulnerable to fishery impacts because they are long-lived; slow-growing, and may exhibit stock structure (Withler et al. 2001, Williams and Ralston 2002, Matala et al. 2004). Traditional management techniques using harvest quotas based on biomass estimates may not be effective due to inadequate sampling by the surveys. A possible alternative is to create a spatial management strategy that may involve marine reserves or harvest limited areas. These types of management strategies would require knowledge of areas of high rockfish diversity, spawner abundance, and spatially persistent rockfish assemblages (Soh et al. 2001).

Persistence of a species assemblage has been defined by analyzing the consistency of species composition, geographic boundaries, and environmental factors such as depth and temperature (Leaman and Nagtegaal 1986, Rogers and Pikitch 1992, Weinberg 1994, Jay 1996, Mayer and Piepenburg 1996, Reuter 1999, Williams and Ralston 2002).

Williams and Ralston (2002) described rockfish assemblages off the coasts of Oregon and California using research data, with an intent to provide useful information for fishery managers to use in developing new management strategies for rockfishes. Rogers and Pikitch (1992) used two years of commercial fishery data off the coasts of Washington and Oregon to determine whether species assemblages were found with various target or commercially important species. In their study, the six species assemblages found were either dominated by a single species or were defined by depth. Other studies using research survey data described similar species assemblages off the U.S. West Coast, and showed how environmental factors such as depth and latitude (or geographic location) affect the structure of these assemblages (Gabriel and Tyler 1980, Jay 1996, Williams and Ralston 2002).

The objectives of this paper are to use fishery-independent trawl survey data to give a preliminary description of rockfish species assemblages in the Aleutian Islands, determine their persistence throughout five surveys conducted over a 12-year period, and describe the environmental attributes that may assist in defining the location of those assemblages.

Materials and methods

Bathymetric, temperature, and species composition data collected from five (1991, 1994, 1997, 2000, and 2002) Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, Aleutian Islands (AI) summer bottom trawl surveys were used for this analysis (Fig. 1). The area covered by the survey ranges from the Islands of Four Mountains in the eastern AI to Stalemate Bank in the western AI, a distance of approximately 1,000 miles, and depths from 50 to 500 m. To ensure comparability of hauls across different years and regions, only hauls with the same gear type were selected. All haul locations were over trawlable bottom, and hauls where the net was hung up or torn were not used. There were a maximum of 425 AI survey stations, and in a given survey year approximately 417 stations were selected using a modified Neyman optimum allocation sampling strategy (Zenger 2004). The study used the high-opening, four-panel polyethylene-nor'eastern trawl net. Although research surveys in the 1980s were conducted, these data were excluded from further analysis, as little information exists regarding comparisons between the differing gear types (Zenger 2004). A total of 1,941 tows were analyzed in this study (Table 1).

The species included in the analysis (Table 2) were rockfish that occurred in greater than 1% of survey hauls across all years combined: Pacific ocean perch (POP), rougheye rockfish (RE), shortraker rockfish (SR), northern rockfish (NR), dusky rockfish, harlequin rockfish, and shortspine thornyhead (SST). Other commercially important species

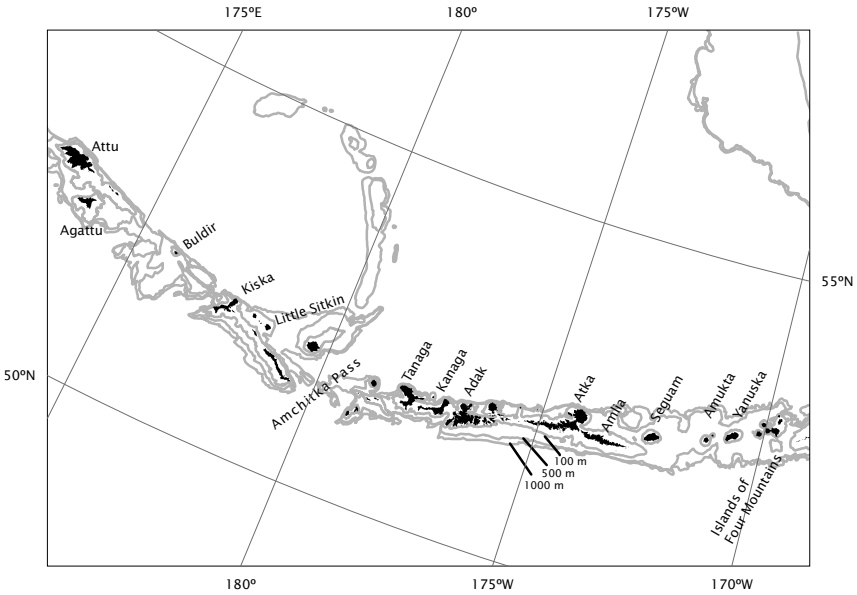


Figure 1. Map of study area showing features described in text.

with primarily benthic adult stages were also included: Atka mackerel (AM), sablefish (Sab), and Pacific cod (Pcod). The catch-per-unit-effort (CPUE; number caught per km^2) of each species was computed as the number caught divided by the total area trawled (the distance trawled times the net width) for each trawl. For those hauls in which net width was not recorded, the net width was estimated from linear regressions of net width on the inverse relationship to bottom depth (C.S. Rose, unpubl., 1993).

A preliminary examination of depth distribution by size revealed that Pacific ocean perch, rougheye rockfish, shortraker rockfish, Pacific cod, and sablefish showed size-specific depth distributions. This suggests a potential delineation of habitat for both juvenile and adults of these species. Therefore, two size categories, small and large, were created for these species. The length that determined the upper boundary of the small category for each species was 25 cm (Pacific ocean perch), 35 cm (rougheye rockfish and shortraker rockfish), 40 cm (Pacific cod), and 50 cm (sablefish). Hauls with no length data for a size category were not used in calculation of CPUE.

For each year of survey data, a hierarchical cluster analysis was conducted to produce haul groups (groups of hauls with similar species composition) and species groups (groups of species with similar

Table 1. Number of hauls per year used in this analysis.

Year	Number of hauls
1991	323
1994	382
1997	420
2000	409
2002	407
Total	1,941

Source: AFSC Aleutian Islands bottom trawl survey.

Table 2. Frequency of occurrence and proportion of total catch in survey hauls for rockfish and other demersal species.

Common name	Species	Frequency of occurrence	Proportion of total catch
Pacific cod	*Gadus macrocephalus*	67.4%	8.1%
Walleye pollock	*Theragra chalcogramma*	60.2%	10.0%
Pacific ocean perch	*Sebastes alutus*	52.4%	28.8%
Northern rockfish	*Sebastes polyspinis*	31.1%	4.9%
Atka mackerel	*Pleurogrammus monopterygius*	29.2%	23.6%
Rougheye rockfish	*Sebastes aleutianus*	24.7%	0.6%
Shortraker rockfish	*Sebastes borealis*	13.5%	1.0%
Shortspine thornyhead	*Sebastolobus alascanus*	13.2%	0.3%
Sablefish	*Anoplopoma fimbria*	9.3%	0.4%
Dusky rockfish	*Sebastes variabilis*	2.8%	0.0%
Light dusky (not separated)		3.8%	0.0%
Dark dusky (not separated)		0.6%	0.0%
Harlequin rockfish	*Sebastes variegatus*	1.9%	0.0%
Redbanded rockfish	*Sebastes babcocki*	0.2%	0.0%
Sharpchin rockfish	*Sebastes zacentrus*	0.2%	0.0%
Emperor rockfish[a]	*Adelosebastes latens*	0.2%	0.0%
Broadbanded thornyhead	*Sebastolobus macrochir*	0.2%	0.0%
Yelloweye rockfish	*Sebastes ruberrimus*	0.1%	0.0%

[a]Emperor rockfish is also known as Aleutian scorpionfish.

Table 3. Species assemblages as identified by hierarchical cluster analysis.

	RE/SR/ SST	POP group	Pcod group	Small POP	NO/ AM	AM
Large rougheye rockfish	**0.19**	0.06	0.00	0.00	0.01	0.05
Small rougheye rockfish	0.03	0.02	0.00	0.02	0.00	0.00
Large POP	**0.15**	**0.32**	0.04	0.08	**0.16**	0.03
Small POP	0.00	0.10	0.03	**0.41**	**0.13**	0.07
Northern rockfish	0.01	**0.14**	0.06	**0.14**	**0.25**	0.00
Large shortraker rockfish	**0.20**	0.01	0.00	0.00	0.00	0.00
Small shortraker rockfish	0.05	0.00	0.00	0.00	0.00	0.00
Shortspine thornyhead	**0.20**	0.03	0.00	0.02	0.01	0.00
Dusky rockfish	0.00	0.02	0.01	0.04	0.04	0.00
Harlequin rockfish	0.00	0.01	0.00	0.00	0.00	0.00
Atka mackerel	0.01	0.08	**0.23**	0.03	**0.24**	**0.73**
Large Pacific cod	0.04	**0.17**	**0.44**	0.07	**0.12**	0.02
Small Pacific cod	0.00	0.02	**0.18**	**0.18**	0.03	0.00
Large sablefish	0.08	0.02	0.00	0.00	0.00	**0.10**
Small sablefish	0.01	0.00	0.00	0.00	0.00	0.00

Individual species are listed in rows, species assemblages in columns. Numbers in each cell represent the proportion of CPUE, on average 1994-2002 only, of each species. Bold numbers indicate species that dominate the composition of each assemblage (>10% of CPUE).

distribution patterns) (Clifford and Stephenson 1975, Jongman et al. 1995). A matrix was created for the cluster analysis that was composed of CPUE data for the individual species by individual hauls from the AI bottom trawl surveys. Prior to the cluster analysis, the data were log transformed using log (CPUE+1) to minimize the influence of outliers and adjust non-normal distributions (Field 1984, Jager and Looman 1995).

S-PLUS statistical software (version 6.2, Insightful Corp.) was used to create a dissimilarity matrix and then perform an agglomerative hierarchical clustering using the average linkage method. (Reference to trade names does not imply endorsement by NOAA Fisheries.) The Bray-Curtis dissimilarity measure is commonly used to provide "ecological patterns" in large data sets. The Bray-Curtis dissimilarity matrix compares each pair of hauls or species (depending on the matrix) using the formula:

$$BC_{ij} = \sum \frac{\left| n_{ik} - n_{jk} \right|}{\left(n_{ik} + n_{jk} \right)}$$

where n is the abundance of k haul or species at i (individual species) and j (individual hauls) group. Each group is defined by its dissimilar-

ity or similarity to the other groups (Clifford and Stephenson 1975, Jongman et al. 1995). The resultant values range from 0 (most similar) to 1 (most dissimilar). Average linkage clustering (van Tongeren 1995) was used to produce an average dissimilarity measure between all possible pairs of points within two groups. Those groups with the smallest average distance between their points are then merged at each step of the clustering analysis.

To obtain haul groups, the resultant dendrogram was separated at two levels: $k = 5$ and $k = 10$ (Fig. 2 a-e). These two levels were used for all five years of trawl survey data. The initial separation, at $k = 5$, was to find any major haul groups within the dendrogram. If certain groups within the $k = 5$ level showed potential for a second separation (large number of hauls within group) then the groups found at the $k = 10$ separation were analyzed to find more meaningful subgroups (Fig. 2 a-e). Once the haul groups were determined, their species compositions were analyzed for persistence of membership for individual species over multiple years.

Haul groups were further described with regard to environmental parameters such as depth, temperature, and longitude; longitude is used as a simple indicator of spatial location within the AI. The average values of those parameters, weighted by total CPUE, were used to evaluate the relationships between environmental variables and haul groups. Geographic persistence over time was evaluated using ArcMap (version 9.0 ESRI). Haul groups (hauls) were summarized into 5 km × 5 km grids for each survey year; these grids were independent from the station grids used during the survey. These grids were then intersected to obtain locations where the particular haul group overlapped during multiple years.

Species groups were described by year for the entire Aleutian Islands region, using all hauls. These groups were used to compare with the species assemblages categorized by the haul groups.

Results

Haul groups

Three major haul groups, Pacific cod group (Pcod), a POP group, and an RE/SR/SST group, were persistent throughout all five survey years (Fig. 2 a-e). Three other haul groups, small POP, AM group, and an NR/AM group, were found during at least two survey years. The three major haul groups were defined by the species with the largest average CPUE (Table 3 shows the combined average for each species within a group): (1) the Pcod was made up mainly of large Pacific cod (44%), followed by Atka mackerel (23%) and small Pacific cod (18%); (2) the POP group was made up mainly of large Pacific ocean perch (32%), followed by large Pacific cod (17%) and northern rockfish (14%); and (3) the third group

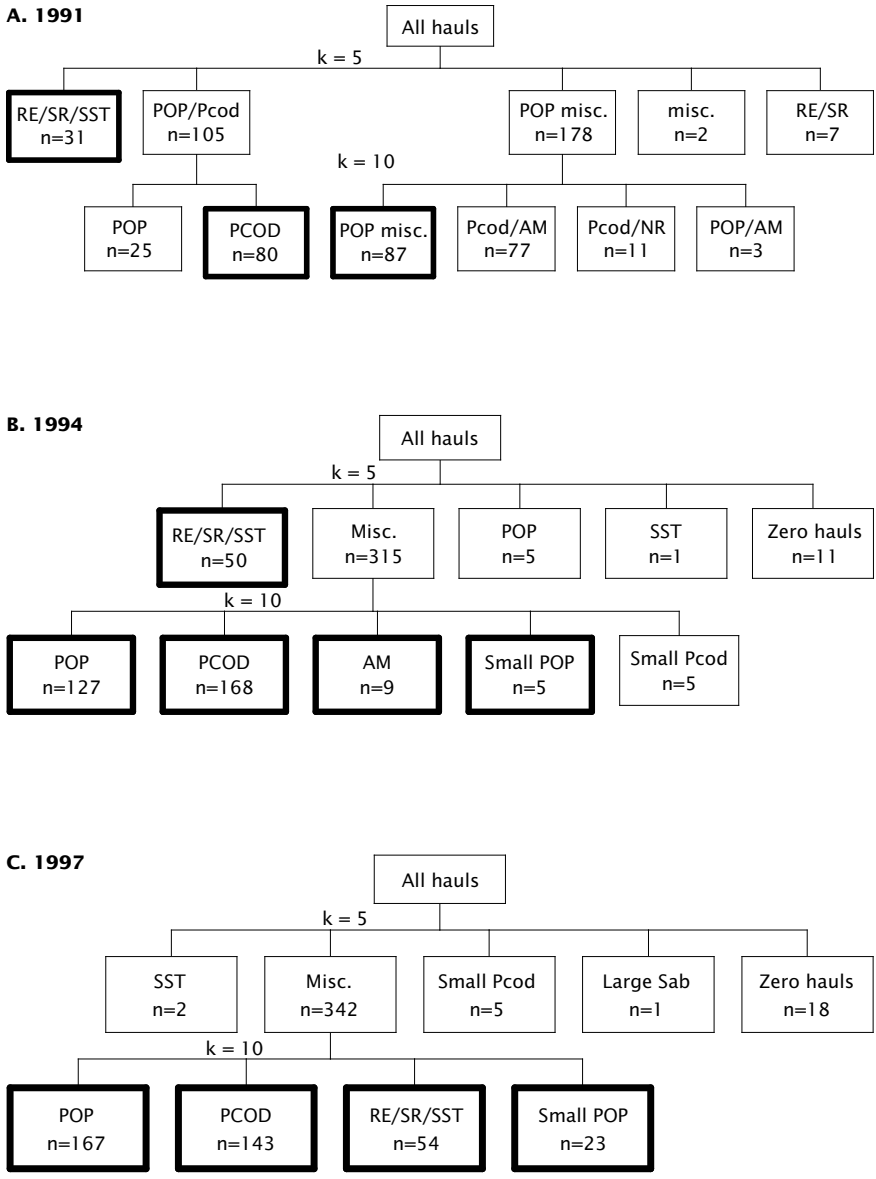
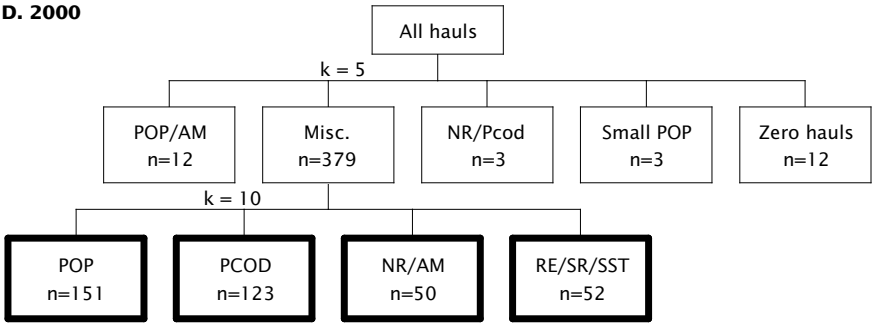


Figure 2. Cluster analysis dendrogram, separated at $k = 5$ and $k = 10$, showing haul groups for (a) 1991, (b) 1994, (c) 1997, (d) 2000, (e) 2002.

AM = Atka mackerel
NR = northern rockfish
Pcod = Pacific cod
POP = Pacific ocean perch
RE = rougheye rockfish
Sab = sablefish
SR = shortraker rockfish
SST = shortspine thornyhead

D. 2000



E. 2002

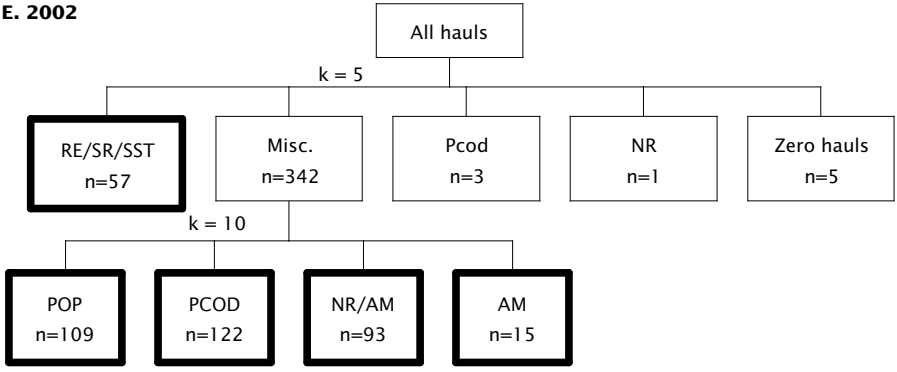


Figure 2. (Continued.)

(RE/SR/SST) was made up of a combination of large rougheye rockfish (19%), large shortraker rockfish (20%), shortspine thornyhead (20%) and large POP (15%). These groups were found at $k = 10$ separation of a larger miscellaneous group composed of mainly POP and Pcod, for each of the survey years (Fig. 2 a-e). The exception was for the RE/SR/SST group which was found at the $k = 5$ separation in the 1991 and 1994 survey data (Fig. 2 a-e).

Three other haul groups occurred during at least two survey years. These groups were a small POP group made up of mainly small POP (41%), followed by small Pacific cod (18%) and northern rockfish (14%); an Atka mackerel group (AM) composed mainly of Atka mackerel (73%) and large sablefish (10%); a northern rockfish and Atka mackerel group (NR/AM) made up mainly of northern rockfish (25%), Atka mackerel (24%), followed by large POP (16%), small POP (13%) and large Pcod (12%) (Table 3).

The spatial distribution of haul groups was described using temperature, depth, and longitude (Fig. 3 a-d). Each group was uniformly distributed throughout the Aleutian Islands chain, and was distinguished by their respective average temperature, depths, and longitudes. Data from 1991 were not used for the following analyses because temperature data were not collected. The deepest haul group was the RE/SST/SR group with an average depth between 350 m and 400 m (Fig. 3 a-d). The longitudinal center of their abundance was 178ºW near Tanaga Island in the middle of the Aleutian chain. The POP haul group was found in the upper slope depths ranging from 200 to 250 m, with a longitudinal range between 177ºW and 179ºW or between Tanaga Island and Amchitka Island shifting eastward in 2000 and 2002. The shallowest haul group, Pcod, was located in the outer shelf between 100 and 150 m. The longitudinal center for this haul group was slightly east from the other two, in 1994 and 1997 at 176.5ºW, and farther east in 2000 and 2002 at 175.5ºW-174.5ºW, or the distance between Adak Island and Amlia Island.

The spatial distribution of the three haul groups that occurred in only two surveys varied (Fig. 3 a-d). One group, the small POP group, was present during the 1994 and 1997 surveys; its average depth was between 100 and 150 m and its longitudinal center of abundance was near 175ºW or Atka Island, shifting less than half a degree between these surveys (Fig. 3a,b). The second group, the AM group, was present in a few hauls during the 1994 (n = 9) and 2002 (n = 15) surveys (Fig. 3a,d). Although the longitudinal center of abundance for this haul group was consistently around 176ºW or near Semisopochnoi Island, its average depth varied between years. In 1994 the average depth was 130 m, and then in 2002 became much deeper at 230 m. The third group, NR/AM group, was found during the 2000 and 2002 surveys and the average depth was similar for both years, around 150 m, but its longitudinal

center of abundance shifted eastward from 2000 to 2002 (Fig. 3c,d). In 2000 the longitudinal center was near 177ºE or near Kiska Island, and in 2002 its longitudinal center was near 179ºE or near Amchitka Island.

Bottom temperature may assist in explaining the shifts in average depth and longitude. Each haul group's average temperature was plotted against depth by year (Fig. 4 a-d). The deepwater RE/SR/SST group had the coldest temperature range between 3.6ºC and 4.1ºC from 1994 to 2002, the warmest year had a weighted average temperature of 4.1ºC in 1997, and the coldest average temperature was 3.7ºC in 2000. The upper slope POP group had a temperature range between 3.8º and 4.4ºC with the warmest year being 1997 and the coldest 2000. The shallowest group, Pcod, had the warmest and broadest temperature range from 3.9º to 4.8ºC with the warmest being 1997 and the coldest 2000, similar to the POP group. The groups that occurred only twice during the five survey years showed a warm shift over time. The small POP group increased from a 4.2ºC average in 1994 to a 4.8ºC average in 1997. Although the AM group in 1997 had an average depth of 130 m and in 2000 an average of 230 m, the average temperatures for 1997 (3.6ºC) were only 0.4ºC cooler than in 2000 (4.1ºC). Water temperature for the NR/AM group increased from 3.8ºC in 2000 to 4.1ºC in 2002.

Spatial persistence was also described geographically using ArcMap (version ESRI). Only the haul groups that occurred in all survey years had sufficient data to show geographic persistence over time (Fig. 5 a-c). The RE/SR/SST group persistently occurred from 1994 to 2002 at locations north of Amlia Island, south of Kanaga Island, and a few west of Attu Island. When 1997-2002 data were used, a few more locations near Kiska Island and one near the Rat Islands were added (Fig. 5a). The POP group persisted over several areas (Fig. 5b). The locations where the POP group occurred from 1994 to 2002 were north of Yanuska Island, north of Amlia Island, in the Delarof Islands area, southwest of Amchitka Island, and several locations west of Buldir Island. Many more locations were added when using data from the 1997-2002 surveys. Using data from the 1994-2002 surveys the Pcod group sites were found at the north end of Seguam Pass, northeast of Atka Island, south of Kanaga and Tanaga Islands, a few locations between Little Sitkin and Kiska Islands, and near Agattu Island (Fig. 5c).

Species groups

Species groups showed similar species relationship to the haul groups. Species groups were similar for each survey year; therefore the aggregated species groups from the 1991-2002 surveys best describe them (Fig. 6). Three groups occurred each year, with little variation between years. One group consisted of the deepwater species: large rougheye, large shortraker, and shortspine thornyhead. Another group consisted of shallower water species such as Pacific ocean perch, Pacific cod (large

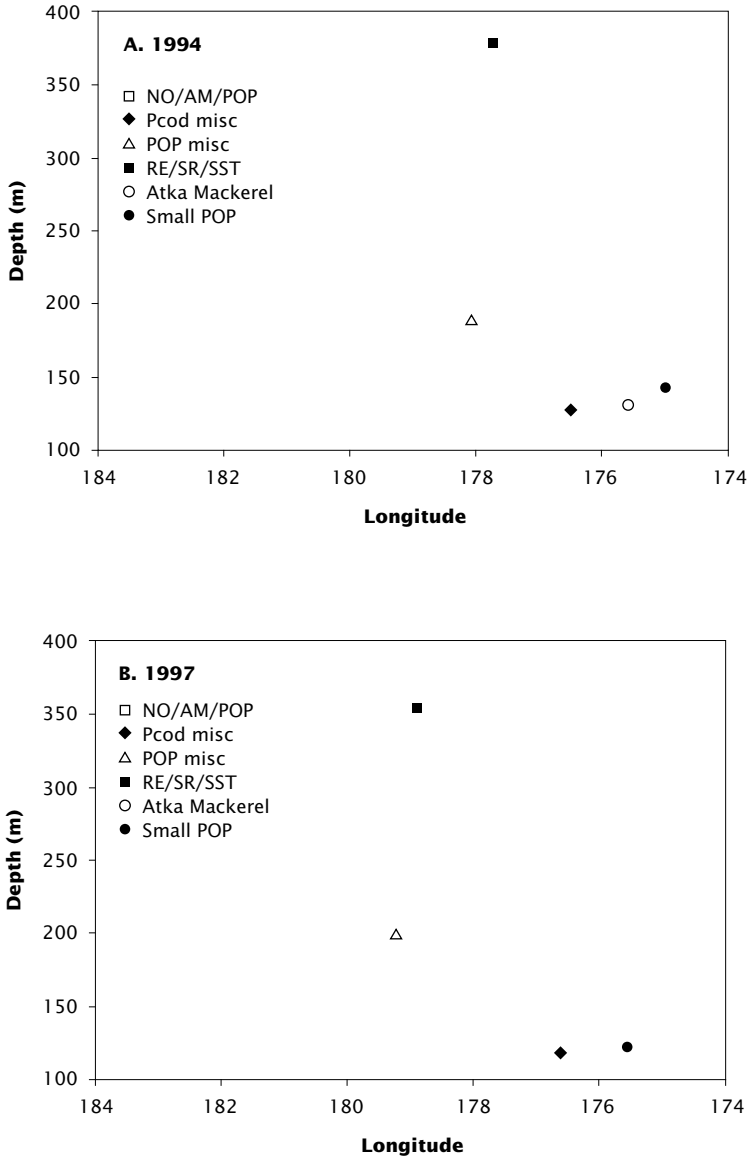
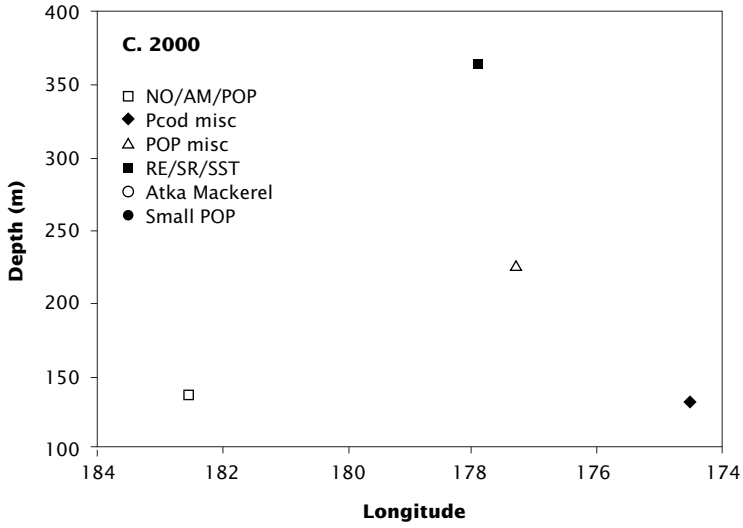


Figure 3. Plots of the weighted average for longitude and depth of each haul group by year. (a) 1994, (b) 1997, (c) 2000, (d) 2002.



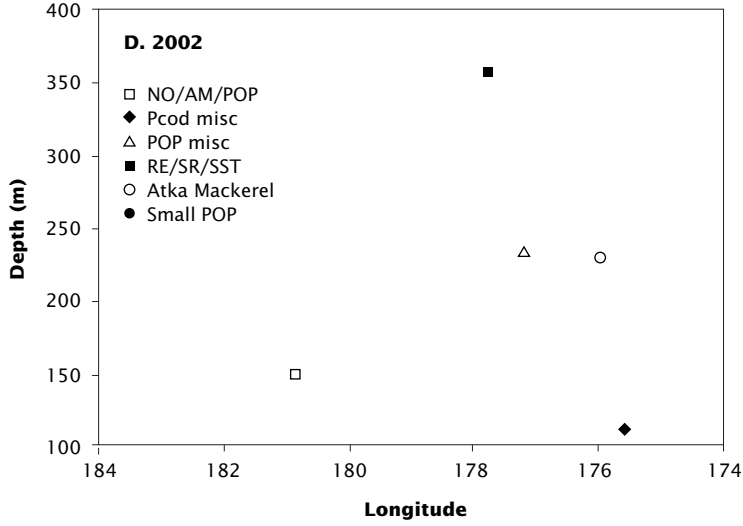


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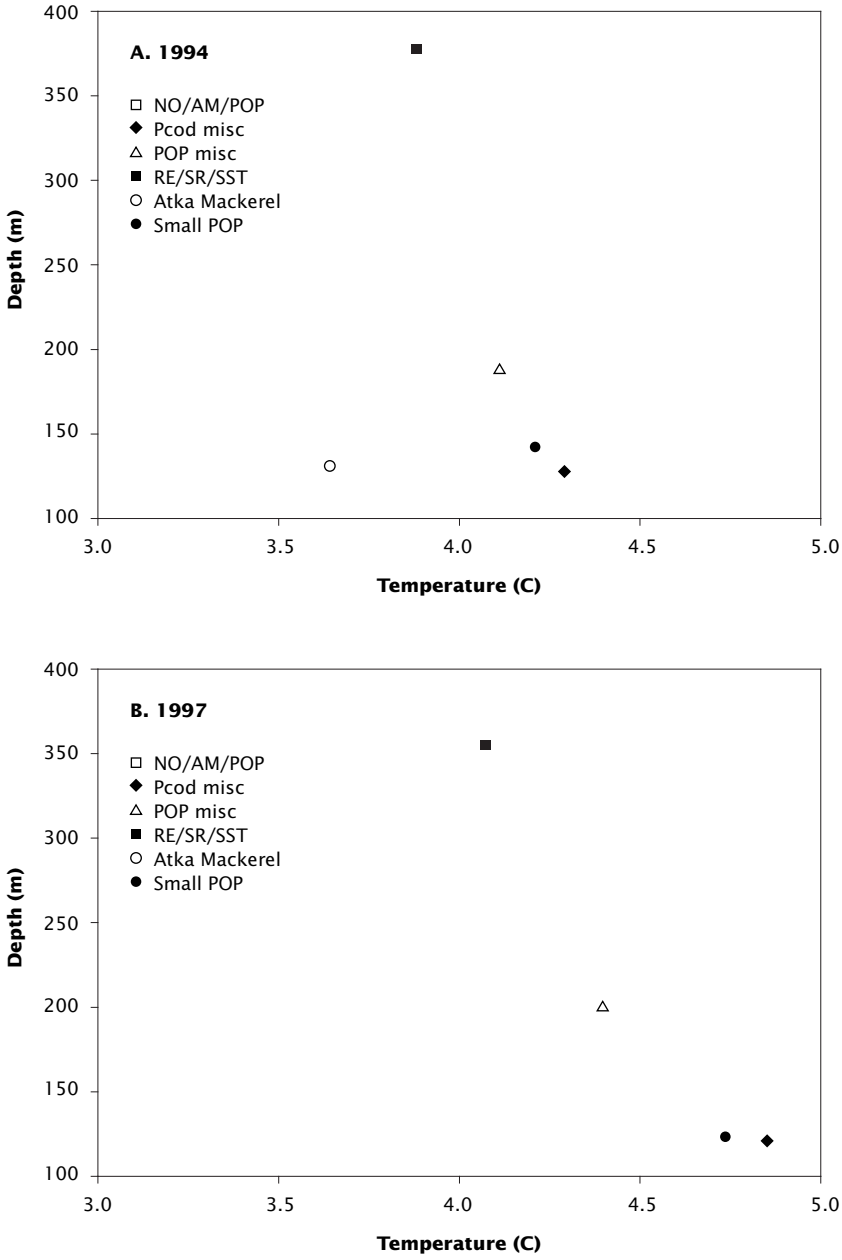
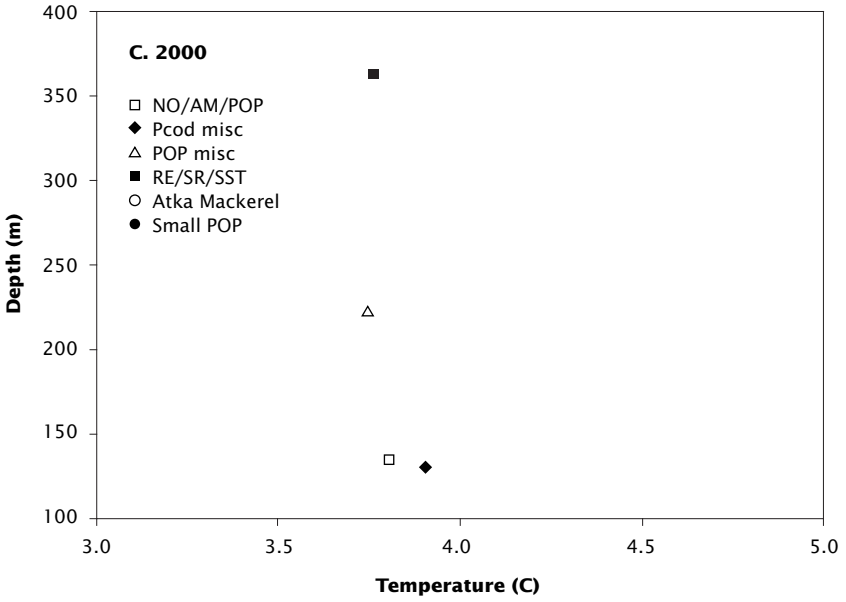


Figure 4. Plots of the weighted average for depth and temperature of each haul group by year. (a) 1994, (b) 1997, (c) 2000, (d) 2002.



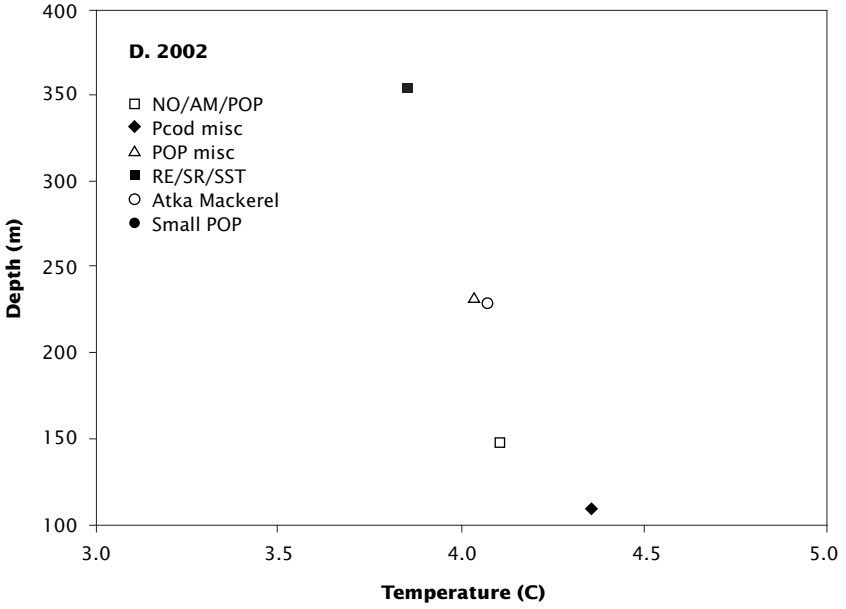


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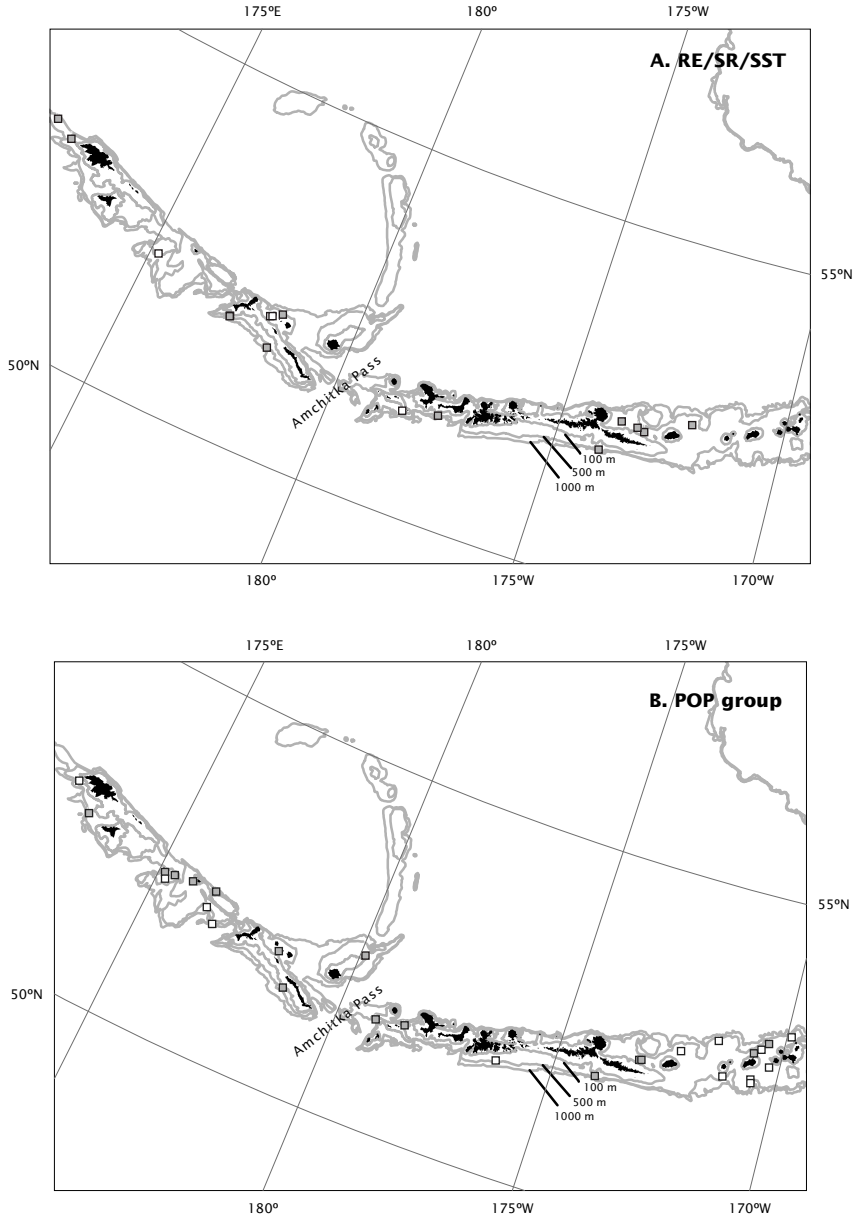


Figure 5. GIS maps illustrating areas where each haul group occurred within a 5 km × 5 km grid during four survey years (1994-2002, shaded box) and three survey years (1997-2002, outlined box). (a) RE/SR/SST group, (b) POP miscellaneous group, (c) Pcod miscellaneous group. Note: Boxes are not to scale.

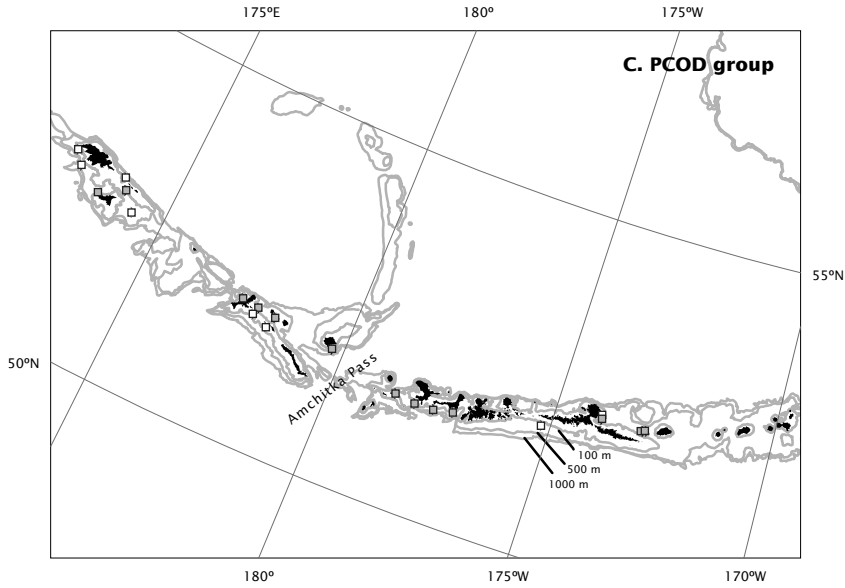


Figure 5. (Continued.)

and small), northern rockfish, and Atka mackerel. A variety of other species were in the third group, including dusky and harlequin rockfish, small rougheye rockfish, and small shortraker rockfish.

Grouping species by environmental parameters

To better understand the formation of the haul groups, depth, longitude, and temperature were analyzed for each individual species and its respective size group (Fig. 7 a-d). Graphing the longitudinal center of abundance and the average depth for individual species within a haul group showed that depth was a defining character for the haul group. When analyzing the average depth for the individual species within the three main haul groups, the species in the Pcod group were the shallowest at ~150 m, those in the POP group were in the mid-range at ~200 m, and those in the RE/SR/SST group were the deepest at >300 m.

Analysis of longitudinal distribution showed that there might be geographic differences in an individual species range that is not captured in the general haul group. Individual species within most haul groups had average longitudes that were within 2-4º, which is analogous to the central AI region. This is the result one would expect if the species were uniformly distributed throughout the AI. In 2000, however,

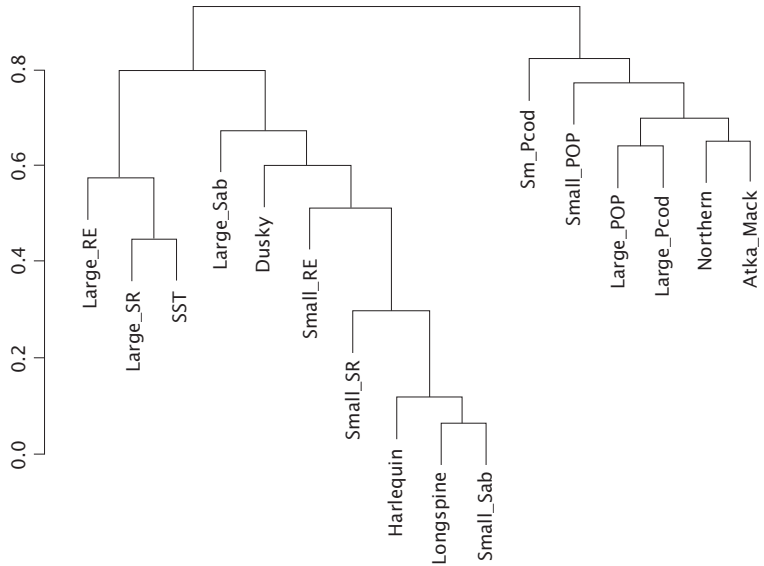


Figure 6. Dendrogram of species groups. Main groups are a deepwater group, a shallow-water group, and a miscellaneous group. Compiled data from 1991-2002 were used.

two members (Atka mackerel and small Pacific cod) of the Pcod group had a 10º difference in average longitude (Fig. 7c).

Average temperature for each individual species also influenced the character of each haul group (Fig. 8a-d). For three of the four years, similar assemblage patterns were found for the main species within the haul groups. For 1994, 1997, and 2002, similar assemblage patterns were found for the main species within the haul groups, whereas in 2000 temperature did not show the same range. The pattern of warmer to cooler, analogous to shallower to deeper, was seen for these haul groups. The Pcod group was the warmest at around 4.2º-4.8ºC (the warmest year being 1997), the POP group ranged from 4.1º to 4.4ºC, and the RE/SR/SST group was the coldest at temperatures ranging from 3.8º to 4.2ºC.

Discussion

The results from this study offer suggestions to why certain rockfish species and species size groups cluster together. Although the trawl survey data used were limited to areas where the gear was less likely to get damaged, the resultant haul groups offer a perspective of species

associations in the Aleutian Islands. The two haul groups that were not persistent throughout the study may suggest that certain species have lower selectivity to the survey trawl gear. Low selectivity may result from factors such as variable movement patterns or their center of abundance is over habitats not sampled during the trawl survey.

Analysis of five years of summer bottom trawl survey data revealed persistence in six distinct haul groups. Three haul groups occurred throughout all five years, whereas three others occurred during two of the survey years. These groups, similar to previous studies, were mainly depth dependent (Gabriel and Tyler 1980, Fargo and Tyler 1991, Rogers and Pikitch 1992, Weinberg 1994, and Jay 1996). The deepest group was the RE/SR/SST group, whose members are made up of deepwater slope rockfish species: rougheye rockfish, shortraker rockfish, and shortspine thornyhead. The other rockfish group, the POP group, was located in the lower shelf region and was made up mainly (32%) of large (>25 cm) Pacific ocean perch. The small POP group, 41% small Pacific ocean perch, was found in the upper shelf region. This finding is consistent with previous studies that found smaller/younger rockfish in shallower waters than the adults (Boehlert 1980, Love and Westphal 1981, Cailliet et al. 1996, Reuter 1999).

Similar to rockfish associations along the U.S. West Coast (Weinberg 1994), the best indicator for a spatial boundary was bathymetry, which separated the RE/SR/SST group from the POP and Pcod groups (Williams and Ralston 2002). Although hauls from across the AI archipelago were combined for this analysis, the results showed specific 25 km^2 geographic locations where these assemblages persist throughout most of the survey years. Two of these locations, north of Amlia Island and near Little Sitkin Island, could be potential locations for a marine protected area for rockfish. It was at these two locations that both the RE/SR/SST group and the POP group were present for four of the five survey years. For the Pcod group, locations such as south of Kanaga and Tanaga islands may be summer foraging areas for Pacific cod. Tagging studies from the Bering Sea and Gulf of Alaska suggest that Pacific cod are highly migratory during the summer (non-spawning) months (Shimada and Kimura 1994), and have specific spawning areas during the winter. The results from this study may suggest that Pacific cod have persistent summer foraging areas. Another finding was that Amchitka Pass (180º longitude) might be a biogeographic boundary. This is suggested by the distribution of the NR/AM group, which was only found west of Amchitka Pass. Studies of rockfish species along the U.S. West Coast found similar patterns that were defined by depth and geographic location (Gabriel and Tyler 1980, Williams and Ralston 2002). An analysis of only rockfish species off the coast of California and Oregon found four depth-related assemblages, a nearshore, a northern shelf, a southern shelf, and a deepwater slope assemblage (Williams and Ralston 2002).

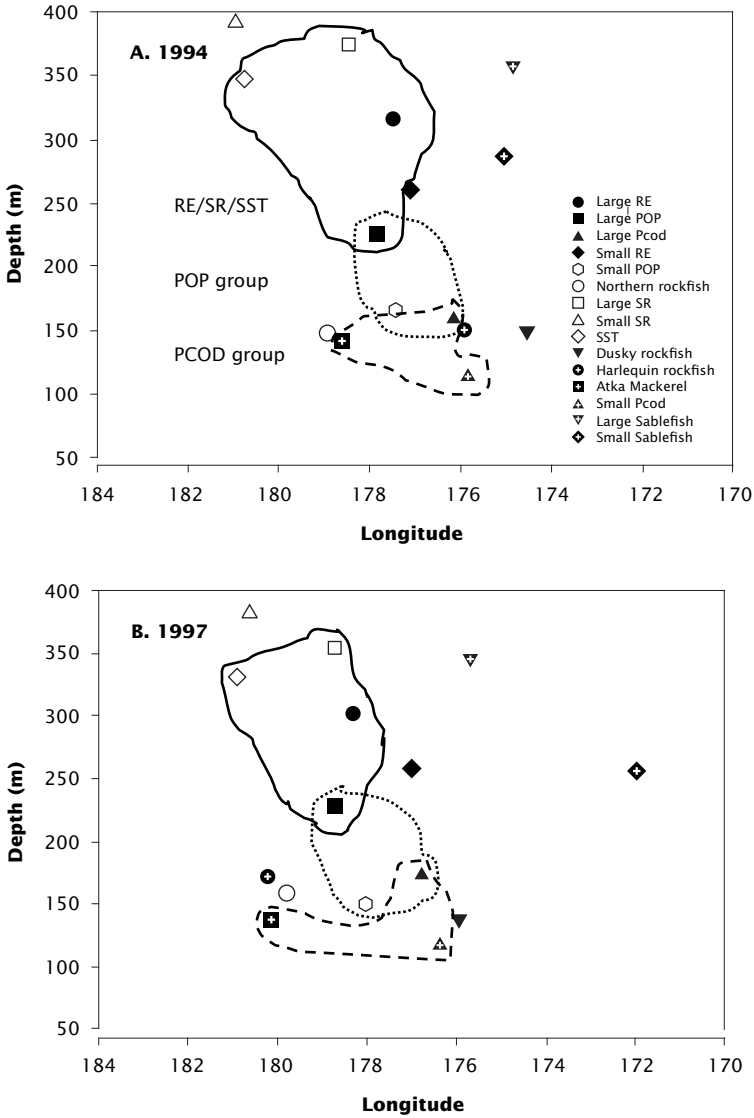


Figure 7. Plots of the weighted average for longitude and depth of each species by year. (a) 1994, (b) 1997, (c) 2000, (d) 2002. Circles denote haul groups where species occurred (>10% CPUE of haul group): solid line = RE/SR/SST group; dotted line = POP miscellaneous group; dashed line = Pcod miscellaneous group.

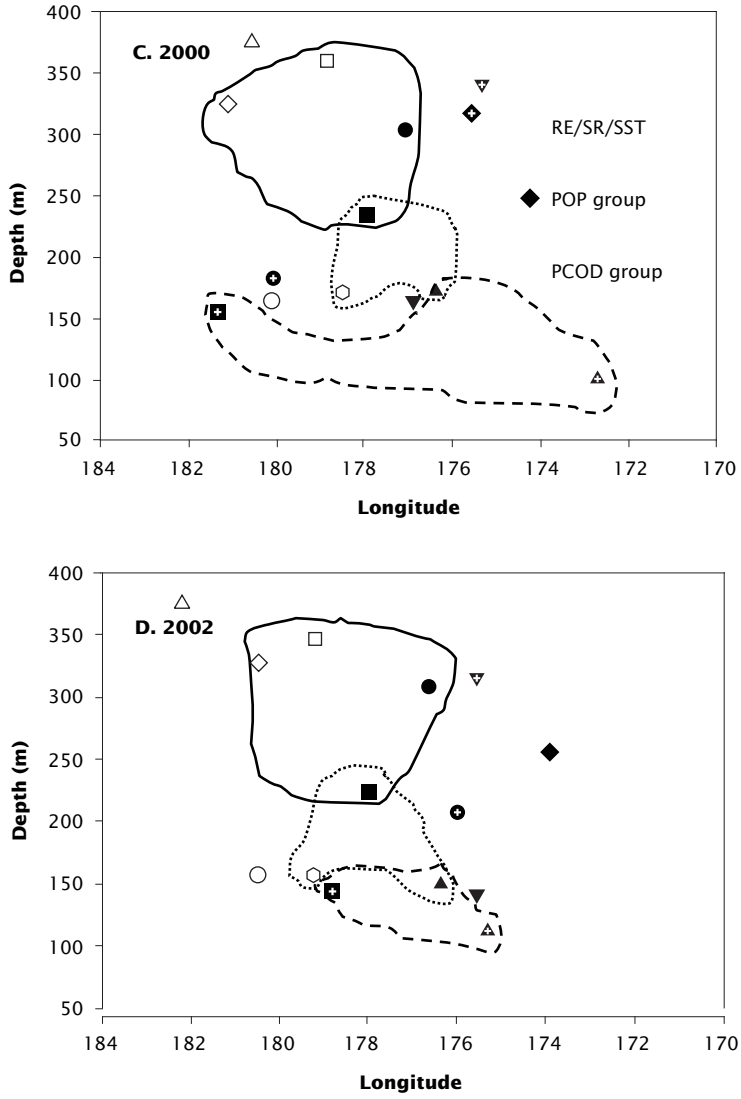


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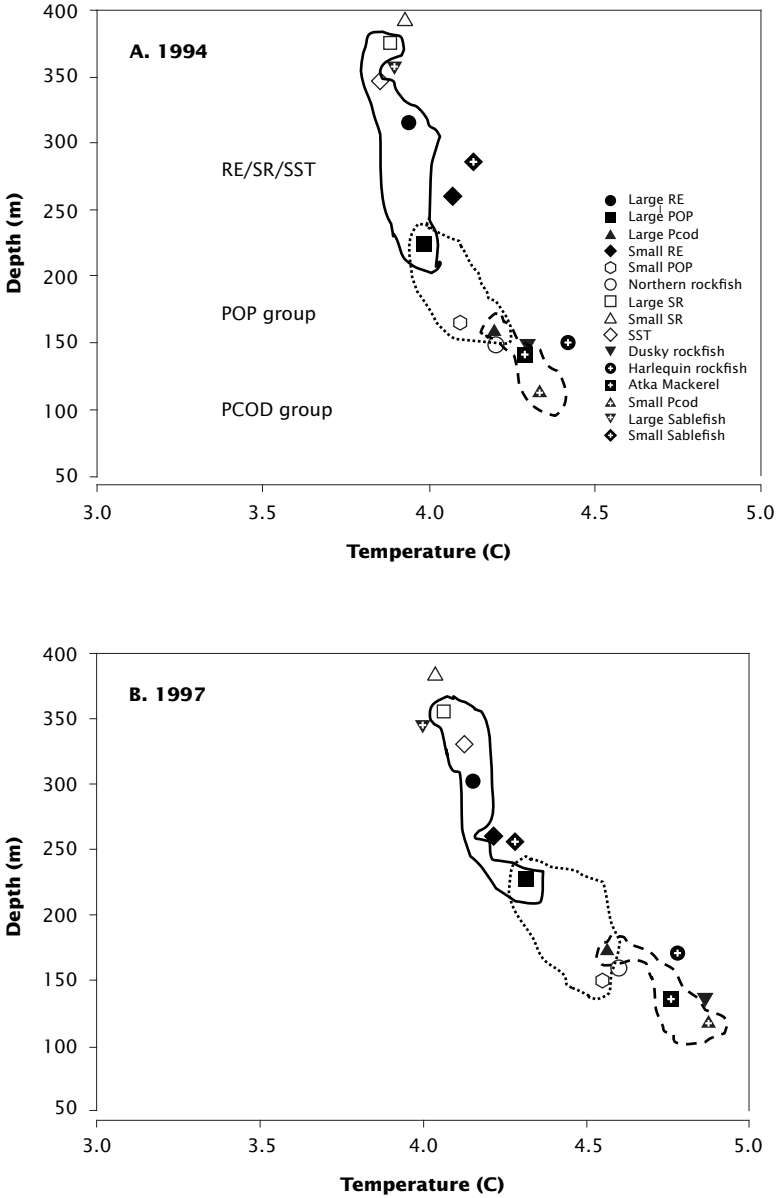
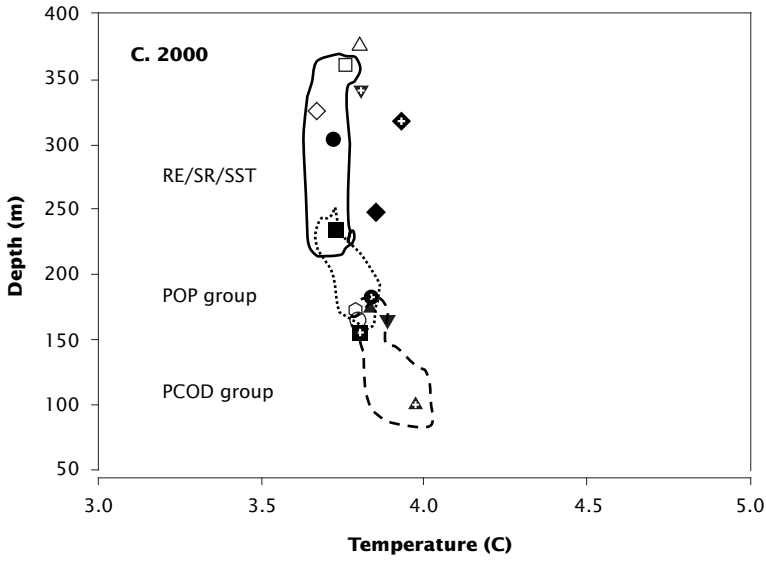


Figure 8. Plots of the weighted average for depth and temperature of each species by year. (a) 1994, (b) 1997, (c) 2000, (d) 2002. Circles denote haul groups where species occurred (>10% CPUE of haul group): solid line = RE/SR/SST group; dotted line = POP miscellaneous group; dashed line = Pcod miscellaneous group.



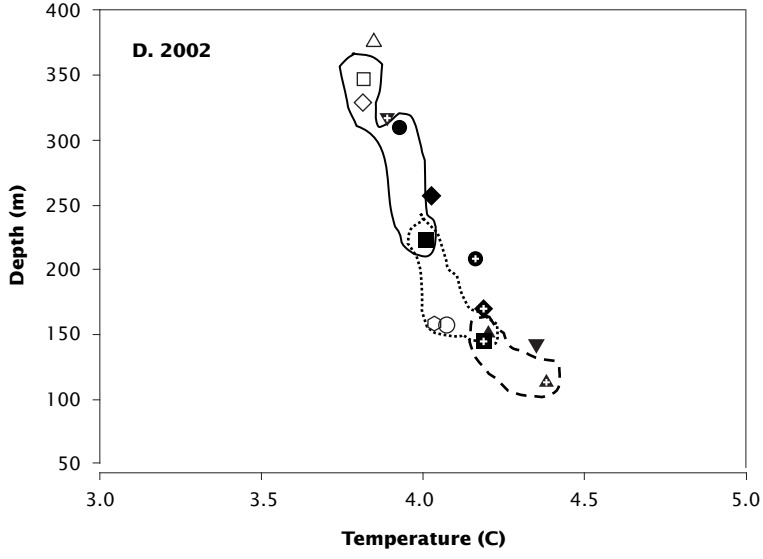


Figure 8. (Continued.)

There were only two species of rockfish, Pacific ocean perch and shortspine thornyhead, in the AI data set that overlapped with the species in the Williams and Ralston (2002) study. Although these two species were in the deepwater assemblage off California and Oregon, they were in separate assemblages in the AI region, the deepwater slope assemblage of the RE/SR/SST group and the shelf assemblage of the POP group.

Although the survey data had a low sample density relative to the entire Aleutian Islands chain, it illustrated areas of possible importance to rockfish. The main drawback is that those species whose center of abundance is not in these trawlable areas, such as rockfishes, are inadequately represented in the survey data (Jagielo et al. 2003). Sampling using bottom trawl gear is not only limited to certain habitats but it may bias the density of certain species. Jagielo et al. (2003) described differences in the density of certain rockfish species in trawlable and untrawlable habitat off the coast of Washington state. Using a manned submersible, it was found that rockfish density was significantly higher over areas that were not trawlable. This suggests that the definition of a marine reserve may not be done using only trawl data. In our study, though, the areas where the haul groups were persistent could be used to further investigate the potential for a marine reserve and to suggest areas for further research on the disparity of density estimates between trawlable and untrawlable areas.

Various factors, other than depth and habitat, may influence a change in the distribution of haul groups and individual species between survey years. Temperature, predator abundance and/or predator-prey interactions are just a few factors to consider (Murawski and Finn 1988, Williams and Ralston 2002). Water temperature, a factor that was considered in this study, may explain why certain haul groups were found in some years but not others. The AM group in 1997 had an average depth of around 150 m and in 2000 had an average depth closer to 250 m, but the average temperatures for 1997 were only 0.4ºC cooler than in 2000. This suggests that Atka mackerel, the main species in the group, went deeper in search of cooler temperatures. Similarly, the small POP group's average temperature shifted from 4.2º to 4.8ºC in depths from 150 to 125 m, respectively. This may suggest that the species in the small POP group follow warmer/shallower waters than typically sampled by the bottom trawl survey. Although diet data are routinely collected aboard the summer bottom trawl surveys, insufficient data exist to do a complete analysis of prey composition over time of rockfish in the AI region or to analyze dietary competition between the rockfish species within the haul groups described in this study. Samples from stomachs of rockfish are difficult to obtain due to a high occurrence of regurgitation. Despite this difficulty, some stomachs from rockfish species have been collected; it has been shown that those spe-

cies in the RE/SR/SST group mainly eat shrimp and miscellaneous fish species (Yang 1996, 2003).

Further research needs to be conducted to validate the rockfish assemblages obtained in this study. This may be accomplished with data from a rockfish specific bottom trawl survey or in situ observations using a submersible or remotely operated vehicle. Although cluster analysis has been used in many studies to determine ecologically linked patterns in data (e.g., Rogers and Pikitch 1992, Jay 1996) other ordination techniques such as nonparametric multidimensional scaling could be explored to assist in explaining relationships between the assemblages, the individual species and their respective environmental variables (Clarke 1993, Clarke and Warwick 2001). Finally, results from this study can be used to assist the design of future rockfish surveys and assemblage studies in the Aleutian Islands.

Acknowledgments

Thanks to all the staff of the AFSC Aleutian Island surveys for their work during the summer surveys included in this study. Thanks to the reviewers for their useful comments and suggestions. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of NOAA Fisheries.

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Variability in Trawl Survey Catches of Pacific Ocean Perch, Shortraker Rockfish, and Rougheye Rockfish in the Gulf of Alaska

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Abstract

Little information is available on the comparative variability of Pacific ocean perch, shortraker rockfish, and rougheye rockfish catches in Alaska trawl surveys. In this study, data were first examined for these three species from three localized experimental bottom trawl surveys in the Gulf of Alaska in 1993, 1998, and 1999 to compare the variability of catch rates for each species. When catch rates were analyzed within favorable fishing areas for each species, the coefficients of variation for Pacific ocean perch were approximately 2.5 to 3 times greater than those of shortraker or rougheye rockfish, indicating that the latter two species are much more even in their distribution. To provide a broader comparison of variability, catch rates of the three species were also examined from seven large-scale bottom trawl surveys conducted in the Gulf of Alaska from 1984 to 2001. Using geographic information systems software, subsets of the hauls in these surveys were selected in what were determined to be favorable fishing areas for either Pacific ocean perch or for shortraker and rougheye rockfish. Analysis of the species' catch rates in these hauls indicated results that were very similar to those of the experimental trawl surveys; the variability of Pacific ocean perch was 2.1-2.3 times greater than that for either shortraker or rougheye rockfish. The results of this study indicate that a trawl survey for shortraker and rougheye rockfish based on a random design may be logistically feasible, but that an alternative design would be needed for Pacific ocean perch in order to be cost effective.

Introduction

Pacific ocean perch (*Sebastes alutus*), shortraker rockfish (*Sebastes borealis*), and rougheye rockfish (*Sebastes aleutianus*) are ecologically important and commercially valuable species that inhabit the outer continental shelf and upper continental slope of the Gulf of Alaska. Pacific ocean perch (POP) as adults are found on the outer shelf and upper slope at depths of ~100-300 m. In contrast, adult shortraker and rougheye rockfish typically inhabit deeper waters of the slope at depths of ~300-500 m (Clausen et al. 2003). Due to the fact that shortraker and rougheye often co-occur in hauls and are superficially similar in appearance, until 2005 the two species were grouped together as an assemblage in the Gulf of Alaska for fishery management purposes, whereas POP has been managed as a single species for many years. POP is the most abundant rockfish in Alaska, and in recent bottom trawl surveys of the Gulf of Alaska has ranked second in biomass among all groundfish species in this region (Martin 1997, Britt and Martin 2001). Shortraker and rougheye rockfish, while of less overall abundance, are nonetheless two of the most common species in the 300-500 m stratum on the slope. POP supports the largest rockfish trawl fishery in the Gulf of Alaska, with catches averaging about 11,000 t in the years 1999-2003 (Hanselman et al. 2003). Catches of shortraker and rougheye rockfish have been much lower, but still substantial, with an average during these years of about 1,600 t for the assemblage (Clausen et al. 2003).

Despite the importance of all three species, there is little information on their comparative variability in trawl catches. POP are known to have a highly clustered distribution (Lunsford 1999); hence, randomly located hauls targeting this species usually result in many hauls with low or zero catches and infrequent hauls with relatively large catches. There has been little published on the variability of shortraker and rougheye rockfish catches, except that Ito (1999) states that they are "contagiously distributed and highly dispersed," which implies the two fish may be similar to POP in having a clustered distribution and a relatively high variability.

Information on the variability in trawl catches for each of these species is particularly needed, as bottom trawl surveys provide much of the data used in assessing their stock condition and in determining appropriate harvest levels. These surveys have been conducted every two or three years by the Alaska Fisheries Science Center (AFSC) since 1984, and they attempt to survey all groundfish species in offshore waters of the Gulf of Alaska out to a depth of 500 m (to 1,000 m in some surveys). However, the surveys have oftentimes been problematic for rockfish due to three major reasons: (1) sampling density in the areas inhabited by rockfish appears to be inadequate for species such as POP with a patchy distribution; (2) the stratified random survey design is a based on a stratification scheme that may not be optimal for POP in the

Gulf of Alaska (Lunsford 1999); and (3) the trawl gear used in the survey is not able to sample many of the rough bottom locations where species such as shortraker and rougheye rockfish are often found. As a consequence of these problems, the present trawl surveys have sometimes yielded wide confidence intervals around biomass estimates (often the case for POP; Hanselman et al. 2003) or uncertain trends in abundance (especially for shortraker and rougheye rockfish; Clausen et al. 2003). Therefore, to improve trawl survey results for rockfish, it appears that new surveys, designed specifically for rockfish, may be necessary.

We undertook the present study to investigate the variability of trawl survey catches of POP, shortraker rockfish, and rougheye rockfish. The main objectives are to determine how the variability of shortraker and rougheye catches compares with that of POP and to provide information that will be needed to design improved trawl surveys for rockfish. In the first part of our study, we examine results from three small, experimental trawl surveys for rockfish conducted by the chartered F/V *Unimak*. We were particularly interested in these surveys because we believe they may represent the best trawl data for these species in Alaska. In the second part of the study, we analyze results from seven of the large-scale AFSC trawl surveys of the Gulf of Alaska. Finally, we compare our results for the *Unimak* and the large-scale gulf-wide surveys and discuss our study's implications for future surveys.

Experimental surveys by F/V *Unimak*

Methods and analysis of Unimak surveys

The AFSC chartered a commercial factory trawler, the 56 m F/V *Unimak*, to conduct specialized experimental bottom trawl surveys of rockfish in 1993, 1998, and 1999. (In 1993 and 1998, the vessel was named the *Unimak Enterprise*). These surveys had some unique advantages when compared with the standard AFSC trawl surveys, especially the following two. (1) In each experimental survey, the vessel was equipped with a rockfish net fitted with "rockhopper" gear along the footrope. Rockhopper gear consists of a series of split automobile tires mounted on the center section of the footrope so the gear can bounce over boulders and obstructions (for a detailed description of the net see Clausen et al. 1999). This allows the net to be fished over much rougher bottom than can the standard AFSC survey net. Rockhopper gear is now routinely used by most commercial vessels in Alaska that bottom trawl for any species of rockfish. (2) The same skipper was used in each of the *Unimak* surveys—a very experienced Alaska rockfish fisherman. This is in contrast to the AFSC surveys, which used many different skippers over the years, most of whom had limited fishing experience for rockfish in Alaska.

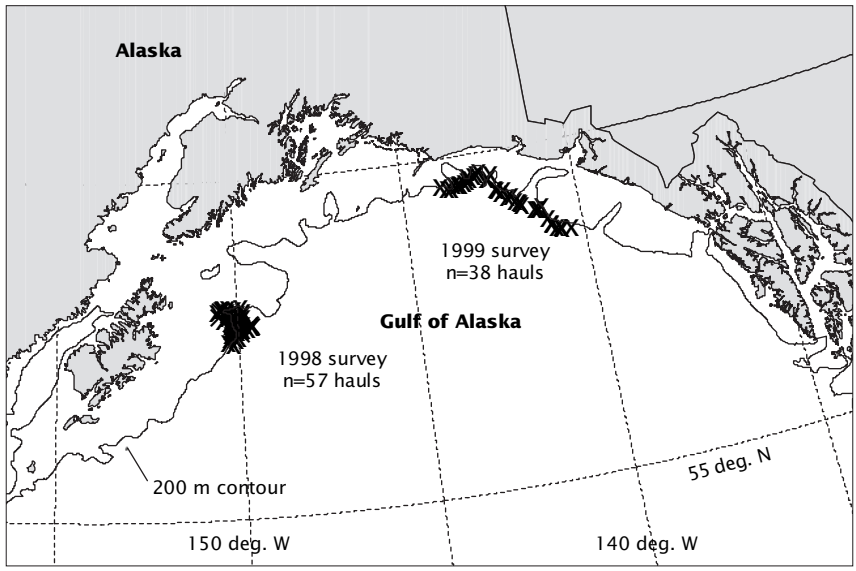


Figure 1. Location of random hauls for Pacific ocean perch (POP) that were sampled in the F/V *Unimak* surveys. Hauls were considered to be in favorable fishing localities for POP.

The actual purpose of the 1993 survey was to use rockhopper gear to conduct a pilot survey of shortraker and rougheye rockfish only (Ito 1999), whereas the purpose of the 1998 and 1999 surveys was to conduct adaptive sampling experiments for these two species as well as for POP (Clausen et al. 1999; Hanselman et al. 2001, 2003). In each survey, a number of hauls were located at random positions, and for the present study we restricted our analysis to just these random hauls. The location and total numbers of hauls used in the analysis are shown in Figs. 1 and 2, which indicate the hauls in each survey covered relatively small geographic areas of the central and eastern Gulf of Alaska. It should also be noted that the number of random hauls fished was relatively small and ranged from 19 for shortraker and rougheye in the 1999 survey to 57 for POP in the 1998 survey. The locations of these random hauls were in what was believed to be "favorable fishing localities" for each species, which for the purpose of this paper we define to be positions where one would reasonably expect to sometimes encounter a large catch. For shortraker and rougheye rockfish in the *Unimak* surveys, favorable fishing localities were considered to be depths of 300-500 m on the slope and, for POP, depths of 150-300 m on the outer shelf and

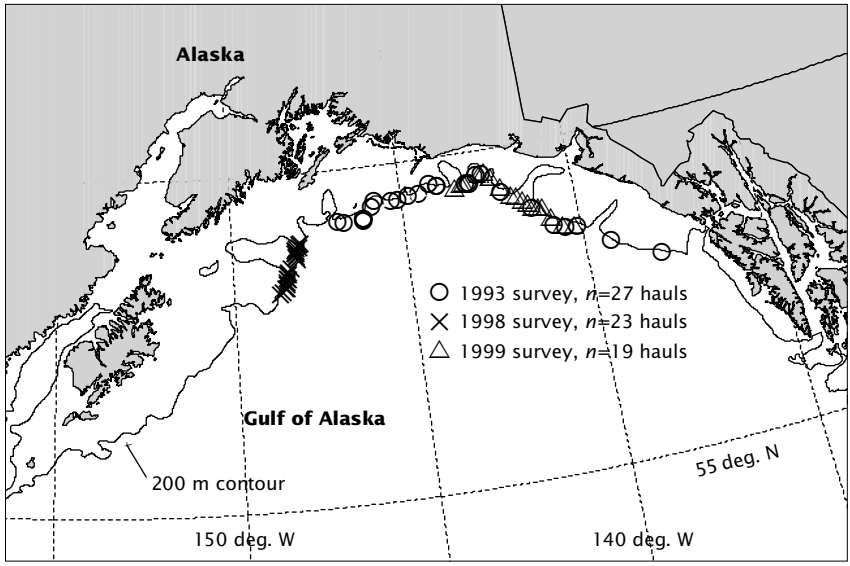


Figure 2. Location of random hauls for shortraker and rougheye rockfish that were sampled in the F/V *Unimak* surveys. Hauls were considered to be in favorable fishing localities for these two species.

upper slope. For our study, it was important to analyze catches only in favorable fishing localities for each species to obtain the best estimate of variability; otherwise the analysis could be biased by the inclusion of hauls located outside the favorable fishing localities with very low or zero catch rates.

Catch-per-unit effort (CPUE) values of shortraker rockfish, rougheye rockfish, and POP in the survey hauls were standardized in terms of kg caught per km towed over the bottom (see Clausen et al. 1999 for details). To compare the variability of the species' CPUE within each survey, coefficients of variation (CV) of the CPUE for each species were computed. It should be emphasized that these CVs are for the "population" of CPUE values in the individual hauls, and not the CVs of abundance estimators such as mean CPUE or biomass that are derived from the individual haul data. The bootstrap percentile method was used to determine 95% confidence intervals for the CVs of CPUE (Efron and Tibshirani 1993). Given n CPUE values, 1,000 replicated sets of size n were randomly drawn with replacement, and a CV value was calculated for each set. The 95% confidence interval was determined from 25th and 975th largest values of the bootstrapped CVs.

Results for Unimak surveys

Summary statistics for the *Unimak* hauls in our analysis show that CPUE values for POP were highly variable compared with the more even distributions of shortraker and rougheye rockfish (Table 1). This high variability for POP is especially evident in its values of skewness and kurtosis relative to those for shortraker and rougheye rockfish. Skewness and kurtosis were much higher for POP, and these statistics reflect the fact that most POP hauls had very low catch rates, approaching zero in some cases, whereas in just a few hauls CPUE was very high. This high variability for POP is similar to the distribution pattern noted for this species by other scientists and fishermen, and that was referred to earlier.

Given the above CPUE statistics, it is not surprising that the CVs for POP in the 1998 and 1999 surveys are 2.5-3 times higher than those for shortraker and rougheye rockfish (Table 1; Fig. 3). Moreover, this difference is statistically significant because the 95% confidence intervals for POP do not overlap those for shortraker and rougheye in the years (1998 and 1999) when all three species were surveyed. Shortraker rockfish are

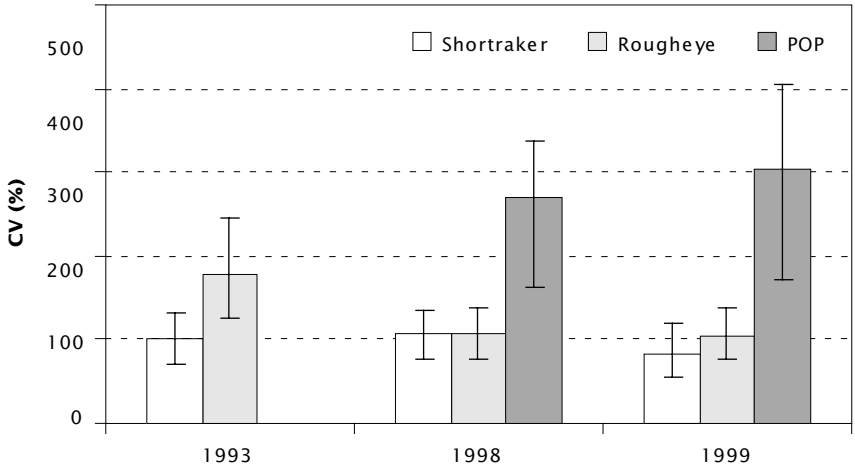


Figure 3. Coefficients of variation (CV) and associated 95% confidence intervals for catch-per-unit-effort of Pacific ocean perch (POP), shortraker rockfish, and rougheye rockfish in random hauls conducted during F/V *Unimak* surveys in 1993, 1998, and 1999. Hauls for each species were considered to be in favorable fishing localities. POP were not part of the survey design in 1993. Confidence intervals were determined by using the bootstrap method.

Table 1. Summary statistics for catch-per-unit effort (CPUE) of Pacific ocean perch, shortraker rockfish, and rougheye rockfish in random hauls conducted during F/V *Unimak* surveys in 1993, 1998, and 1998. Hauls were considered to be in favorable fishing localities for each species, and CPUE is in kg per km. POP were not part of the survey design in 1993. CV = coefficient of variation.

Species	No. hauls	Mean CPUE	Standard deviation	CV (%)	Min. value	2.5 percentile	Median value	97.5 percentile	Max. value	Skewness	Kurtosis
1993											
Shortraker	27	339.4	341.0	100.4	7.0	8.5	215.7	1,037.4	1,504.7	1.7	3.9
Rougheye	27	155.5	277.2	178.3	0.0	0.6	31.7	871.8	1,135.6	2.4	5.6
1998											
POP	57	349.3	944.1	270.3	3.3	5.6	64.3	2,395.2	6,290.0	5.1	29.2
Shortraker	23	217.7	235.1	108.0	0.0	16.6	113.1	771.7	969.7	1.9	3.7
Rougheye	23	303.7	325.4	107.1	1.8	10.9	201.9	1,057.4	1,148.5	1.4	1.1
1999											
POP	38	678.3	2,050.7	304.3	4.3	9.2	73.8	4,221.6	11,998.7	4.9	26.4
Shortraker	19	355.5	297.6	83.7	6.3	13.6	325.5	824.5	843.6	0.2	−1.6
Rougheye	19	72.1	76.2	105.6	0.0	1.4	36.7	215.0	217.0	1.0	−0.6

Table 2. Summary statistics for catch-per-unit effort (CPUE) of Pacific ocean perch, shortraker rockfish, and rougheye rockfish in random hauls determined to be in favorable fishing localities for each species during large scale surveys of the Gulf of Alaska, 1984-2001. CPUE is in kg per km². CV = coefficient of variation.

Species	No. hauls	Mean CPUE	Standard deviation	CV (%)	Min. value	2.5 percentile	Median value	97.5 percentile	Max. value	Skewness	Kurtosis
POP	1,030	9,980.5	41,766.6	418.5	0.0	0.0	780.1	87,800.9	830,312.9	10.9	167.5
Shortraker	297	1,837.6	3,604.3	196.1	0.0	0.0	678.3	9,790.9	36,015.7	5.2	37.0
Rougheye	297	2,320.2	4,178.1	180.1	0.0	0.0	653.1	15,133.0	30,354.2	3.2	12.8

remarkably consistent in their CVs, with values of about 100% for each survey. Rougheye rockfish have CVs similar to shortraker in the 1998 and 1999 surveys, although their CV is somewhat higher than shortraker in the 1993 survey. The generally low CPUE values for rougheye rockfish in the 1993 and 1999 surveys (Table 1) may make results for this species in these two years less meaningful; these surveys were both conducted offshore the Yakutat area, and rougheye in this region have been documented to have consistently low catch rates in longline surveys (Clausen et al. 2003).

Large-scale trawl surveys of the Gulf of Alaska

Methods and analysis of large-scale Gulf of Alaska surveys

To determine the comparative variability of POP, shortraker rockfish, and rougheye rockfish in the large-scale trawl surveys of the Gulf of Alaska, we analyzed data from seven of these surveys conducted in the following years: 1984, 1987, 1990, 1993, 1996, 1999, and 2001. A total of 5,254 valid hauls were completed during these surveys throughout the shelf and slope of the Gulf of Alaska. As previously stated, haul location was determined by using a stratified random design, and as much as possible, the surveys were standardized in terms of fishing gear and operations (Britt and Martin 2001). The stratification scheme divided the area surveyed in the Gulf of Alaska into 59 strata based on a combination of depth (1-100 m, 101-200 m, 201-300 m, 301-500 m, etc.) and broad geographic types (e.g., shelf, gullies, slope). For each haul, direct measurements or estimates were made of the bottom area swept by the net, which allowed us to standardize CPUE for POP, shortraker rockfish, and rougheye rockfish in units of kg caught per km^2. Simple two-way analysis of variance for each species did not reveal any significant differences in CPUE by year or by region of the Gulf of Alaska, which allowed us to pool all the hauls in the data set.

For our investigation of POP, we selected hauls from this data set that we determined to be in favorable POP fishing localities. Early in the selection process, it became evident that we could not use the survey's stratification scheme to make these selections. For example, many survey strata on the shelf at depths 101-200 m often included relatively small geographic areas on the outer shelf where large catches of POP had been encountered. However, most of the shoreward area of these strata consisted of large expanses in which the survey's catches of POP were sparse or zero. Inclusion of all hauls within these strata as "favorable fishing localities" for POP would clearly not be appropriate for determining the comparative variability of POP catch rates.

Consequently, we elected to use our own selection procedure that followed an iterative process. (1) We started by including all the hauls that were in the survey's previously established 201-300 m slope strata, as we knew from past trawl survey data reports that these strata contained a large proportion of the POP biomass and many of the hauls with the highest catch rates. (2) We then used geographic information systems (GIS) software to plot all the hauls outside these strata that had POP catch rates greater than 10,000 kg per km^2 ("large" hauls). This value, although arbitrary, represents a relatively large catch rate; for example, the rate roughly corresponds to a catch of 7,000 kg taken in the area swept by the net of a rockfish factory trawler during a typical fishery tow (Clausen and Heifetz 2002). This amount of catch would likely be considered a commercially valuable haul by most skippers. In the western and central Gulf of Alaska, all the hauls with this catch rate (except for the hauls in the 201-300 m slope strata that we had already selected) were located in shelf strata at depths less than 200 m or in gully strata 201-300 m deep that extended into the shelf. In the eastern Gulf of Alaska, the large hauls were also located in these types of strata, but a few large hauls were also found at depths greater than 300 m in slope strata or in deepwater gully strata greater than 300 m that extended into the slope and shelf. (3) After selecting the large hauls, we used GIS to select adjacent hauls within a distance of one nautical mile, together with all other hauls that were located in a seaward direction between the large hauls and the 201-300 m slope strata. (For those large hauls in the eastern Gulf of Alaska on the slope at depths greater than 300 m, we selected other hauls in a shoreward direction toward the 201-300 m slope). (4) We next examined many of the selected hauls on a case by case basis in GIS to see if it was reasonable to include them as "favorable fishing localities"; if not, they were rejected. In particular, a few large hauls on the shelf were a considerable distance shoreward from the slope and had many intervening hauls between them and the slope with zero catches of POP. These large hauls appeared to be isolated and anomalous, and including them and all the intervening hauls as being in favorable fishing localities for POP would definitely bias the analysis; therefore, they were excluded. After completing this whole selection procedure, we identified a total of 1,030 survey hauls as being in favorable fishing localities for POP (Fig. 4). We believe that the area encompassed by these hauls is a reasonable representation of the preferred area for POP in the Gulf of Alaska, at least for the summer months when the surveys occurred. The hauls are all contiguously located along a relatively narrow band on the outer shelf and upper slope, except the band is wider where it includes gully locations. Depth range of the favorable hauls is from 102 to 346 m. Of the 155 hauls that had a POP catch rate of more than 10,000 kg per km^2, 150 (97%) were included in our selection.

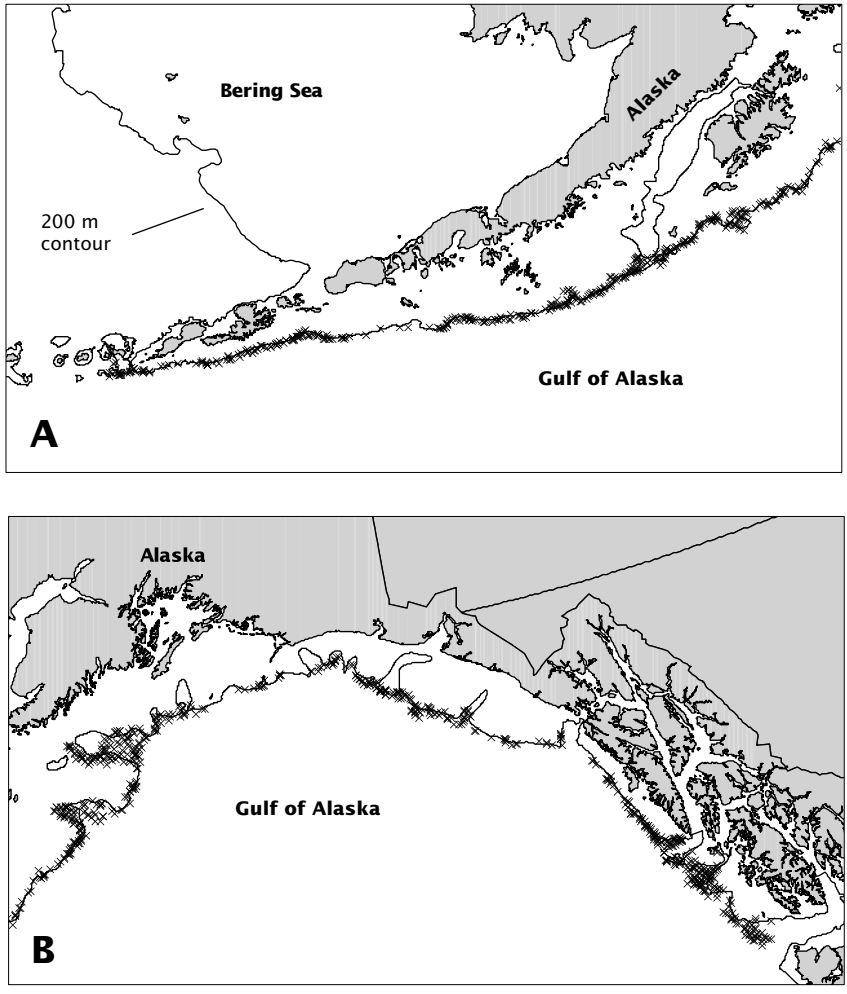


Figure 4. Location of hauls determined to be in favorable fishing localities for Pacific ocean perch in large-scale trawl surveys of the Gulf of Alaska, 1984-2001. A: hauls in the western half of the Gulf of Alaska. B: hauls in the eastern half of the Gulf of Alaska.

Hauls in shortraker and rougheye rockfish favorable fishing localities were selected by a similar procedure. The only differences were that we started by including all hauls in the survey's 301-500 m slope strata, which were known to contain a large proportion of the hauls with high catch rates for these fish, and that we used a CPUE value of more than 5,000 kg per km^2 as our criterion for a "large" haul for each species. This catch rate was used rather than POPs higher value of over 10,000 kg per km^2 because relatively few hauls had a CPUE over 10,000 kg per km^2 for either shortraker or rougheye rockfish. Although before we began this study we knew that shortraker and rougheye rockfish generally shared a preference for the same depths on the slope, we were somewhat surprised in our analysis of survey catches to find no distinct difference between the two species in terms of favorable fishing localities. Large catches for each species were frequently encountered in the same individual hauls or in hauls of close proximity. Consequently, we ended up selecting for both shortraker and rougheye rockfish the same set of 297 hauls that comprised favorable fishing localities for either species (Fig. 5). These hauls were all located on a very narrow band along the slope, except for a group that were in two deepwater gullies off southeastern Alaska. Depth range of the hauls is from 256 to 649 m. Of the 28 hauls that had a shortraker catch rate over 5,000 kg per km^2, 27 (96%) were included in our selection; of the 43 hauls that had a rougheye catch rate of more than 5,000 kg per km^2, 37 (86%) were included. The six large hauls for rougheye rockfish that were not selected as being in favorable fishing localities were mostly located far inshore on the shelf and consisted of catches of small juvenile fish.

Similar to our analysis of the *Unimak* data, we computed CVs and associated 95% bootstrapped confidence intervals for CPUE values of POP, shortraker rockfish, and rougheye rockfish in the favorable fishing localities. The bootstrapping procedures were identical to those described for the *Unimak* data.

Results for large-scale Gulf of Alaska surveys

Summary statistics for hauls in the large-scale surveys show that CPUE values for POP in favorable fishing localities were much more variable than those for shortraker and rougheye rockfish (Table 2). These results are very similar to those for the *Unimak* surveys. Although the median values for each species are nearly equal, standard deviation, skewness, and kurtosis are substantially higher for POP. The statistics indicate that the POP distribution consists of a relatively small number of very large catches, as well as large numbers of zero or small catches. In contrast, the statistics for shortraker and rougheye rockfish show a distribution that is less extreme and more even. Also notable is a remarkable similarity in the statistics for shortraker and rougheye rockfish. For each of these two species, mean CPUE, standard deviation, median, and

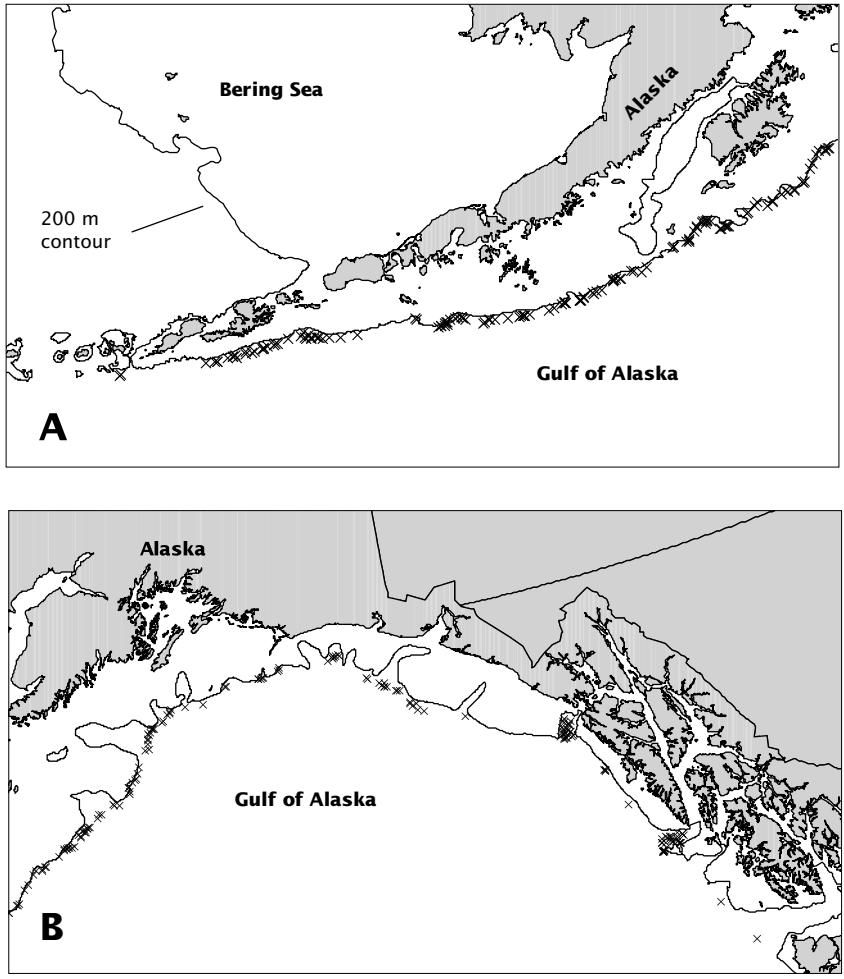


Figure 5. Location of hauls determined to be in favorable fishing localities for shortraker and rougheye rockfish in large-scale trawl surveys of the Gulf of Alaska, 1984-2001. A: hauls in the western half of the Gulf of Alaska. B: hauls in the eastern half of the Gulf of Alaska.

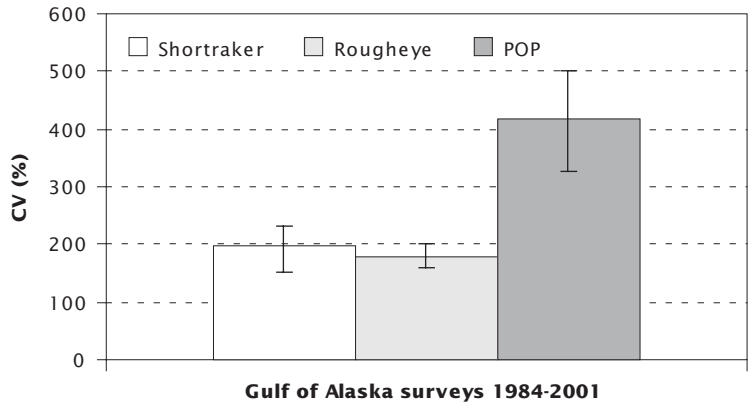


Figure 6. Coefficients of variation (CV) and associated 95% confidence intervals for catch-per-unit effort of Pacific ocean perch (POP), shortraker rockfish, and rougheye rockfish in hauls conducted in favorable fishing localities in large-scale trawl surveys of the Gulf of Alaska (GOA), 1984-2001. Confidence intervals were determined by using the bootstrap method.

maximum value are nearly equivalent, although skewness and kurtosis are somewhat higher for shortraker. Thus, not only do shortraker and rougheye appear to share the same favorable fishing localities, within these localities they share a similar pattern of CPUE distribution.

CV values for each species in the Gulf of Alaska surveys reflect their corresponding CPUE distributional patterns (Table 2; Fig. 6). CVs for shortraker and rougheye rockfish are nearly equal at about 180-200%, whereas the CV for POP is over twice as high at about 420%. The 95% confidence interval for POP does not overlap those for shortraker and rougheye, which indicates POP variability is significantly higher Therefore, within the area of favorable fishing localities for each species, shortraker and rougheye rockfish are distributed much more evenly than are POP.

Discussion and implications for future trawl surveys

Both the *Unimak* surveys and the Gulf of Alaska surveys showed similar results concerning the variability of trawl catches of POP, shortraker rockfish, and rougheye rockfish. This was true despite the fact that they were very different datasets. The *Unimak* surveys were small-scale, had relatively few hauls, and were restricted in area and time. The Gulf of

Alaska surveys were large-scale in area and time and had many hauls, especially when combined over years. The relative variability between species is quite similar in each dataset (compare Fig. 3 and Fig. 6), although the CVs are higher in the Gulf of Alaska surveys. Thus, the *Unimak* and Gulf of Alaska surveys agree that shortraker and rougheye rockfish have a similar and relatively low variability, whereas the variability of POP is 2-3 times higher.

The fact that CVs for each species in the Gulf of Alaska surveys were higher than in the *Unimak* surveys is likely due to gear, operational, and design differences between each survey type. Although the Gulf of Alaska surveys were standardized in terms of gear and procedures, the *Unimak* surveys used more up-to-date and optimized gear for catching rockfish and also had the same skipper each year who was very experienced in fishing this gear. This may have resulted in more consistent catches aboard the *Unimak*. In addition, the *Unimak* survey areas were relatively small in size and were selected to be in localities that had a history of especially good rockfish catches in the commercial fishery. Thus, it is possible that the distribution of POP, shortraker rockfish, and rougheye rockfish CPUE in the gulf-wide "favorable fishing areas" may be more variable than what was found at the smaller areas fished by the *Unimak*.

Results of this study were used to compute the hypothetical number of survey hauls that would yield a desired level of survey precision for each species. For this, we followed the analytic procedures described in Snedecor and Cochran (1967; see p. 512-513) which are based on use of a population's CV, as well as a "finite population correction." For the desired level of precision, we chose a confidence interval of 50% around the abundance estimators; in this study, the abundance estimators are the mean CPUE values for each species in each survey. The 50% confidence interval was chosen as one that would represent a reasonably precise estimate for detecting changes in abundance between surveys. In the computations for the finite population correction, an estimate of the maximum size of the population is required. Our "population" in this case consists of survey hauls, so an estimate of the maximum number of possible survey hauls (or defined another way, the maximum number of individual sampling units) for each survey is needed. We suggest a reasonable estimate of the size of an individual sampling unit would be a square measuring 1.5 km on each side (2.25 km^2), a dimension that equals the average distance over the bottom covered by a net in a typical survey tow of 15 minutes standard duration. To compute the maximum number of possible hauls for each of the surveys examined in this study, an estimate is also needed of the overall size of the favorable fishing localities encompassed by each survey. Approximations of these sizes were made based on the size measurements listed in Britt and Martin (2001) for sampling strata in the Gulf of Alaska. The area size

Table 3. Summary of data and results for determining the number of hauls needed to obtain a 50% confidence interval for mean CPUE of Pacific ocean perch, shortraker rockfish, and rougheye rockfish in the four trawl surveys examined in this study. Pacific ocean perch were not part of the survey design in the 1993 *Unimak* survey.

	1993 *Unimak*	1998 *Unimak*	1999 *Unimak*	Gulf of Alaska
Pacific ocean perch				
Approx. survey area[a] (km^2)	–	1,500	1,500	24,914
Max. sampling units	–	667	667	11,073
No. hauls for 50% conf. int.	–	100	120	275
Density[b] of hauls (no./km^2)	–	0.066	0.080	0.011
Shortraker rockfish				
Approx. survey area[a] (km^2)	1,521	600	900	10,341
Max. sampling units	676	267	400	4,596
No. hauls for 50% conf. int.	16	17	11	61
Density[b] of hauls (no./km^2)	0.010	0.029	0.012	0.006
Rougheye rockfish				
Approx. survey area[a] (km^2)	1,521	600	900	10,341
Max. sampling units	676	267	400	4,596
No. hauls for 50% conf. int.	47	17	17	51
Density[b] of hauls (no./km^2)	0.031	0.029	0.019	0.005

[a]For Gulf of Alaska surveys, area is the area encompassing favorable fishing localities for each species.

[b]Density of the hauls needed to obtain a 50% confidence interval.

approximations, estimated maximum number of sampling units within these areas, calculated number of hauls required to obtain confidence intervals of 50%, and density of these hauls are listed in Table 3.

The results in Table 3 indicate that in comparison to POP, surveys for shortraker and rougheye rockfish would require considerably fewer hauls to obtain an acceptable confidence interval. For example, in the 1998 *Unimak* survey, 17 hauls in the area surveyed for shortraker and rougheye would be needed for a 50% confidence interval versus 100 hauls needed in the area surveyed for POP. Similarly, in the Gulf of Alaska surveys, 50-60 hauls would be needed for shortraker and rougheye rockfish versus 275 hauls for POP. Much of this difference is simply due to the fact that the area of "favorable fishing localities" required for sampling for POP is larger; in the Gulf of Alaska, the estimated survey area needed for POP is 2.4 times greater than the area for shortraker and rougheye. However, the variability of each species' CPUE within these

areas is also a major factor affecting how many hauls are necessary. This is indicated in Table 3 by the values for "density of hauls." In the 1998 *Unimak* survey, required haul density in the survey area for POP (0.066 hauls per km^2) is approximately twice the density required in the shortraker and rougheye survey areas (0.029 hauls per km^2). Likewise, the density of hauls necessary in the Gulf of Alaska survey area for POP (0.011 hauls per km^2) is about twice that necessary for shortraker and rougheye rockfish (0.006 and 0.005 hauls per km^2, respectively). The lower density needed for shortraker and rougheye is directly related to the fact that variability (CVs) for these two species was much lower than that for POP.

One seemingly paradoxical aspect of the results in Table 3 is that for POP, relatively few hauls (275) would be required for a survey of their favorable fishing localities in the entire Gulf of Alaska compared to the relatively many hauls needed in the small areas fished by the *Unimak* in 1998 and 1999 (100 and 120 hauls needed, respectively). Snedecor and Cochran (1967) also point out that many people initially find such results counter-intuitive, but that the results are indeed correct. Their explanation is that for a large population (such as our large number of possible hauls in favorable POP localities in the Gulf of Alaska), the standard error of the mean depends mostly on the sample size, rather than on the fraction of the population that is sampled.

The computed number of hauls in Table 3 required for a Gulf of Alaska survey of shortraker and rougheye rockfish indicate that a random survey of these species may be logistically feasible. However, a similar random survey of POP would be less feasible. For shortraker and rougheye, a total of 61 random hauls gulf-wide within the area encompassed by the favorable fishing localities would yield an acceptable confidence interval of 50% for either species. The present Gulf of Alaska surveys average ~42 hauls within these areas (a density of 0.009 hauls per km^2), which means an increase of only 19 hauls would be needed. This relatively small increase in survey effort could be accomplished in a reasonably short time at a modest additional cost. Moreover, if optimal sampling gear and an experienced skipper were used in such a survey (i.e., like that used in the *Unimak* surveys), variability of catches might be less and even fewer hauls would be necessary. For POP, however, Table 3 indicates that a total of 275 hauls are needed in favorable fishing localities to obtain a 50% confidence interval. The current Gulf of Alaska surveys average ~147 hauls in favorable POP fishing localities (a density of 0.006 hauls per km^2), so that 128 additional random hauls would be required to attain the desired level of precision. This relatively large number of additional hauls would likely be prohibitively costly, especially in terms of increased manpower, and it is doubtful that such an augmented survey would be conducted. Consequently, to improve

survey results for POP, investigations of alternative survey methods other than random sampling are needed.

Finally, we believe that our analysis of the Gulf of Alaska surveys, in which we geographically identified broad-scale favorable fishing localities for Pacific ocean perch and for shortraker and rougheye rockfish, should prove useful in the design of future surveys for these species. Knowing what geographic locations need to be sampled, and excluding those that do not, are essential to maximize efficiency and cost effectiveness of a survey. Before this study, detailed information was not available on the geographic location of preferred areas inhabited by these species. In particular, the stratification pattern of the gulf-wide trawl surveys did not allow easy identification of favorable fishing localities for POP on the outer shelf. Future surveys of POP and of shortraker and rougheye rockfish should be able to use our analysis of favorable fishing localities as the initial basis for determining where to locate hauls or sampling positions.

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Extending Statistical Age-Structured Assessment Approaches to Gulf of Alaska Rockfish (*Sebastes* spp.)

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Abstract

Modern age-structured stock assessments typically involve use of a complex "packaged" model or programming of a customized model. For Gulf of Alaska (GOA) rockfish, a customized model has been developed for use with four rockfish species: northern rockfish (*Sebastes polyspinis*), Pacific ocean perch (*S. alutus*), dusky rockfish (*S. variabilis*), and rougheye rockfish (*S. aleutianus*). Each species has particular differences in fishery, survey, and biology, and changes to the customized model structure have allowed for the additional data types and special fishery and biological characteristics. Compared with large, more feature-rich packaged programs, the software developed for GOA rockfish is efficient and relatively straightforward to implement. We describe the customized model and compare differences in model structure among the four applications, the relative impact of different data sources, and factors affecting the uncertainty of key parameter estimates. Modifications needed to adapt the customized model to the different rockfish species were relatively minor, and comparisons among assumptions were easy to compile. Comparison of diagnostics of model fits and estimates of

uncertainty in key parameters among species indicated that the variance specified for most data components was consistent with characteristics of the data and the biological aspects unique to each rockfish species. The development of a customized age-structured model for several rockfish species proved to be adaptable for evaluating uncertainty and the information content of diverse types of data.

Introduction

Rockfish (*Sebastes* spp.) stocks off Alaska represent a valuable component of the groundfish fisheries of the North Pacific (Hiatt 2005). Management of rockfish off Alaska is by region-specific annual quotas that depend on regular assessments based on fishery and fishery-independent data (e.g., Heifetz and Ianelli 1992). In general, rockfish are characterized as relatively long-lived and susceptible to large fluctuations in recruitment. Furthermore, species-specific rockfish data can be scarce (e.g., patchy sampling effort, lack of age composition data), and survey methods for rockfish are problematic (Hanselman et al. 2003b). As such, statistical age-structured methods (e.g., Fournier and Archibald 1982, Methot 1990, Quinn and Deriso 1999) are favored as an assessment approach.

Modern age-structured stock assessment analyses typically involve learning a complex "packaged" program, e.g., Multifan CL (Fournier et al. 1998) or involve programming a customized stock assessment model. The advantage of packaged programs is that they have typically undergone tests and require less debugging and development time for the experienced user. The disadvantage is that the complexities of packaged programs can be so great that even a moderately experienced user may be prone to inadvertent errors in model specifications. The advantage of a customized model is the removal of unnecessary complexity. The disadvantage of a customized model is an increased potential for inadvertent coding errors. Arguably, errors in implementing complex packaged programs offset the disadvantages of programming customized models. A side benefit of programming customized models is the fostering of innovative approaches to stock assessment modeling. Recently, as software advanced and the level of biological realism that could be built into models increased, approaches for modeling diverged. On the one hand, developments in highly efficient software (e.g., ADMB™, Otter Research Ltd. 2001) have made programming and implementation of customized models much simpler. On the other hand, "packaged" programs such as Stock Synthesis (Methot 1990) have become more complex and difficult to use, with features that often go unused.

Previously, Stock Synthesis software was used to provide management advice for Alaska rockfish stock assessments (Heifetz and Ianelli 1992). Using this comprehensive software package as a modeling frame-

work was an improvement over previous practices since the number of assumptions required for management was much lower. Prior to the implementation of Stock Synthesis, scientific quota recommendations were based on either simplistic models requiring a number of assumptions or simply some fraction of the (highly imprecise) survey biomass estimates. For Alaska rockfish, assessment models were re-coded using C++ (with the ADMB libraries) and simplified relative to the Stock Synthesis versions. Initial benchmarks with Stock Synthesis results aided the development of the new approach, but with the benefit of adding features only as needed.

The customized model for rockfish was developed for use with four Gulf of Alaska (GOA) rockfish species: northern rockfish (*Sebastes polyspinis*), Pacific ocean perch (*S. alutus*), dusky rockfish (*S. variabilis*), and rougheye rockfish (*S. aleutianus*) (Courtney et al. 1999, 2003; Hanselman et al. 2003a; Hanselman and Fujioka 2004; Lunsford et al. 2004). These species have different data types and specifications that were easily accommodated. The objectives of our study were to compare differences in model structure among the four applications, including specification of the stock-recruitment relationship, recruitment variability assumptions, and the relative impact of different data sources. Factors affecting the uncertainty of key parameter estimates were compared using both multivariate approximations of the covariance matrix and by integrating Bayesian posterior distributions obtained from Markov Chain Monte Carlo (MCMC).

Methods

The available data for these species were variably incomplete over time and included total commercial catch, survey biomass indices, and age and length compositions from both survey and fishery observer collections (Table 1). Note that for rougheye rockfish an additional index of abundance with corresponding length compositions was available from a NMFS longline survey that covered the deeper-water areas of the GOA slope (200-1,000 m).

Biological parameters estimated independently for each species included length-at-age, weight-at-length (or weight-at-age), female maturity-at-age, and prior assumptions about natural mortality, survey catchability, recruitment variability, and stock-recruitment productivity (e.g., steepness; Table 2). Both an age-to-length transition matrix and an age-error transition matrix were provided as input data (e.g., see Courtney et al. 1999). The age-to-length transition matrix was developed from the estimated Von Bertalanffy growth curve fitted to length and age data collected from NMFS trawl surveys. Age-error matrices were constructed by assuming that the break-and-burn ages were unbiased but had a given amount of normal error around each age determined

Table 1. Years of available data for Gulf of Alaska northern rockfish, Pacific ocean perch, dusky rockfish, and rougheye rockfish used in stock assessment models.

	Northern rockfish	Pacific ocean perch	Dusky rockfish	Rougheye rockfish
Trawl survey biomass[a]	1984, 1987, 1990, 1993, 1996, 1999, 2001, 2003			
Trawl survey ages	1984, 1987, 1990, 1993, 1996, 1999, 2001	1984, 1987, 1990, 1993, 1996, 1999	1984, 1987, 1990, 1993, 1996, 1999, 2001, 2003	1990, 1999
Trawl survey lengths				1984, 1987, 1993, 1996, 2003
Total catch biomass	1977-2003	1961-2003	1977-2004	1977-2004
Trawl fishery ages	1998-2002	1998-2002	2000-2002	
Trawl fishery lengths	1990-2003	1963-1997	1991-2004	1988, 1990-1993, 2000-2004
Longline survey index				1990-2004
Longline survey lengths				1990-2004

[a]Trawl survey biomass data are available for all species, all years.

from between reader comparisons. Known age comparisons were not available for GOA rockfish.

Model specification can be thought of as a state-space approach (e.g., Schnute and Richards 1995) where the unobservable numbers-at-age were projected forward from an initial state and modified by recruitment and mortality processes (Appendix A). Converting these underlying values to observable quantities (e.g., catch proportions-at-age) was done using "observation equations" and resulted in sets of model-predicted "observations." These model predictions were then compared to actual observations for the years in which they were available. Parameters were specified to control the underlying processes and were modified to achieve the best overall fit among the different data components. Additional penalties (or priors) were included to condition the model for appropriate behavior. For example, the coefficients of selectivity-at-age as specified could, in principle, vary widely from one age to the next. However, penalty specifications (akin to non-parametric smoothing) were used so that this variability was moderated unless strongly supported by available data (Ianelli 2002).

Rockfish recruitment is characterized by high inter-annual variability, and the influence of modeling stock-recruitment relationships was evaluated. For one case, northern rockfish, recruitment (R_y) was mod-

Table 2. Life history parameters and prior assumptions about key stock assessment parameters for Gulf of Alaska northern rockfish, Pacific ocean perch, dusky rockfish, and rougheye rockfish populations.

	Northern rockfish	Pacific ocean perch	Dusky rockfish	Rougheye rockfish
A_0	2	2	4	3
A_+	23	25	21	25
Maximum age	67	90	59	129
Age at 50% maturity	12.8	10	11.3	19
Length at 50% maturity (cm FL)	36.1	35.7	42.8	43.9
Growth parameters				
L_∞ (cm FL)	38.3	41.4	45.9	51.2
k	0.17	0.19	0.24	0.08
t_0	−0.76	−0.47	1.18	−1.15
$\theta_1, \theta_2 : \sigma_a^l = \theta_1 + \theta_2 \ln(a)$	13.82, 4.17	13.05, 5.53	14.07, 5.71	45.95, 3.42
Prior assumptions, mean, (CV)				
M, natural mortality	0.06, (0.0)	0.05 (0.10)	0.09, (0.0)	0.03, (0.10)
q, bottom-trawl survey catchability	1.0, (0.45)	1.0, (0.45)	1.0, (0.45)	1.0, (0.45)
σ_r, recruitment variability	0.9, (0.45)	1.7, (0.45)	1.7, (0.45)	1.1, (0.03)
h, steepness	0.9, (0.45)			

Note that σ_a^l represents the standard deviation in length given age a, and maximum age is based on data used in these assessments.

eled as a stochastic process about a Beverton-Holt stock-recruitment relationship (e.g., see Butterworth et al. 2003). The relationship was parameterized following Mace and Doonan (1988). Parameters of the stock-recruitment relationship included steepness (h) and annual average pre-exploitation recruitment (R_0). Recruitment residuals, $\tau_y \sim (0, \sigma_r^2)$ about average R_0, were also estimated 21 years ($a_+ - a_0 - 1$) prior to the initial model year (1977) so that the population age structure distribution was allowed to differ from equilibrium to the extent that the data suggested. For the other rockfish species presented here, recruitment was modeled in a similar manner except that the variability occurred about an average annual recruitment independent of stock size.

Fishing mortality was partitioned into constant age-dependent gear selectivity and annual fishing mortality levels. Total catch biomass was typically assumed to be known most precisely and largely determined the annual fishing mortality estimates (the assumed CV for catch biomass was less than 15% in all four models). Survey biomass

indices were scaled to the total population using a survey catchability (q) parameter.

Parameter estimation is facilitated in the ADMB libraries through the use of automatic calculation of gradients and an aggressive quasi-Newton search algorithm. Finding the maximum of the likelihood surface thus involved probing parameters over a wide range of multivariate space in an efficient manner. Certain parameters were estimated in successive phases to avoid pathologies that can arise. For example, parameters that effectively scale the population appropriately were estimated prior to other parameters that may have highly nonlinear effects (e.g., natural mortality). Estimation of the key parameters such as q, M, h, and recruitment variability (σ_r) was constrained within the overall objective function by minimizing deviations from assumed log-normal prior probability distributions with pre-specified mean and variances (Table 2, Appendix A).

For comparing among species, a method was developed to judge how well models fit data given the assumed component variances. The approach taken was to standardize output variances and compare them with assumed input values. For survey indices, this was calculated as the ratio of the model root-mean squared error (RMSE) divided by the average standard deviation specified for the index. For age and length composition data, the standard deviations of Pearson (normalized) residuals were computed. The Pearson residuals are defined as

$$\rho_{y,a}^{g} = \frac{\left(P_{y,a}^{g} - \hat{P}_{y,a}^{g}\right)}{\sqrt{\hat{P}_{y,a}^{g}\left(1 - \hat{P}_{y,a}^{g}\right) / \psi_{y}^{g}}}$$

where $P_{y,a}^{g}$ is the observed vector of proportions-at-age, $\hat{P}_{y,a}^{g}$ are the predicted values, and ψ_{y}^{g} denotes the assumed multinomial sample size corresponding to year y. Standard deviations of $\rho_{y,a}^{g}$ should be near 1.0 if the model is fitting the data according to the specified variances. Values greater than 1.0 suggest that the model is fitting poorly given the specified level of data precision. Values less than 1.0 indicate that the model is fitting the data better than the magnitude of the variance (or sample size) specified would indicate.

Standard errors of parameter estimates were computed based on an approximated multivariate normal covariance matrix and by computing marginal distributions from the posterior distribution Markov Chain Monte Carlo (MCMC) integration technique (Gelman et al. 1995). MCMC distributions were presented as Bayesian credible intervals, even though the model is only quasi-Bayesian in that prior distributions were not formally developed for each species. For implementation of MCMC integrations, the first 500,000 samples were omitted as "burn-in" out of a chain of five million. After that, every one-thousandth sample was saved out of the remaining 4.5 million MCMC iterations to remove auto-

Table 3. Ratio of root-mean squared error (RMSE) of observed and predicted values over the mean standard error specified for biomass indices (rows 1-2) and the average standard deviations of normalized residuals (rows 3-7).

	Northern rockfish	Pacific ocean perch	Dusky rockfish	Rougheye rockfish
Trawl survey index	1.751	1.389	1.634	1.002
Longline survey index				1.096
Standard deviation of normalized residuals				
Fishery age compositions	0.720	0.535	0.693	0.850
Fishery length compositions	0.807	0.503	0.636	0.599
Trawl survey age compositions	1.984	0.737	0.909	0.835
Trawl survey length compositions				0.869
Longline survey length compositions				0.528

Values greater than 1 indicate that the model fit was poorer than the input variance specified whereas values less than 1 indicate that the model fit the data better than indicated by the input specification.

correlation. Assurance that the chain had converged was obtained by comparing the mean of the first half of the chain with the mean of the second half after removing the "burn-in." If these two values were similar, then convergence to the true posterior distribution was concluded. Chains were run from different initial starting values to compare for similar converged distributions. Uncertainty estimates are shown for q, M, σ_r, and terminal year spawning biomass.

Results

The diagnostics of model fits indicated that the variances specified for the data components of the model were consistent with what is known about these rockfish species (Table 3). That is, the species that are most difficult to survey with NMFS bottom-trawl gear (due to their patchy distributions) fit the survey trends the poorest. Northern rockfish tend to be the most patchily distributed, and the model fit was least consistent with the survey time series for this species. Rougheye rockfish tend to be the least patchily distributed, and the model fit was most consistent with the survey time series for rougheye rockfish. Dusky rockfish and Pacific ocean perch were in between in their consistency with survey biomass sample-variance estimates.

For age and length composition data, the standard deviations of the normalized residuals tended to be less than 1.0. This suggests that the sample-sizes specified for the multinomial might be too low or that the model structure allowed for accommodation of the observed age or size composition data. Northern rockfish survey age compositions were

the exception in that the effective sample size input for those data were 10-fold higher than for the other multinomial data components. Hence, standardizing those residuals made for more than expected variability, since the denominator reflected more precision (lower value) than the model was able to accommodate. Full plots of model fits to data can be found in Courtney et al. (2003), Hanselman et al. (2003a), Lunsford et al. (2004), and Hanselman and Fujioka (2004).

The marginal posterior probability distributions for M, q, and σ_r revealed considerable overlap between some species (Fig. 1). For example, the estimated marginal posterior distribution for dusky rockfish q overlapped considerably with rougheye, whereas most of the distribution for Pacific ocean perch was outside the range estimated for northern rockfish and dusky rockfish. This is consistent with the biological aspects of these species and their availability to the survey gear; i.e., northern rockfish and dusky rockfish are thought to be less available to survey gear than Pacific ocean perch and rougheye rockfish. Marginal posterior distributions of σ_r were informative in that they departed considerably from their maximum likelihood estimates (MLE) for some species; e.g., the MLE of σ_r for northern rockfish was 0.9 while the mean of the marginal posterior distribution was approximately 1.4 (Fig. 1, Table 4). Model sensitivity analyses to alternative informative prior assumptions for M and σ_r relative to q and h can easily be conducted using the model framework developed here as discussed below. Marginal posterior distributions were also created for the time series of recruitment and biomass so that the Bayesian credibility interval could be compared with the normal approximation (based on the Delta method). An example is provided for northern rockfish (Fig. 2). As expected, the Bayesian credibility intervals were slightly larger than the normal approximations.

Discussion

Maximum likelihood estimates and means of the marginal posterior distribution of trawl survey catchability, q, ranged from approximately 0.5 for northern rockfish to 2 for Pacific ocean perch (Fig. 1, Table 4). Northern rockfish are often encountered over hard untrawlable bottom while Pacific ocean perch are thought to occur over softer more trawlable bottom (Krieger and Sigler 1996). Consequently, estimated values for q are plausible given what is known about the life history of these stocks. Maximum likelihood estimates and means of the marginal posterior distribution of natural mortality, M, ranged from 0.03 for rougheye rockfish to 0.05 for Pacific ocean perch (Fig. 1, Table 4). Marginal posterior distributions of M were narrow (CV 10%, Table 4) as a result of informative prior distributions (CV 10%, Table 2).

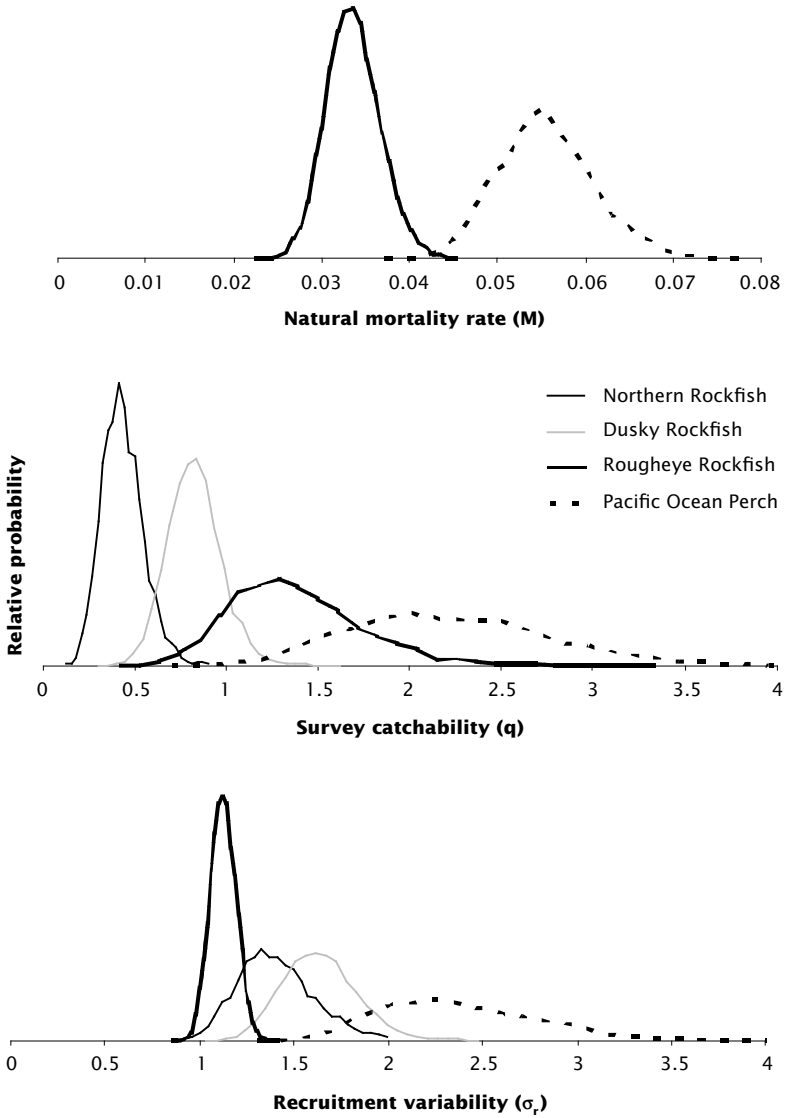


Figure 1. Marginal posterior distributions for natural mortality (*M*), trawl survey catchability (*q*), and recruitment variability (σ_r) for Gulf of Alaska northern rockfish, Pacific ocean perch, dusky rockfish, and rougheye rockfish.

Table 4. Maximum likelihood estimates (MLE), and approximate coefficients of variation (CV) for Gulf of Alaska rockfish computed using the normal distribution approximation (inversed Hessian matrix) and by computing the marginal distribution integrated over the full posterior distribution (MCMC).

	Northern rockfish			Pacific ocean perch			Dusky rockfish			Rougheye rockfish		
		CV			CV			CV			CV	
Parameters	MLE	Normal	MCMC	MLE	Normal	MCMC	MLE	Normal	MCMC	MLE	Normal	MCMC
q	0.46	25%	25%	1.88	28%	30%	0.81	17%	18%	1.30	30%	30%
M				0.05	10%	10%				0.03	9%	10%
σ_r	0.89	12%	22%	1.02	10%	42%	1.13	12%	19%	0.094	6%	7%
Spawning biomass	38,446	37%	52%	95,762	34%	39%	17,766	26%	35%	12,496	37%	57%

Note that female spawning biomass is from the terminal year in each model.
MCMC = Markov Chain Monte Carlo.

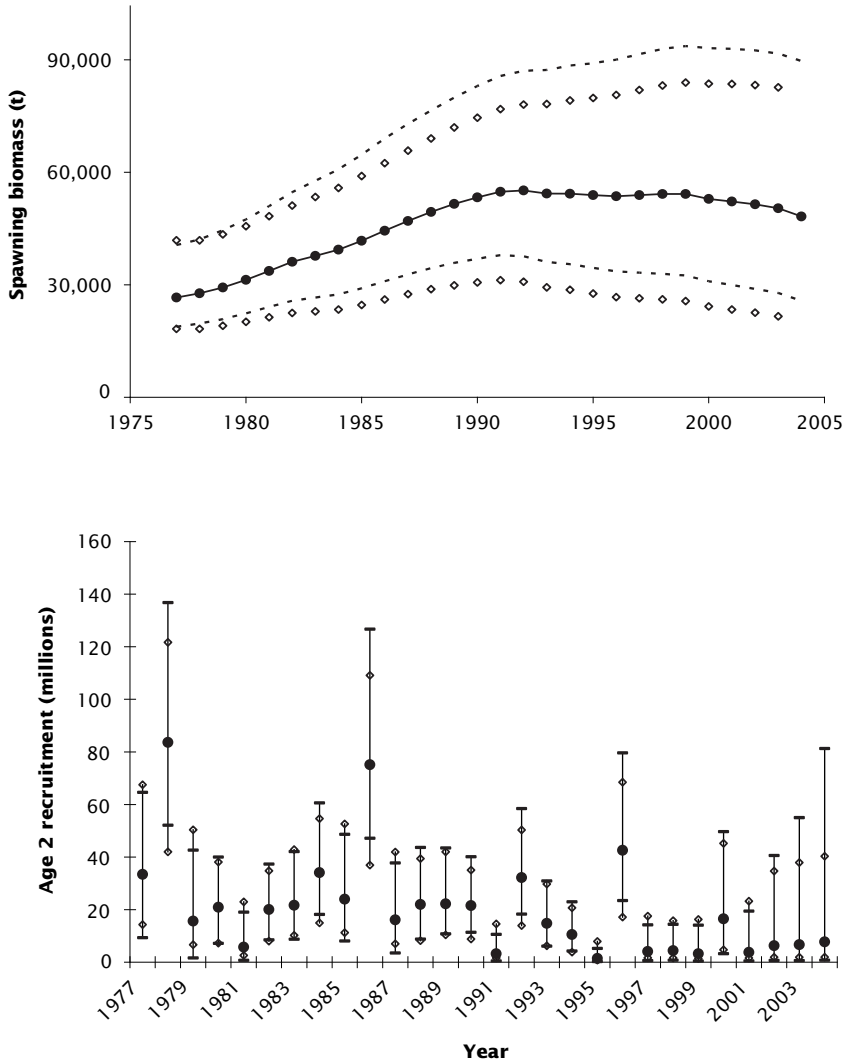


Figure 2. Gulf of Alaska northern rockfish estimates of female spawning biomass (top) and recruitment (bottom) with median (solid dots) and 5th and 95th percentile credibility intervals (dashes) based on the marginal distribution from the Bayesian posterior distribution. Diamonds plotted are the analogous lower and upper confidence intervals derived from the normal approximation to the posterior distribution (no integration was involved).

In these analyses, estimation of the parameters M and q had a large effect on Pacific ocean perch and rougheye rockfish model output when they were allowed to vary simultaneously. Estimation of M within stock assessments can be confounded with other parameters such as q and fishing mortality (Fu and Quinn 2000). Similarly, incorrect specification of natural mortality can have dramatic repercussions on harvest rate recommendations (Thompson 1994). Exploration of parameter estimation for q and M was performed in the Pacific ocean perch model by loosening the prior constraint on q, estimating M from within the model, and comparing MCMC posterior distributions to the maximum likelihood output of the model (Heifetz et al. 2002). Estimating M tended to have a substantial effect on the model outputs for ending biomass and resulting management recommendations for sustainable catch. Specifying a less informative (CV 45%) prior distribution on q when M was constrained by an informative (CV 10%) prior distribution reduced the sensitivity of results for Pacific ocean perch and allowed for the stable estimation of q (Table 2, Heifetz et al. 2002, Hanselman et al. 2003a).

A similar exploration of both the trawl survey q and longline survey q relative to M for the rougheye rockfish model determined that estimates of M *and* q converged at reasonable values when allowed to vary simultaneously (Hanselman and Fujioka 2004). Convergence occurred even though only two years of age data were available for the rougheye rockfish model (trawl survey ages 1990, 1999; Table 1). Either the addition of the longline survey data or the more consistent trawl survey biomass estimates over time (relative to the other rockfish species) may have provided sufficient data contrast to estimate M and q at the same time (Table 2). Simultaneous estimation of q and M for northern and dusky rockfish converged at unreasonable values, and M was fixed at independently estimated values for those stocks by setting the prior CV to 0.0 (Table 2).

Estimates of marginal posterior distributions of σ_r departed considerably from the MLEs for some species (Tables 2, 4, Fig. 1). Maunder and Deriso (2003) evaluated this and found similar results if age data were missing over a number of years. In practice, the ability to estimate σ_r is contingent on good (and abundant) age data. When these are lacking, σ_r can be fixed by the analyst at a value that allows for reasonable recruitment variability as determined by prior knowledge of the stock or by meta-analysis of similar stocks. An alternative to fixing σ_r was accomplished in these rockfish model applications by constraining estimation of σ_r with a lognormal prior probability distribution assigned by the analyst. In the northern rockfish application, σ_r represented the standard deviation of log recruitment residuals about the Beverton-Holt stock-recruit relationship (Courtney et al. 1999). Courtney et al. (2003) found that for northern rockfish a prior arithmetic mean for σ_r of 0.9

and an uninformative prior CV of 45% were sufficient to allow for reasonable variability in estimated recruitment. This mean value is also consistent with Ianelli and Heifetz (1995) who fixed σ_r for Pacific ocean perch at 1.08 based on residuals of the MLE fit to a similar model formulation, and slightly higher than Ianelli (2002) who fixed σ_r at 0.6 in an analogous model used for U.S. West Coast Pacific ocean perch.

Considering that rockfish populations are thought to be characterized by rare large recruitment levels, Hanselman et al. (2003a) concluded that a prior arithmetic mean for σ_r of 0.9 resulted in estimates of low recruitment variability (CV of 25%) for Pacific ocean perch. Hanselman et al. (2003a) and Lunsford et al. (2004) found that a prior arithmetic mean for σ_r of 1.7 and an uninformative CV of 45% were sufficient to allow for reasonable recruitment variability for Pacific ocean perch and dusky rockfish. This is consistent with a meta-analysis of Atlantic groundfish data sets by Beddington and Cooke (1983) that identified values of σ_r, defined there as the standard deviation of log recruitment about the mean, ranging from 0.07 to 2.84. Unlike for the other rockfish species here, Hanselman and Fujioka (2004) found that with only two years of age data, a prior arithmetic mean for σ_r of 1.1 and an *informative* prior CV of 3% were required to allow for reasonable recruitment variability in the rougheye rockfish model.

The four rockfish species modeled here had different amounts of length and age composition data available. The multinomial likelihood components for age and length compositions required assumptions about input sample size. These values affected precision and the degree to which some data were fit compared to other data components. Age compositions in the northern rockfish assessment showed consistent patterns over time, and age determination practices resulted in relatively more precise estimates compared to other rockfish species. As a consequence, relatively heavier weight was placed on age data in the northern rockfish model (Courtney et al. 2003). Sample size in early model development for application to northern rockfish was estimated as the number of hauls from which age or length specimens were collected scaled to a maximum of 100 (Courtney et al. 2003). In later model development for applications to Pacific ocean perch, dusky rockfish, and rougheye rockfish, the square root of the number of ages or lengths was used so that sample size was directly proportional to sample variance (Hanselman et al. 2003a, Hanselman and Fujioka 2004, Lunsford et al. 2004). The diagnostics of model fits to data presented here indicated that reliance on relatively heavier weight in the northern rockfish model reflected more precision in the age data than the model was able to accommodate (standard deviations of the normalized residuals = 2; Table 3). However, the diagnostics of model fits to data also suggested that in general, the sample-sizes specified for the multinomial might be too low (standard deviations of the normalized residuals all <1; Table

3). Based on these diagnostics, alternative values for assumed sample sizes could easily be re-evaluated.

Including a stochastic stock-recruitment relationship in the northern rockfish had little effect on fits to the available data (Courtney et al. 2003; Appendix A). If productivity measures are to be estimated for rockfish stocks, Ianelli (2002) suggests that estimating stock-recruitment relationships is best done internal to integrated models as presented here for northern rockfish. However, if a stock-recruit relationship is used, precautions should be taken to evaluate autocorrelation patterns of stock-recruitment residuals since they affect the precision of critical parameters such as steepness. Even when autocorrelation of recruitment residuals is accounted for, careful analysis of the stock-recruitment relationship given the available data is required in order to evaluate stock productivity in age-structured models (e.g., Butterworth et al. 2003). For the rockfish stocks presented here, recruitment appeared largely independent of current spawning biomass and was likely more dependent upon environmental conditions (Hanselman et al. 2003a, Hanselman and Fujioka 2004, Lunsford et al. 2004). As a result, model interpretation in later applications to Pacific ocean perch, dusky rockfish, and rougheye rockfish was simplified by removal of the stock-recruit relationship from within the integrated models.

Conclusions and future directions

In conclusion, development of a customized age-structured model for several rockfish species proved to be adaptable for evaluating uncertainty and the information content of diverse types of data. The modifications needed to customize the model to the different rockfish species were relatively minor, and comparisons among assumptions were easy to compile. The code executed quickly (for example, an MCMC chain of length 5 million was completed in just over 3 hours on a 2005 desktop computer).

The next steps being considered include evaluation of consistency among species by modeling related species simultaneously and sharing parameters in a hierarchical meta-analytic approach. This would allow a more careful analysis of the stock-recruitment relationship given the available data that are required in order to evaluate stock productivity in age-structured models. Similarly, patterns in recruitment (and their variability) and other vital parameters could easily be evaluated. A more fully Bayesian approach could be developed by utilizing more meaningful prior distributions from meta-analyses such as Myers et al. (1995) or by utilizing truly uninformative prior distributions (Punt and Hilborn 1997). Other ongoing improvements to GOA rockfish assessment not discussed here include (1) reconstruction of historic catch (1965-1976) for GOA rockfish species other than Pacific ocean perch (Ito 1982,

Ackley and Heifetz 2001, Clausen and Heifetz 2002), (2) assessment of age determination error and sample size (Kimura 1990, Coggins and Quinn 1998), (3) evaluation of error in maturity and growth schedules, and (4) assessment of different selectivity curves, likelihood functions, and the potential of time-varying parameters (Bence et al. 1993, Radomski et al. 2005).

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Appendix A. Model details

Notation	Model description
Y	Year, $y = 1, 2, \ldots T$
T	Terminal year of the model
A	Model age class, $a = a_0, a_0 + 1, \ldots, a_+$
a_0	Age at recruitment to the model
a_+	Plus-group age class (oldest age considered plus all older ages)
L	Length class
Ω	Number of length bins (for length composition data)
G	Gear-type (g = survey or fishery)
X	Index for likelihood component
w_a	Average weight at age
φ_a	Mature female population proportion at age
μ_r	Average log-recruitment
μ_f	Average log-fishing mortality
ϕ_y	Annual fishing mortality deviation
τ_y	Annual recruitment deviation ~ $(0,\sigma)$
σ_r	Recruitment standard deviation
$N_{y,a}$	Numbers of fish at age a in year y
M	Natural mortality
$F_{y,a}$	Fishing mortality for year y and age class $a\left(= s_a^g \mu_f e^{\phi_y}\right)$
$Z_{y,a}$	Total mortality for year y and age class $a\left(= F_{y,a} + M\right)$

Notation	Model description (Continued)
R_y	Recruitment in year y
R_0	Unfished average recruitment
B_y	Spawning biomass in year y
B_0	Unfished average spawning biomass
ω	Set mean recruitment to average (=0) or to stock-recruitment curve (=1)
s_a^g	Selectivities at age a for gear type g
$\mathbf{A}$	Age error matrix dimensioned
$\mathbf{A}^1$	Age-to-length transition matrix dimensioned
$\rho_{y,a}^g$	Pearson residual of proportion at age (or length) a for gear g and year y
Q	Survey catchability coefficient
λ_x	Statistical weight (penalty) for component x
$I_y, \hat{I}_y$	Observed and predicted survey index in year y
$P_{y,l}^g, \hat{P}_{y,l}^g$	Observed and predicted proportion at length l for gear g in year y
$P_{y,a}^g, \hat{P}_{y,a}^g$	Observed and predicted proportion at observed age a for gear g in year y
ψ_y^g	Sample size assumed for gear g in year y (for multinomial likelihood)
n_g	Number of years that age (or length) composition is available for gear g
h,σ_h	Prior mean, standard deviation for steepness
q,σ_q	Prior mean, standard deviation catchability coefficient
M,σ_M	Prior mean, standard deviation for natural mortality
$\sigma_{r_\mu},\sigma_{\sigma_r}$	Prior mean, standard deviation for recruitment variability

Equations describing state dynamics	Model description (Continued)
$N_{1,a} = \begin{cases} R_1, & a = a_0 \\ e^{\left(\mu_r + \tau_{a_0-a+1}\right)} e^{-(a-a_0)M}, & a_0 < a < a_+ \\ e^{(\mu_r)} e^{-(a-a_0)M} \left(1 - e^{-M}\right)^{-1}, & a = a_+ \end{cases}$	Initial year recruitment and numbers at ages.
$N_{y,a} = \begin{cases} R_y, & a = a_0 \\ N_{y-1,a-1} e^{-Z_{y-1,a-1}}, & a_0 < a < a_+ \\ N_{y-1,a-1} e^{-Z_{y-1,a-1}} + N_{y-1,a} e^{-Z_{y-1,a}}, & a = a_+ \end{cases}$	Subsequent years recruitment and numbers at ages
$R_y = \begin{cases} e^{\left(\mu_r + \tau_y\right)}, & \omega = 0 \\ \dfrac{B_{y-a_0} e^{\tau_y}}{\alpha + \beta B_{y-a_0}}, & \omega = 1 \end{cases}$	Recruitment
where $\alpha = \dfrac{B_0}{R_0}\left(1 - \dfrac{h-2}{0.8h}\right)$, $\beta = \dfrac{5h-1}{4hR_0}$	
$B_0 = \sum_{a_0}^{a_+ - 1} R_0 e^{-(a-a_0)M} \varphi_a w_a + R_0 e^{-(a_+ - a_0)M} \varphi_{a_0} w_{a_0} \Big/ \left(1 - e^{-M}\right)$	
and $B_y = \begin{cases} B_0, & y = 1 \\ \sum_a \varphi_a w_a N_{y,a}, & y > 1 \end{cases}$	
Observation equations	
$\hat{C}_y = \sum w_a N_{y,a} F_{y,a} \left(1 - e^{-Z_{y,a}}\right) Z_{y,a}^{-1}$	Catch biomass in year y
$\hat{I}_y = q^g \sum_{a_0}^{a_+} N_{y,a} \dfrac{s_a^g}{\max\left(s_a^g\right)} w_a$	Survey biomass index
$\hat{P}_{y,\cdot}^g = N_y s^g \left(\sum_{a_0}^{a_+} N_{y,a} s_a^g\right)^{-1} \mathbf{A}$	Vector of fishery or survey predicted proportions at age
$\hat{P}_{y,\cdot}^g = N_y s^g \left(\sum_{a_0}^{a_+} N_{y,a} s_a^g\right)^{-1} \mathbf{A}^l$	Vector of fishery or survey predicted proportions at length

Posterior distribution components	Model description (Continued)
$L_C = \lambda_c \sum_y \left(\ln C_y - \ln \hat{C}_y\right)^2 / \left(2\sigma_C^2\right)$	Catch likelihood
$L_I = \lambda_I \sum_y \left(\ln I_y - \ln \hat{I}_y\right)^2 / \left(2\sigma_I^2\right)$	Survey biomass index likelihood
$L_{age} = \lambda_{age} \sum_{i=1}^{n_g} -\psi_y^g \sum_{a_0}^{a_+} \left(P_{i,a}^g + \nu\right) \ln\left(\hat{P}_{i,a}^g + \nu\right)$	Age composition likelihood
$L_{length} = \lambda_{length} \sum_{i=1}^{n_g} -\psi_y^g \sum_{l=1}^{\Omega} \left(P_{i,l}^g + \nu\right) \ln\left(\hat{P}_{i,l}^g + \nu\right)$	Length composition likelihood (ψ_y^g = sample size, n_g = number of years of data per gear g, i = year of data availability, ν is a constant set at 0.01)
$L_h = \left(\ln \hat{h} - \ln h_\mu\right)^2 / 2\sigma_h^2$	Prior for stock-recruitment steepness, when estimated
$L_q = \left(\ln \hat{q}^g - \ln q_\mu^g\right)^2 / 2\sigma_q^2$	Prior on survey catchability coefficient for gear g
$L_M = \left(\ln \hat{M} - \ln M_\mu\right)^2 / 2\sigma_M^2$	Prior for natural mortality
$L_{\sigma_r} = \left(\ln \hat{\sigma}_r - \ln \sigma_{r_\mu}\right)^2 / 2\sigma_{\sigma_r}^2$	Prior distribution for σ_r
$L_\tau = \sum_{y=1}^{T} \frac{\tau_y^2}{2\hat{\sigma}_r^2} + \ln \hat{\sigma}_r$	Prior on recruitment deviations
$L_f = \lambda_f \sum_{y=1}^{T} \phi_y^2$	Regularity penalty on fishing mortality
$L_s = \lambda_s \sum_{a_0+1}^{a_+} \mathrm{I}\left(s_a^g < s_{a-1}^g\right)\left(s_{a-1}^g - s_a^g\right)^2$	Selectivity non-decreasing penalty—"I" represents indicator function (1 if true, 0 if false)
$L_{s_a} = \lambda_{s_a} \sum_{a_0}^{a_+-2} \left(s_{a+2}^g + s_a^g + 2s_{a+1}^g\right)^2$	Selectivity smoothness penalty (squared second differences)
$L_{Total} = \sum_x L_x$	Total objective function value

Population Dynamics of an Unexploited Rockfish (*Sebastes jordani*) in the California Current

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Abstract

The shortbelly rockfish, *Sebastes jordani*, is one of the most abundant rockfish species in the California Current, and is a key forage species for many fish, birds, and marine mammals. This species has not been the target of commercial fisheries, and consequently catch data are limited. Nevertheless, available evidence suggests that the population has undergone significant fluctuations in abundance over the last several

decades, presumably in response to variable environmental conditions. We present a population model, using standard methods and a variety of both traditional and untraditional data, to investigate population changes for this ecologically important species. The results from this analysis provide an opportunity to consider the dynamic nature of an unexploited rockfish population, and should ultimately provide insight into the potential causes and consequences of natural population variability on both exploited and non-exploited populations throughout the California Current.

Introduction

The shortbelly rockfish (*Sebastes jordani*) is best characterized by small size (individuals are rarely longer than 30 cm), rapid growth and maturity (in our data, 50% of females are mature by age 2, 99% by age 3), and high natural mortality rate (Pearson et al. 1991, Love et al. 2002). Shortbelly rockfish range from Punta Baja in Baja California as far north as La Perouse Bank off of British Columbia. However, they are most abundant along the continental shelf break between the northern end of Monterey Bay and Point Reyes, California, and around the Channel Islands in the Southern California Bight. Although stock structure is poorly understood, genetic analysis of fish collected between San Diego and Cape Mendocino (California) suggest a single, coastwide stock, with slight differences in allele frequencies across Point Conception (Constable 2006). Our paper considers only the shortbelly rockfish population in this region, which is shown in Fig. 1 along with the approximate spatial coverage and duration of the principal data time series used in the model.

Shortbelly rockfish feed primarily on juvenile and adult euphausiids, and are an important prey item to a wide range of piscivorous fishes, seabirds, and marine mammals (Chess et al. 1988, Sydeman et al. 2001). Merkel (1957) reported that juvenile rockfish were important prey of chinook salmon along the central California coast in late spring and summer, with shortbelly accounting for more than 60% of those identified to species. Although both juvenile and adult rockfish have rarely been identified to the species level in the diets of many California Current marine mammals (Antonelis and Fiscus 1980, Stroud et al. 1981), shortbelly rockfish were among the five most significant prey items for California sea lion (*Zalophus californianus*) in the Channel Islands (Lowry and Carretta 1999). Consequently, shortbelly rockfish have a trophic position and life history traits more similar to forage fishes than most other *Sebastes*.

Large catches of shortbelly rockfish were made during foreign fisheries of the 1960s and 1970s, although these were presumably incidental to the targeting of other rockfish and Pacific hake (*Merluccius*

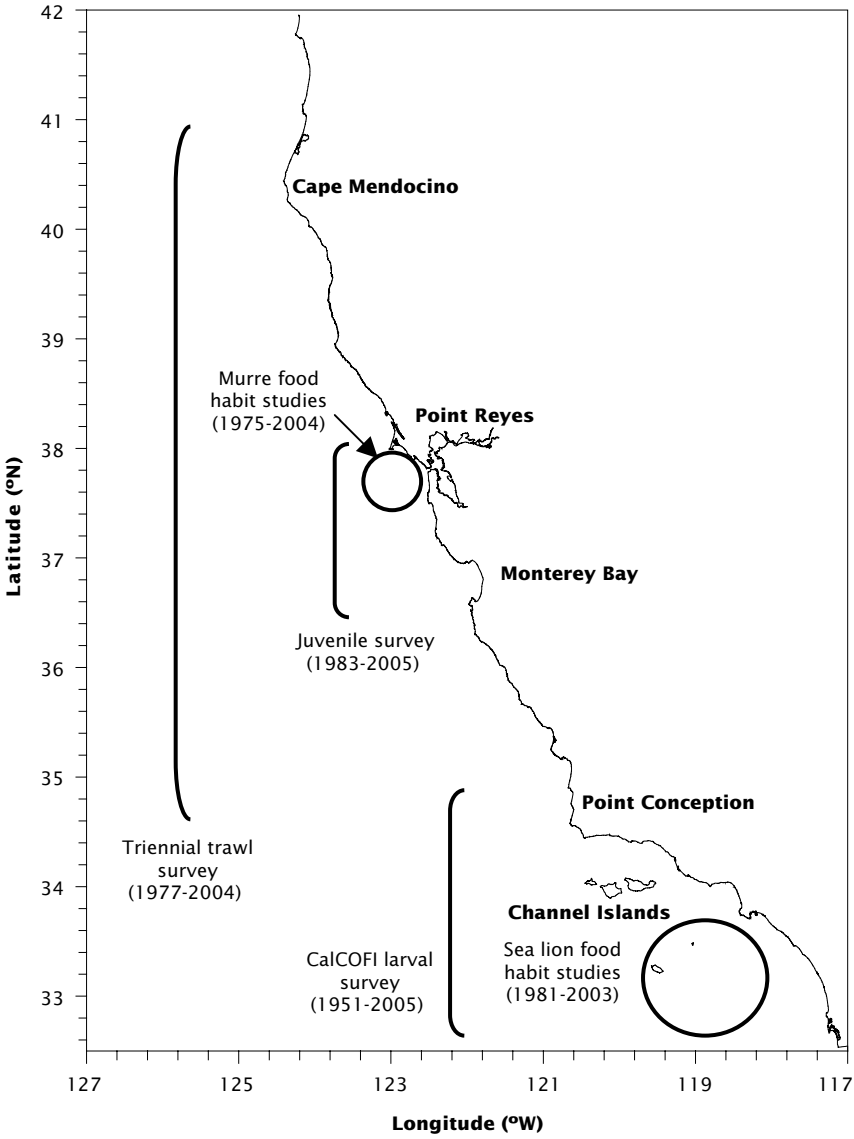


Figure 1. Approximate spatial coverage of major data sources used in this study. Note that actual coverage varied among years for many surveys; areas shown approximate the core areas sampled with consistency throughout the duration of the time series.

productus) (Rogers 2003). The expectation of eventual development of a domestic commercial fishery led to past efforts to estimate stock abundance and productivity (Lenarz 1980) as well as evaluations of commercial potential (Kato 1981). Pearson et al. (1989, 1991) estimated that allowable catches for shortbelly could range from 13,900 to 47,000 tons per year, based on life history data and hydroacoustic survey estimates of abundance. Subsequently, the Pacific Fishery Management Council established an acceptable biological catch (ABC) of 23,500 tons for shortbelly, which was reduced to 13,900 tons in 2001 based on observations of poor recruitment throughout the 1990s. Only modest landings (10 to 70 tons per year) have been reported in California over the last 20 years. Discards may be somewhat greater, as shortbelly can be caught incidentally by trawl gear when targeting other semi-pelagic rockfish. A very modest amount of early data on bycatch rates off of Central California suggests that shortbelly rockfish were often encountered in intermediate depth tows (100 to 200 meters), and comprised approximately 7.8% of the rockfish catch by volume at this depth range (Heimann 1963). However, the desire and ability of fishermen to avoid shortbelly suggest that more recent bycatch rates are likely to be considerably less (T. Ghio, Groundfish Advisory Subpanel, Pacific Fishery Management Council, pers. comm.). Recent estimates of discards from the West Coast groundfish observer program have been on the order of five tons per year (or less) for 2002 and 2003, although these may not represent historical rates.

As the overall impacts of fisheries can be considered to be modest to inconsequential, the objectives of this paper and model are focused on an evaluation of the variability and change exhibited by this population over time, including the potential to infer such changes using non-traditional data. Fisheries management typically presumes that we understand population behavior even in unfished systems. Consequently, understanding changes in unexploited populations could be insightful with respect to appreciating the dynamic nature of productivity and abundance for a wide range of species throughout the California Current ecosystem.

Materials and methods

The population was modeled using an age and size structured statistical model, Stock Synthesis 2, a modeling framework used for most recent California Current groundfish assessments. A full description of the population dynamics, selectivity and catch equations, and associated likelihood functions are given in Methot 2005. In our application, parameters for growth, fecundity, and maturity were estimated externally from the model and input as fixed values. Although shortbelly rockfish have been aged to 30 years, we found that 95% of all aged

shortbelly available to us (~8,500) were 12 years of age or less, and 99% of the shortbelly available to us were less than 17 years of age or less, consistent with estimates of natural mortality of 0.25 to 0.27 based on the Hoenig (1983) rule of thumb approach. We used a fixed natural mortality rate of 0.26, consistent with these observations, the range estimated by Pearson et al. (1991) and the point estimate by Ralston et al. (2003).

Ralston et al. (2003) used larval production methods to estimate that the spawning biomass in the Monterey to San Francisco area of approximately 65,000 tons in 1991, considerably less than the hydroacoustic estimates of 153,000 to 295,000 tons (in 1980 and 1977 respectively). The latter estimates are considered to be highly uncertain, since there is no estimate of target strength for shortbelly rockfish and the hydroacoustic estimates assumed a target strength equivalent to Pacific hake. MacGregor (1986) had earlier reported that 53% of shortbelly larvae occurred in the Monterey area, 35% occurred in the Channel Islands area, with the remaining ~12% occurring near the central coast. This suggests that a doubling of the Ralston et al. (2003) biomass estimate may be reasonable, giving a total biomass of 115,000 tons in 1991. This was incorporated as a point estimate of biomass with a coefficient of variation of 0.2 (based on Ralston et al. 2003), with a selectivity curve set identical to the maturity function. In order to evaluate the sensitivity of model behavior to potential bycatch, estimates of plausible bycatch streams were developed based on the Heimann (1963) data, extrapolated to what might have been caught based on historical shelf rockfish landings, and entered into the model as catches.

CalCOFI larval abundance data

Egg or larval abundance data from the California Cooperative Oceanic and Fisheries Investigations (CalCOFI) surveys have been used in stock assessments for a number of commercially important West Coast species, including bocaccio rockfish (MacCall 2003), sheephead (Alonzo et al. 2004), and several coastal pelagic species. Shortbelly larvae are the most frequently occurring of the rockfish larvae identifiable to species, accounting for approximately 15% of the total rockfish larvae in the survey (Moser et al. 2000). High levels of larvae abundance in CalCOFI surveys were observed throughout most of the 1950s, and the late 1980s through the early 1990s, while very low abundance levels occurred during the 1958-1959 El Niño, from the mid-1970s through the early 1980s, and in the late 1990s.

We used tow-specific information and a Delta-GLM approach, which combines a binomial model for presence/absence information with a model of catch per unit effort (CPUE) for positive tows (Stefansson 1996, Maunder and Punt 2004), to generate a relative index of spawning biomass. The data included over 11,200 observations during 1951-2005

for the regularly sampled survey grid, although from 1967 to 1984 this survey was limited to a triennial frequency. Presence/absence (π) was modeled with a binomial GLM using a logit link (where the logit (π) = log [$\pi/(1-\pi)$]), and the density (μ) of shortbelly rockfish larvae in positive tows was modeled with a Gaussian distribution of the log transformed data. Specification of the error distribution for the positive observation was determined based on Akaike Information Criteria, as in Dick (2004). Models included year, month, and station effects, and the product of the year effects of the two models ($\pi\mu$) was used as the final index of abundance.

Triennial Trawl Survey

A primary source of fishery independent information for many groundfish species in the California Current are area-swept estimates of abundance based on the Triennial Trawl Survey (Weinberg et al. 2002). However, for semi-pelagic species the patchiness of catches in the survey is particularly problematic, and area-swept estimates of abundance are highly uncertain. For example, out of nearly 1,500 tows made south of Cape Mendocino between 1977 and 2004, over half the total catch of shortbelly rockfish was made in only six tows, and over 95% of the catch was made in only fifty tows. Rather than use area-swept estimates, we developed a delta-GLM approach that estimated year, latitude (2º bins), and depth (50 meter bins) effects to estimate annual indices for each survey year, consistent with the approach of He et al. (2006) for another semi-pelagic species, widow rockfish (*S. entomelas*). We obtained haul-specific survey data from 1977 to 2004 (M. Wilkins, AFSC, pers. comm.; B. Horness, NWFSC, pers. comm.), and excluded bad performance tows based on Zimmermann et al. (2001). We included all tows south of Cape Mendocino (40ºN) that occurred between depths of 55 to 366 meters for all years, with the exception of a small number of tows made south of 34º30' in 1977 (as the survey did not cover this region in subsequent years). Catch per unit effort was estimated for each tow as in Weinberg et al. (2002). Length frequency data were also generated for each survey year, with the effective sample size based on the number of tows in which length samples were taken. Due to differences in the depth strata sampled in 1977, and low sample sizes in 1980-1986, only length data from 1989-2004 were used in the analysis. Length data demonstrate a movement to deeper water with size, as shown by Lenarz (1980).

Juvenile survey

Estimates of juvenile shortbelly rockfish abundance are available for 1983-2005 from the NMFS/SWFSC midwater trawl survey. Studies have shown that indices of year-class strength derived from the survey are effective at gauging impending recruitment (Ralston and Howard 1995), and consequently these indices have been used in forecasting year-class

strength for a number of groundfish species, including widow rockfish (He et al. 2006), Pacific hake (Helser et al. 2006) and chilipepper rockfish (Ralston et al. 1998). Similar to other surveys, we used a delta-GLM to remove spatial and seasonal effects. Shortbelly rockfish are by far the most abundant rockfish species in the juvenile survey data, and the results of the survey time series suggest a high degree of covariance among juveniles of different species (S. Ralston, unpubl. data). Although a power coefficient has been used in other assessments to transform juvenile indices, based on the assumed compensatory relationship between pelagic juvenile abundance and subsequent recruitment to the adult population (Adams and Howard 1996), the paucity of reliable age information necessary to estimate this parameter led to our decision to use the index as an absolute reflection of juvenile abundance. Consequently, the catchability of age-0 rockfish from this survey was treated as a nuisance parameter.

Seabird food habits data

The abundance, biology, and food habits of several species of seabirds have been monitored by the Point Reyes Bird Observatory on the southeast Farallon Islands (west of San Francisco, California) since the early 1970s, providing a thirty-year time series of food habits for some species (Sydeman et al. 2001). Juvenile rockfish have traditionally dominated the diets of common murre (*Uria aalge*) and many other seabird species during their breeding seasons. However, the proportion of rockfish in seabird diets declined severely through most of the 1990s, likely related to ocean conditions (Sydeman et al. 2001, Miller and Sydeman 2004). Although seabird food habits data can be informative in the evaluation of stock status or recruitment for some species (Cairns 1992, Montevecchi and Myers 1995), behavioral complications can also undermine the utility of such data in population models. Food habits data may reflect relative prey availability more than abundance, as predators tend to concentrate foraging effort on the most available prey. However, these are complications that similarly undermine the integrity of fisheries-dependent time series (Cairns 1992, Walters 2003).

Several factors make the utility of this data set as an indicator of year-class strength appealing. First, shortbelly are generally quite easy to distinguish in the sampling regime, and are the overwhelmingly dominant rockfish species found in murre diets (Ainley et al. 1996). Second, research has shown that common murres prefer to forage locally for juvenile rockfish during their breeding season (May-June, when juvenile rockfish are most abundant), because the close proximity to the breeding grounds reduces foraging trip duration. In years when juvenile rockfish are less abundant, murres forage in coastal waters for northern anchovy and other forage fishes (Ainley and Boekelheide 1990, Miller and Sydeman 2004). Third, the species composition of common

murre prey has been at least partially validated by comparisons with rhinoceros auklet (*Cerorhinca monocerata*) food habits for 1987-2004, in which prey are physically taken from the sampled birds and identified to species in a controlled setting (Sydeman et al. 2001). Finally, the proportion of juvenile rockfish in murre diets is highly correlated to the NMFS midwater trawl estimates of juvenile abundance, which indexes juvenile rockfish abundance over a larger spatial extent (Ainley et al. 1993; K. Mills, PRBO, pers. comm.). Individual prey observations were treated with a binomial GLM to obtain annual indices and remove calendar date effects. Annual indices were arcsine transformed, as is appropriate for indices of proportionality (Zar 1996). The resulting index was included in the model as an index of age 0 abundance for the period from 1975 to 2004.

Sea lion food habits data

Another source of food habits data is based on ongoing monitoring of California sea lion (*Zalophus californianus*) food habits in the Channel Islands (Lowry et al. 1990, 1991; Lowry and Carretta 1999). Scat samples have been collected at regular (monthly to quarterly) intervals from 1981 to the present, from San Nicolas, San Clemente, and Santa Barbara islands. Prey species have been identified to the lowest possible taxon based on recovered hard parts (otoliths, cephalopod beaks, shark teeth, and invertebrate exoskeletal fragments). During 1981-2003, over 9,300 samples with identifiable prey remains were collected and enumerated. Shortbelly rockfish were among the most frequently occurring prey, generally present in 10 to 30% of samples (other *Sebastes* were relatively infrequent). The presence/absence sample data were treated with a binomial GLM (logit link) with year, island, and seasonal effects, and the arcsine transformed year effects were used as an index of relative abundance. Length frequency information was also available to assess the vulnerable portion of the shortbelly stock being predated upon, with lengths reconstructed from otolith lengths in specimens that were not eroded by digestion, based on the otolith to fish length regression reported in Wyllie Echeverria (1987). A total of over 4,500 reconstructed lengths were available, in which strong cohorts are clearly visible over time (Fig. 2). The rapid decline of fish larger than 20 cm suggests that sea lions are primarily foraging on younger, more shallowly distributed shortbelly rockfish, which may become less vulnerable as they move into deeper water with age and size. Although California sea lions usually forage between depths of 20 to 280 meters, Melin and DeLong (2002) found that most dives for female sea lions tended to be shallower than 80 meters, such that fish in deeper waters could be less vulnerable. Effective sample sizes were iteratively adjusted from the number of observations to the effective sample size estimated by the model.

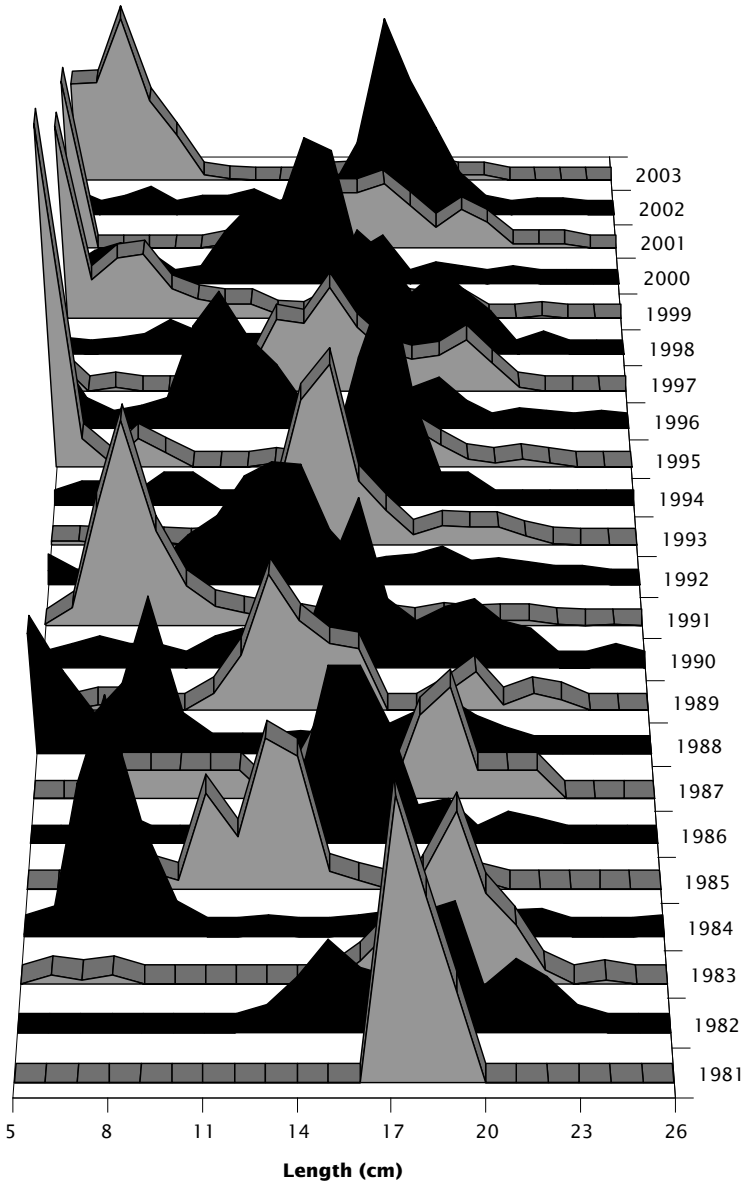


Figure 2. Length frequency composition derived from otoliths collected in sea lion scat samples from the Southern California Bight, 1981-2003, based on otolith length/fish length regressions.

Model configuration

We explored a wide range of model structures and trade-offs between model complexity and the informative limits of the data. Through the process of evaluating alternative model configurations, we developed a base model that had growth and the natural mortality rate estimated externally, and sigma-*R* (the standard deviation of the lognormally distributed recruitment deviations) fixed at 1. The model uses a Mace-Doonan (Mace and Doonan 1988) stock recruitment relationship, where R_0, or equilibrium recruitment, represents the number of recruits that would be expected on average for an unfished stock, and steepness (h) refers to the amount of compensation in the spawner-recruit relationship. We estimated equilibrium recruitment (R_0), but found that the data were inadequate to provide a meaningful estimate of steepness. As steepness values close to 1 represent high compensation and those close to 0.2 represent little or no compensation, we fixed steepness at 0.65, consistent with Dorn (2002). Similar approaches are taken for most West Coast groundfish assessments of commercially exploited species.

An additional parameter estimated in this model was a scaling factor for the initial biomass, which allows the starting biomass value to deviate from the model estimated equilibrium biomass. As marine populations are typically not stationary, the equilibrium biomass is best described as the theoretical average level of biomass (or spawning biomass) around which the population would fluctuate in the absence of fishing. Allowing the starting biomass to be higher or lower than this value is typically not done in assessments for commercially exploited species, where historical catches are believed to have a greater impact on population trajectories than recruitment variability, but is a logical approach for this model. Other parameters that were freely estimated include recruitment deviations from 1960 to 2004 (which reflect relatively stronger or weaker year classes than would be expected from the spawner-recruit relationship), logistic selectivity curve parameters for fisheries catches (based on measurements of landed fish) and the Triennial Trawl Survey length data, and parameters for a double-logistic selectivity curve for the sea lion prey length composition data (in which only the descending limb of the double logistic was estimated; fish were assumed to be fully selected at 5 cm length). Selectivity curves for the CalCOFI data and the larval production point estimate were fixed at the maturity function. Selectivity for the pelagic juvenile (age-0) indices (the juvenile survey and the seabird data) were age-based; fish were assumed to be fully vulnerable at age 0, and fully invulnerable at all ages thereafter. The total number of freely estimated parameters in the model was 54; most were recruitment deviations (46) or selectivity parameters (6), and the remaining two were the mean unfished recruitment level and the ratio of starting biomass to the mean unfished biomass. We also evaluated the sensitivity of the model to a wide range

of different parameter values, including freeing up parameters such as natural mortality, the duration over which recruitment deviations were freed (e.g., to 1950, or beginning in 1975), the standard deviation of lognormal recruitment (sigma-*R*), selectivity curve parameterization, and other factors. For brevity, only a summary of model sensitivities is provided here.

Results

The results demonstrate that the biomass of shortbelly rockfish has fluctuated substantially over time, with major declines apparent between the 1950s and 1960s, and from the early 1990s to the present (Fig. 3). The model estimated a mean "unfished" spawning biomass level of 48,000 tons, an initial (1950) spawning biomass of 187,000 tons, and a total spawning biomass in 2005 of 35,000 tons. By basing the equilibrium spawning biomass on the long-term average biomass level, the resulting "depletion" level of the stock in 2005 was 73% of the averaged unfished level, although it was less than 20% of the estimated 1950 abundance and 50% of the estimated 1991 abundance. Although recruitment was estimated from 1960 onward, only years after 1974 were meaningfully informed by data; prior to this the model was fitting to the trends inferred by CalCOFI data. The model clearly suggests a long period of poor recruitment through most of the 1990s, associated with a significant decline in biomass, a trend that is reflected in all of the recruitment and biomass indices used in the model. The consequence of fisheries was estimated to be negligible (an exploitation rate less than 0.01) in all years except the mid-1960s, suggesting that fishing mortality has probably not had a substantive impact on this stock since the days of the foreign fisheries, although very modest impacts may be plausible.

The fits to the survey data, particularly the CalCOFI data, demonstrated the challenge of interpreting a low frequency signal from highly variable time series (Fig. 4). For the fit to the CalCOFI data in particular, note that the recruitment deviations for the period between 1950 and 1960 were fixed at the equilibrium recruitment, in order to phase in a mean recruitment level for the early part of the time series. Relative abundance levels were highly sensitive to the time in which recruitment deviations were free, particularly given the very rapid decline in the CalCOFI index associated with the 1958-1959 El Niño event. Tuning to an equilibrium recruitment that captured both the high and the low index values throughout the early part of the time series is a reasonable balancing of model freedom and the limitations of the data. Furthermore, there is considerable high frequency variability in larval distribution and abundance inferred in the CalCOFI time series, that may be partially related to variability in ocean conditions and reproductive output (as

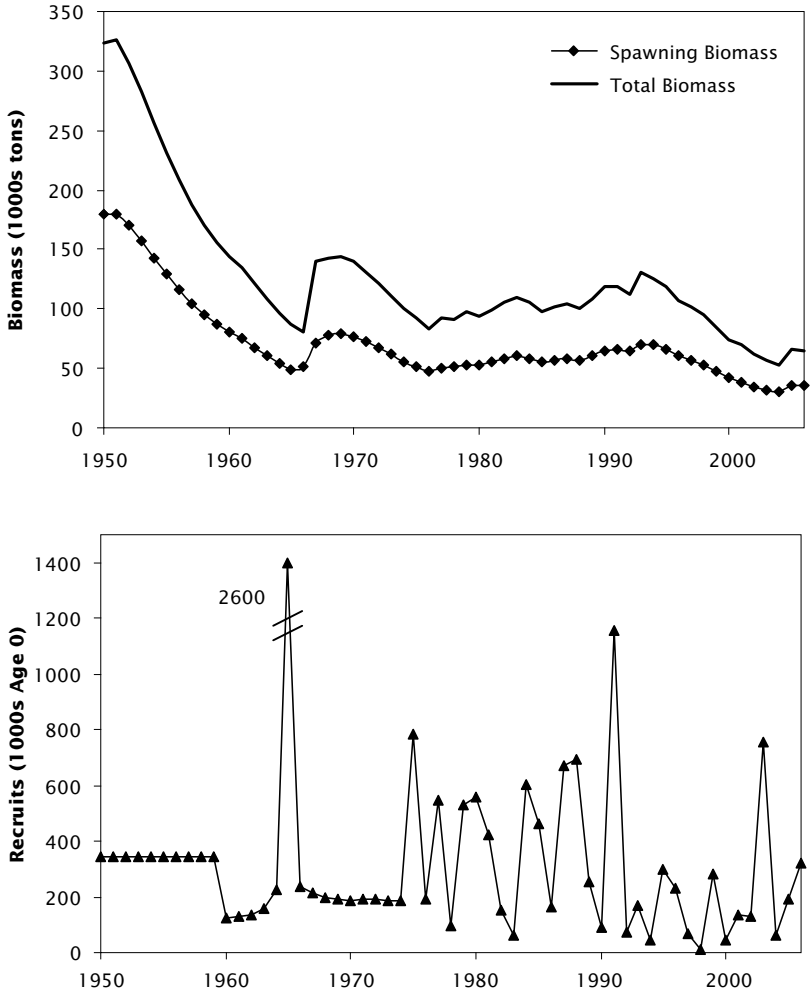


Figure 3. Results of the shortbelly rockfish base model. Total biomass and spawning stock biomass (SSB) estimates (top) and estimates of annual recruitment (bottom).

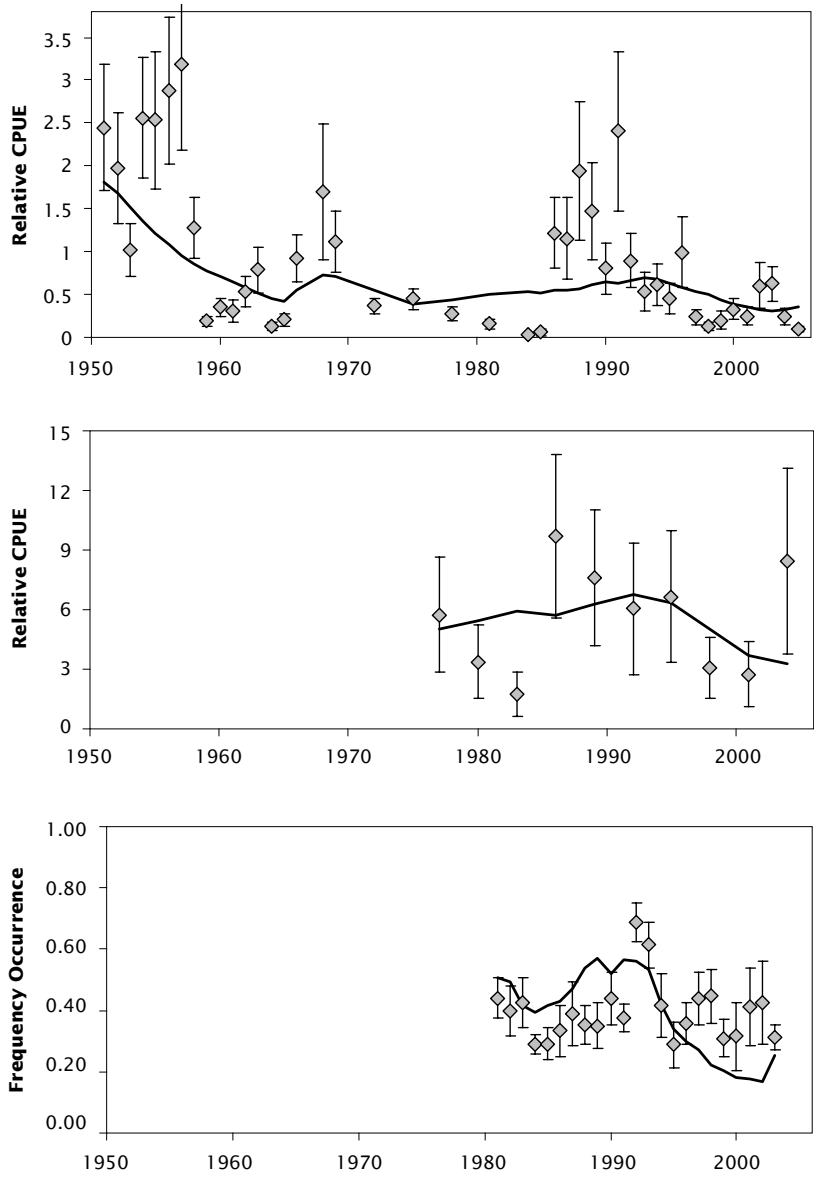


Figure 4. Model fits to relative abundance data: CalCOFI larval abundance (top), Triennial Trawl Survey (middle), and sea lion frequency of occurrence (bottom). Data are shown as points with standard error bars; model predicted fits are lines.

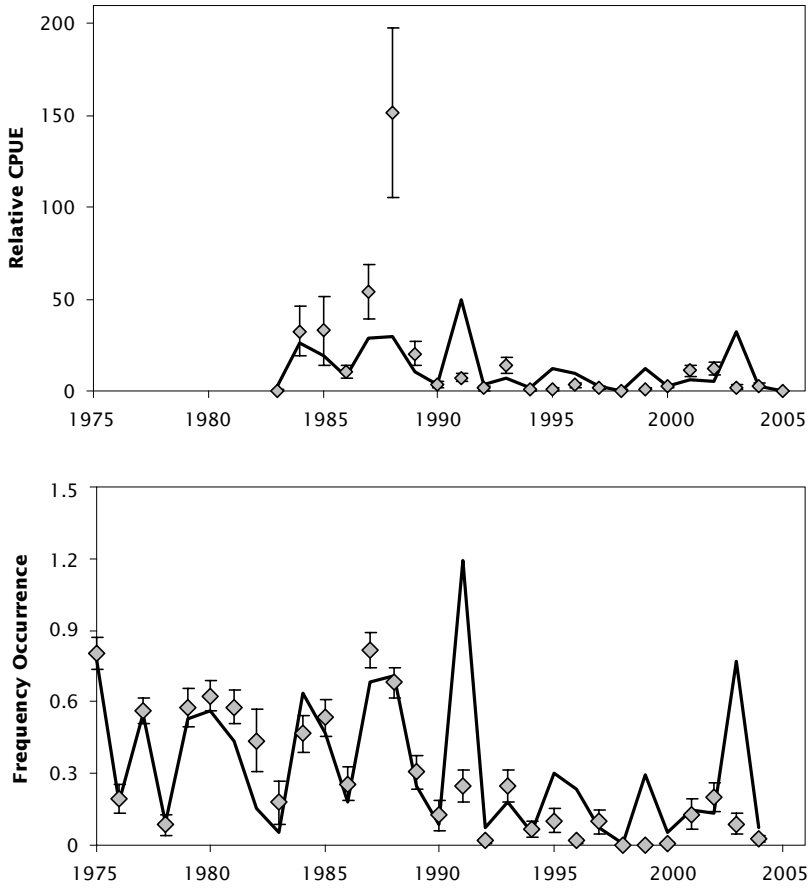


Figure 5. Model fits to Central California juvenile trawl survey (top) and arcsin transformed murre food habits data (bottom). Data are shown as points with standard error bars; model predicted fits are lines.

well as observation error), rather than actual interannual changes in abundance (MacGregor 1986, Moser et al. 2000; see also Lenarz and Wyllie Echeverria 1986). The fit to the Triennial Trawl Survey index is not remarkable, and the index itself is not very informative, which is not surprising for a patchily distributed, semi-pelagic species. Although the model does capture the declining trend from the late 1980s through 2001, the model estimates nearly identical trends in the absence of this data series. The fits to the juvenile trawl survey data and the common murre food habits data (Fig. 5) are reasonable, and are consistent with

the observation that these two time series are highly correlated. Finally, we note that although the relative abundance index generated from the sea lion food habits data seems to be somewhat uninformative, the length composition data associated with this index are very informative, and clearly reflect strong cohorts moving through the fishery (Fig. 6). Although the model fit to the smallest size classes of the length frequency data is poor, reflecting a mismatch between the actual size of pelagic juveniles (age 3 to 6 months) and the growth model predictions of size at age 6 months, fits to the larger size classes in the length composition data are reasonable.

In general, the model estimated a higher natural mortality rate (0.35) and greater recruitment deviation (sigma-*R*, 1.6) when these parameters were freely estimated. This was largely due to the improvement in model fit to the variability in the CalCOFI data; fits to other data were generally the same or eroded. Although it is possible that a higher natural mortality rate, or possibly a time or age-varying rate, could be reasonable for this species, we currently have inadequate information to justify such changes. As with any population model, the benefits and drawbacks of freely estimating parameters such as natural mortality are complex. We also considered the consequences of removing data sets sequentially on the model trend and behavior. Although different results were obtained when the CalCOFI index was excluded, due to the fact that no other indices extend further back in time than 1975, the trends from the late 1970s through 2005 were very similar even without these data. Similarly, the estimated recruitments changed significantly when the sea lion length composition data were removed, as these data tended to be more informative than either the juvenile survey or seabird data. This spoke to a key issue that arose often during the model development and evaluation, as data strongly suggest differences in recruitment north and south of Point Conception, suggesting that individual models for these two regions are likely to be appropriate. The lack of a consistent time series of age data with which to better validate the recruitment variability, and the problems inherent in using both proportional indices of abundance based on food habits data, are also noteworthy, as well as problems commonly faced in assessments of exploited species.

Discussion

Although there is considerable uncertainty surrounding the model results, and the lack of fishery-dependent data has led us to rely primarily on less traditional sources of information, the results of the model are consistent with both what is known about shortbelly life history and the available data regarding juvenile and adult abundance. Even without having a clear sense of the causes of such fluctuations,

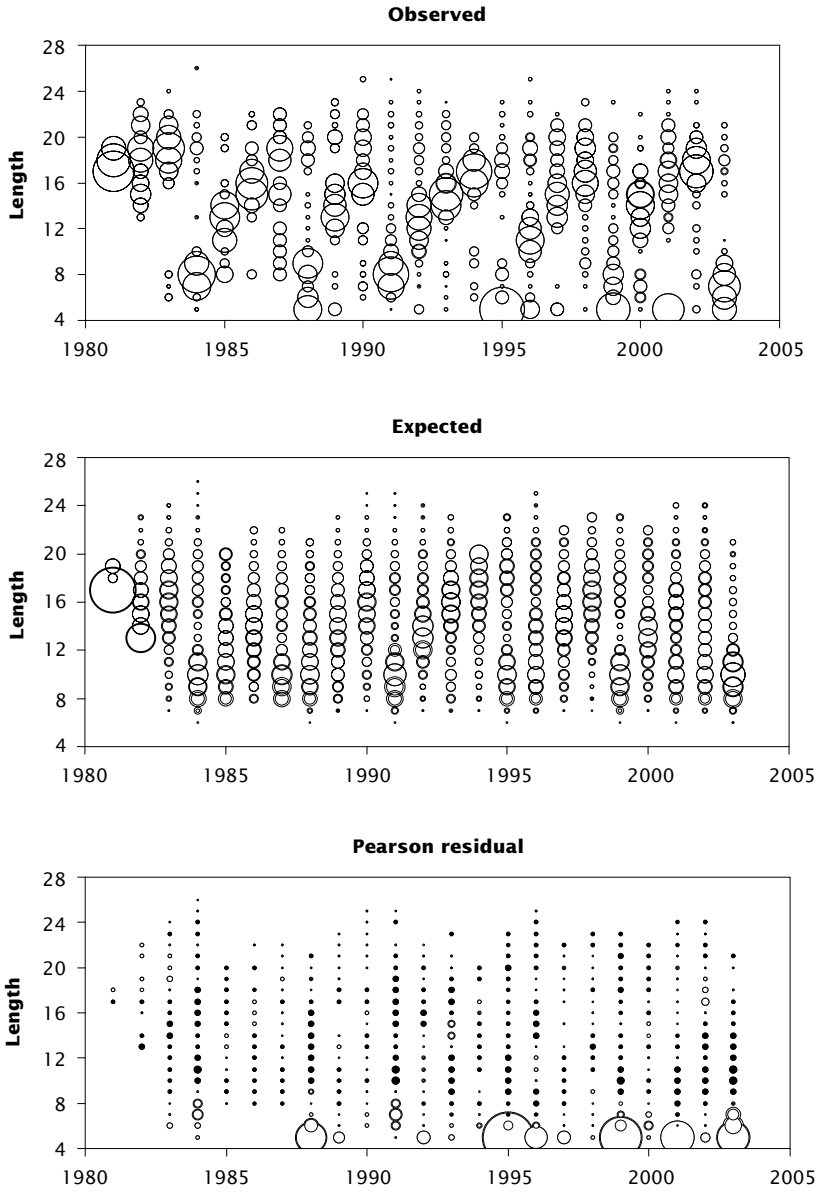


Figure 6. Plots of fits to the sea lion length frequency data, with observed data (top), predicted length composition (middle), and Pearson residuals (bottom). For the residuals, solid circles reflect negative values, open circles reflect positive values. Note that the poor fit to the smallest size classes of the length frequency data reflects the mismatch between the actual size of age zero juveniles and the growth model predictions of size at age zero.

the most important result is the insight that substantive population variability has occurred for an (effectively) unexploited species in the California Current. Although fishery-independent drivers of population variability have been described for many other California Current species (Baumgartner et al. 1992, MacCall 1996), comparable changes are less evident for groundfish, for which management tends to rely on equilibrium-based assessment methods and biological reference points. Such reference points have proven critical to implementing sustainable management measures, by portraying the consequences of exceeding biological limits to decision makers in terms of the risk to the resource (Mace 2001). Yet such reference points are unavoidably based on the assumption of stationarity, such that the biomass at the beginning of the exploitation history is assumed to represent a steady-state unfished equilibrium. However, it should be acknowledged that the life history traits of shortbelly rockfish, which is more similar to a forage fish than most longer-lived, slower growing and larger *Sebastes*, may impede the utility of considering this species as a "control" for commercially important stocks with different life history types.

As Hollowed et al. (2000) suggest, the role of all fisheries models, whether single or multispecies, is to understand and inform decision-makers of the consequences of fishing or other activities on living resources and the ecosystem in which they exist. They described three fundamental processes that structure populations: competition, predation (including fishing), and environmental variability. Any of these factors could plausibly account for the observed changes in the abundance of shortbelly rockfish in the California Current. For example, California sea lions, important predators of shortbelly rockfish, were severely depleted throughout the early part of the twentieth century as a result of hunting and culling (Cass 1985). Following increasing levels of protection from such impacts from the 1950s through 1970s, rapid population increases have been observed. Currently population growth rates regularly approach 9% per year, such that the population is thought to be well over 200,000 animals (Carretta et al. 2002). Models that account for changing natural mortality rates, by incorporating relative changes in the abundance of key predators, have been shown to be plausible for some species (Livingston and Methot 1998), and are worth exploring here. Environmental variability is also likely to be a factor. Large-scale changes in both physical and biological conditions throughout the California Current, including monotonic changes, have been well documented (McGowan et al. 1998, Francis et al. 1998, Mendelssohn et al. 2003), and climate information has the potential to inform population models under some circumstances (Maunder and Watters 2003, Schirripa and Colbert 2005). It has also been suggested that the observed long-term dynamics of many marine populations in the Northeast Pacific may not be a direct function of low frequency cli-

mate variation, but rather are responses to nonlinear amplification of physical forcing by ecological processes (Hsieh et al. 2005). Regardless of the mechanism, shortbelly rockfish have a potentially important role as a species from which further exploration can be made of the linkages between population variability and environmental factors.

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Stratification by Echosounder Signal to Improve Trawl Survey Precision for Pacific Ocean Perch

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Abstract

In 1998 echograms were recorded during individual bottom trawl hauls conducted in a study of Pacific ocean perch *(Sebastes alutus)* survey methods. Categorization criteria were developed on a subset of the echogram data based on signal patterns, shapes, and color. Blind tests were then conducted by individual scientists on a subset of hauls. Between-scientist agreement of high and low categories of rockfish abundance varied from 76% to 87%. Data were collected again in 1999 and categorized using the same criteria. Onboard scientists agreed with categorizations done by a shoreside scientist 65% of the time. The mean catch rate for hauls in the low echogram category was always lower than mean catch rate for the high category and statistically significant in all but one haul. Variance estimates that would result from simple double sampling using the echogram categorizations as strata definitions were predicted using the observed within-category variances at various levels of first stage (echosounder) sampling. Echosounder samples are considerably less expensive in time and cost than trawl sampling, and when 10 times as many echosounder samples were taken to stratify the trawl samples, variance improved 18-37% compared to simple random sampling, depending on the data set and the categorizer. If trawl hauls were allocated optimally, the improvement increased to 44-60% over simple random sampling. To match the variance obtained by double sampling with echosounder primary sampling, the number of random trawl hauls would have to be increased 1.8-2.5 fold depending on data set and categorizer.

Introduction

Trawl survey estimates of slope rockfish (*Sebastes* spp.) abundance in the North Pacific Ocean have high variability, leading to a high degree of uncertainty in their stock assessment and management measures (Ianelli and Heifetz 1995). Various studies have evaluated aspects of the survey methods (Lunsford et al. 2001) and methods to improve survey efficiency (Quinn et al. 1999, Lunsford et al. 2001, Hanselman et al. 2003). In Alaska, hydroacoustics are used extensively to survey fish such as walleye Pollock (*Theragra chalcogramma*) and Pacific hake (*Merluccius productus*), which distribute in midwater in large schools. The size and the density of the schools are estimated by integrating transects of the calibrated echosounder signal over the survey area. Stanley et al. (1998) have explored the potential of assessing rockfish in British Columbia waters using this approach. The school density, size, and shape of Atlantic redfish (Gauthier and Rose 2002) and widow rockfish (Wilkins 1986, Stanley et al. 2002) have been estimated hydroacoustically. In the Gulf of Alaska, the behavior of slope rockfish and the abundant presence of other organisms may preclude quantitative interpretation of the integrated hydroacoustic signal.

In Alaska, scientists have explored other uses of hydroacoustic technology to improve rockfish surveys. Von Szalay (1998) explored hydroacoustic techniques for bottom type identification, which would enable improved stratification of the survey area by bottom type. Rockfish are believed to prefer different bottom types. Krieger et al. (2001) showed a correlation with echosounder signals and catches of slope rockfish during trawl surveys, and Ito (1999) showed a correlation of signal strength with shortraker *(S. borealis*) and rougheye (*S. aleutianus*) rockfish catch rates at a single site in the Gulf of Alaska.

United Kingdom scientists (Everson et al. 1996) describe a method of using echosounder signals in a double sampling design to improve bottom trawl surveys of patchily distributed fish such as the mackerel icefish (*Champsocephalus gunnari*). Their design, Trawl and Acoustic Presence/Absence Survey (TAPAS), uses echosounder data to estimate the presence and size of possible high-density patches of the species. Trawl samples are then made in each high-density patch and in the low-density background. TAPAS is a variant of adaptive double sampling (Thompson 1992) but differs from the adaptive cluster sampling approach examined by Hanselman et al. (2001) by using echosounder signals, or the echogram, to determine the presence of a cluster. TAPAS, like the method we employ here, can use a simple binomial categorization of the echogram that correlates with catch rate. Unlike the approach used to assess walleye pollock and Pacific hake, our approach does not rely on a quantified interpretation or integration of the hydroacoustic signal, but a binomial (or multinomial) categorization of the signal.

Adaptive approaches such as TAPAS or the method we propose here could likely be applied to rockfish aggregations such as found off Southeastern Alaska by Leaman and Nagtegaal (1986) in their encounter response survey of rockfish.

Our study provides an evaluation of using the echogram to improve survey efficiency and precision for rockfish. Our approach is similar to TAPAS or adaptive double sampling, but is simpler because it does not rely on the concept of clusters or patches and can be thought of as two-phased sampling or double sampling for stratification (Cochran 1977). The first sample is the echosounder sample, which indicates the strata being sampled, and the second sampling is with trawl hauls allocated to each stratum.

Methods and results

Data description

In 1998 and 1999, as part of a study to evaluate adaptive sampling (Thompson and Seber 1996, Clausen et al. 1999, Quinn et al. 1999), we collected copies of the echogram screen images during many of the trawl hauls. A Simrad ES-380 (38 khz, 10º transducer cone angle) echosounder was used. Settings were chosen by the vessel captain to best indicate presence of Pacific ocean perch (POP) and did not change during the 1998 data collection. During the 1999 study, sounder settings were inadvertently not set to the 1998 values until the latter part of the data collection. While this led to less confidence in categorizations, sample size limitations did not allow us to determine if there was a significant effect on survey improvement.

During the 1998 study, the echosounder settings provided a view of the total water column and an expanded view of the water column within 5 meters of the bottom. There were approximately 12 depth cell display units within the 5 meter vertical range of the expanded bottom view, providing a vertical resolution of approximately 0.4 meter. Relative echogram signal strength for each depth cell was indicated by its color—green, yellow, or red—in respective ascending order of signal strength. Trawl catch rates were in kilograms per nautical mile (nmi) towed on bottom. Trawl hauls were for 15 minutes and typically covered 1 nmi. Details of the gear used and catch sampling methods are in Clausen et al. (1999). Evaluation of the echogram observations was conducted in the following steps:

1. Use half of the 1998 data for a learning subset to produce criteria for categorization.

2. Categorize the 1998 test subset and compare for repeatability.

3. Compare the categorizations of the 1998 test subset to the haul catch rates.
4. Categorize a subset of the 1999 data and compare to the haul catch rates.
5. Compute hypothetical potential improvements in biomass estimates using categorization results.

Categorization criteria

There were 80 data points (joint haul echogram and catch) collected in 1998. Missing data points can result from failure to save the echogram hard copy or an invalid trawl haul. The data set was divided into two subsets, placing the 42 odd numbered hauls in one subset and the 38 even numbered hauls in the other subset. The odd numbered subset was used as the learning set, and the even numbered subset was set aside for testing the categorization scheme.

Initially, for each datum in the learning subset, the amount of red, yellow, and green depth cells observed in the total water column and in the near-bottom expanded view were given subjective category value ranks. Shape or pattern categories were used to attempt to quantify the number of depth cells, not as primary indicators in themselves. Emphasis was on quantifying the number of depth cells by color. Various combinations and weighting of these signal categories for each haul were compared to the POP catch rates. Correlations or discriminatory power of this first attempt was not satisfactory.

In a subsequent categorization, the patterns of depth cell distribution in the total water column and in the near-bottom view were categorized. The amount of depth cell color was not the primary description, but was used to supplement the pattern descriptions. The descriptive categories were as follows:

Category 1: Nothing, nearly blank.

Category 2: Green haze, few if any yellow or red depth cells (Fig. 1) (green cells are shown in a light shade of gray, yellow cells are shown in a medium shade of gray, and red cells are shown in black).

Category 3: Single, or small, but strong target signals (Fig. 2). This can be seen when occurrence is in the bottom zoom view; they appear as green, yellow, or red depth cell groups that are only one depth cell high, often the cluster has a horizontal, or slightly sloping, orientation, or the classic inverted "V" shape indicating a single or concentrated echo source.

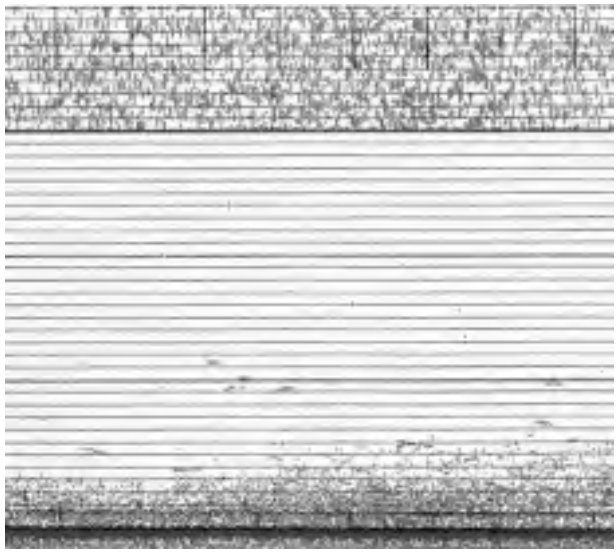


Figure 1. Descriptive category 2: green haze. Light shades of gray represent yellow, medium shades green, and dark shades red. Expanded view of bottom 5 m of echogram is shown at the top of the figure.

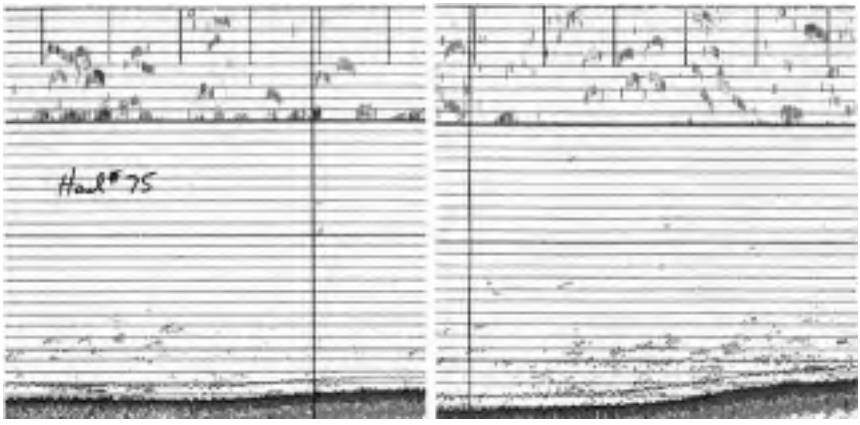


Figure 2. Descriptive category 3: single, or small, but strong target signals. Light shades of gray represent yellow, medium shades green, and dark shades red. Expanded view of bottom 5 m of echogram is shown at the top.

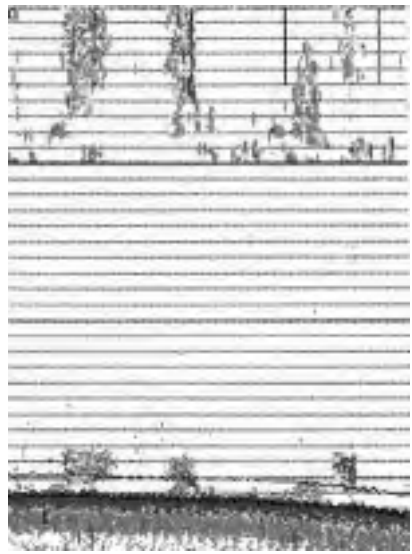


Figure 3. Descriptive category 4: multi-depth cell height clusters. Light shades of gray represent yellow, medium shades green, and dark shades red. Expanded view of bottom 5 m of echogram is shown at the top.

Category 4: Multi-cell height clusters of green, yellow, and red cells (Fig. 3). Clusters tend to have rounded or vertically extended shapes, with the tendency of red distributed toward the center surrounded by yellow, then green cells on the outside. Figure 3 shows at least four of these clusters clearly on the right side of the recording, in the zoomed area as well as extending 10-15 meters above the bottom. Figure 4 compares blowups of the single-cell-height category (3) on the top, with the multi-cell height cluster category (4) on the bottom.

Category 5: Cloud layer extended horizontally typically showing red in the center, surrounded by yellow and green to the outside (Fig. 5). Figure 5 shows a typical layer centered approximately 15-20 meters above the bottom. Distinguishing whether strong signals (red cells) were in single-cell-height clusters or in multi-cell-height clusters improved the ability to distinguish high and low catch rates. Separating catch rates above or below 400 kg per nmi provided approximately equal accuracy to the high and low echogram signal categories.

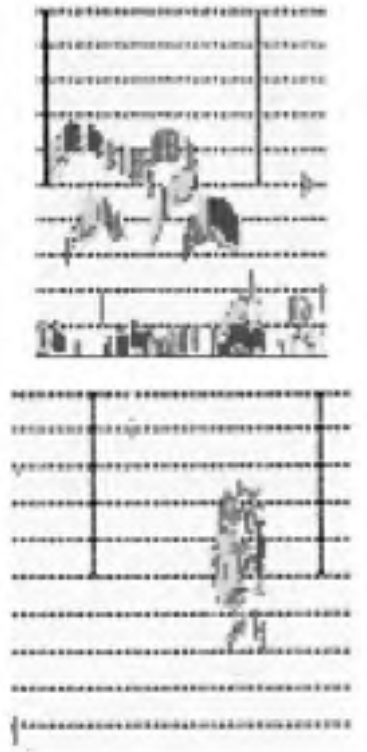


Figure 4. Comparison of single depth cell height (upper figure) and multi-cell height (lower figure). Light shades of gray represent yellow, medium shades green, and dark shades red.

Comparison of these categories to the 42 haul catches in the test subset resulted in the following:

Category 1 or Category 2: Of the seven hauls within either of these categories, five were below the 400 kg per nmi catch rate of POP.

Category 3: Of the 10 hauls with echogram signal pattern of this type, without any category 4 or category 5 patterns, eight were below the 400 kg per nmi catch rate of POP.

Category 4: This pattern category is the predominant positive indicator during daylight; 13 of 15 catches with the echogram signal classified in this category were >400 kg per nmi.

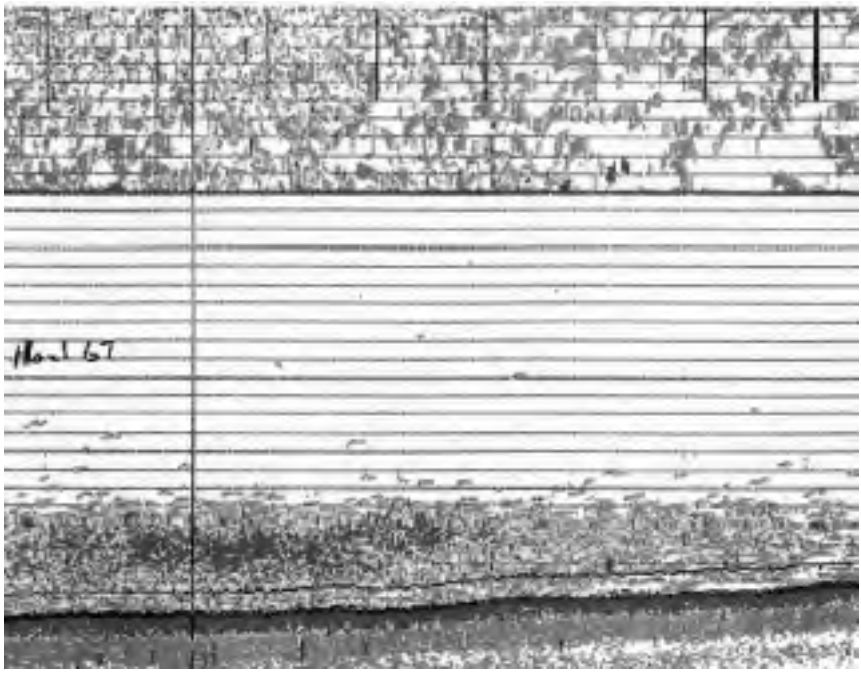


Figure 5. Descriptive category 5: cloud layer showing red in center. Light shades of gray represent yellow, medium shades green, and dark shades red. Expanded view of the bottom 5 m of echogram is shown at the top.

Category 5: This is the positive indicator of POP during night; 8 of 10 catches were >400 kg per nmi. For 6 of the 42 hauls in the learning subset, the signal had a pattern of fading at regular intervals for an unknown reason. Two of the hauls corresponded with the two low hauls considered to be in category 5. In subsequent analyses categories 1-3 are considered to indicate a low catch rate, and categories 4 and 5 a high catch rate.

Repeatability of categorizations

To evaluate the between-scientist categorization error, five scientists were given descriptions of the category criteria and asked to categorize the 1998 test subset. In addition, to test the within-person error, scientist I repeated the categorization. To eliminate possible influence from adjacent hauls, the haul sequence was scrambled and each haul was given a secondary identifier. Scientist I was the initial analyst and generated the categories.

Table 1. Comparison of classification of 1998 echograms by five individuals.

Scientist	II			III			IV			V			I′		
Category	1-3	4,5	Total	1-3	4,5	Total	1-3	4,5	Total	1-3	4,5	Total	1-3	4,5	Total
1-3	19	1	20	20	0	20	20	0	20	18	2	20	20	0	20
4,5	5	13	18	5	13	18	7	11	18	7	11	18	1	17	18
Total	24	14	38	25	13	38	27	11	38	25	13	38	21	17	38

Table 2. Comparison of echogram categorizations to haul catch rates.

	Scientist	I			II			III			IV			V		
Catch	Category	1-3	4	5	1-3	4	5	1-3	4	5	1-3	4	5	1-3	4	5
Low (obs n = 14)		11	2	1	14	0	0	13	0	1	14	0	0	13	1	0
High (obs n = 24)		9	12	3	10	12	2	12	10	2	13	10	1	12	10	2
		20	14	4	24	12	2	25	10	3	27	10	1	25	11	2

Table 1 shows the classification of scientist I compared to each of the other participants and himself (I′). The closest correspondence of scientist I was with himself (37 of 38), the next closest correspondence between scientist I was with scientist III (33 of 38), and the poorest correspondence was with scientist V (29 of 38). Scientist I classified more hauls (18, 17) as being in the high-catch category (4 or 5) than did any of the other scientists (14, 13, 11, and 13).

Categorization of 1998 data and comparison catch rate

Comparisons of the observed catch relative to the echogram categorization are shown in Table 2 for each of the five scientists. Scientist II's categories had the most correspondence with the observed catch rates, categorizing all 14 low catches as low, and 14 of the 24 high catches as high. Scientist I classified three of the low catch rates as categories 4 or 5 (high), whereas the other scientists classified at most one low catch as high. Conversely, scientist I, being more likely to classify signals as high, identified more of the high catches (15 of 24) than the other participants.

Of the high catches that were rated low, five were only marginally high ranging from 400 to 606 kg per nmi. Eight catches ≥1,000 kg per nmi were rated low by at least one person, three of which were rated low by everyone.

Table 3. Comparison of captains' and scientists' categorizations of 1999 echograms.

Captains' categories	Shipboard scientists' categorizations						Scientist I's categorizations					Total
	Blank	1	2	3	4	5	1	2	3	4	5	
No comment	2		1	2	1	2		5	1	2		8
Poor		4	13	4	2	1	1	16	3	2	2	24
Light			1		2					3		3
Maybe			3		3	1		7				7
Okay						1		1				1
Good					1	5		3		2	1	6
Total	2	4	18	6	9	10	1	32	4	9	3	49

Numbers represent the joint frequency of captains' categories and scientists' categorizations.

Categorization of 1999 data and comparison to catch rate

The 1999 data were also split into odd-numbered and even-numbered haul subsets. One subset was set aside for further testing steps. The working subset was categorized using the same criteria developed from the 1998 data. Echogram categorization of each haul was done by the scientist(s) in the wheelhouse during the haul before the catch was brought aboard. The individual scientist doing the categorization varied depending on rotation of duties and work hours. Onboard categorizations by multiple scientists were done to represent actual survey conditions. Categorization was also done back at the office by scientist I. A categorization (or comment) on each haul was also solicited from the captain (or first mate, depending on shift). The captains' responses varied from no response, no comment, various forms of maybes, various indications of likely poor catch, to definite optimism. We attempted to group the captains' responses into six groups, and compared these to the scientists' categorizations for 49 odd-numbered hauls taken in POP strata (Table 3).

The shipboard scientists and scientist I categorized 19 and 12 hauls, respectively, out of 49 hauls as having high (categories 4 or 5) echogram signals, and the captains considered six hauls as "good," one as "okay," seven as "maybe," and three as "light." The seven signals the captains designated as "okay" and "good" were also identified as high by the shipboard scientists, whereas scientist I classified only three of those seven as high, and four of them as category 2 clouds indicating low POP catch rate. The captains designated 24 signals as "poor." Of these, the shipboard scientists classified 21 as low and three as high, and scientist I classified 20 as low and four as high (Table 4). Agreement of high and

Table 4. Comparison between scientist I's and shipboard scientists' categorizations of 1999 echograms.

		Scientist I categorizations					
		1	2	3	4	5	Total
Shipboard scientists	1		2	2			4
	2		14	1	3		18
	3	1	4		1		6
	4		5		3	1	9
	5		6		2	2	10
	Blank		1	1			2
	Total	1	32	4	9	3	49

Table 5. Comparison of trawl catch to echogram categorization by captains and scientists.

			Scientists				
	Captains		Shipboard		Scientist I		
Trawl catch	High	Low	High	Low	High	Low	Total
> Median	6	18	12	12	8	16	24
≤ Median	1	24	7	18	4	21	25
Total	7	42	19	30	12	37	49

low echogram signals between shipboard scientists and scientist I in the 1999 data was 32 of 49 (65%), compared to 76% to 87% in the blind test of the 1998 data.

The classification of haul echogram signals by the captains and scientists was compared to whether the haul catch rates were greater than, less than, or equal to the median catch rate (Table 5). A "good" or "okay" comment by the captain was considered as high. In each case, of the hauls that were classified as high or low, more than half were appropriately classified as above or below the median catch rate. That is, of the seven haul signals that the captains classified as high, six were greater than the median catch rate, whereas 12 of 19 and 8 of 12 hauls classified high by the shipboard scientists and scientist I, respectively, were greater than the median catch rate. Similarly, for hauls rated as low, most were less than or equal to the median.

Although there is a relationship between categorizations and catch rates, the relationship is imperfect. The following section will evaluate whether using the echograms has the potential to improve survey precision.

Potential survey improvement from using echogram categorizations

One simple application of the echogram is as a criterion for stratifying the samples, much as depth is a stratum criterion. For example, an echogram reading of categories 1, 2, or 3 would indicate one stratum, the low stratum, and echogram categories 4 or 5 would indicate a second stratum, the high stratum. A stratified estimate for the abundance measure could then be computed and compared to a strictly random estimate. When stratifying by depth, the stratum sizes are often known (from a map), and estimating the stratum sizes does not contribute to the computed variance. In our case, one needs to estimate the size of the echogram-defined strata, and the variance of this estimate is taken into account. This application fits into the procedure of double sampling or 2-stage sampling theory first described by Neyman (1938), and explained by Cochran (1977) and Thompson (1992).

Following Cochran's (1977) notation, the first stage of sampling would be n' random echogram samples, which fall into L categories, or strata. Of the n' samples, n'_h fall into stratum h and $w_h = n'_h/n$ is the estimate of $W_h = N_h/N$, the proportion of all possible echogram samples falling into stratum h. In our example, the echogram samples are categorized into only $L = 2$ strata, high or low.

The second stage of sampling would be n stratified random samples by trawl hauls of the 2 strata (echogram categories), where the estimate of $\bar{Y}_h$, mean density for stratum h is obtained from the mean of the n_h density measurements, $\bar{y}_h$.

The stratified estimate of the population mean $\bar{Y} = \sum W_h \bar{Y}_h$ is estimated by

$$\bar{y}_{st} = \sum_{h=1}^{2} w_h \bar{y}_h$$

Following Cochran (1977, equation 12.3) the equation for the variance of the estimate is

$$V(\bar{y}_{st}) = S^2\left(\frac{1}{n'} - \frac{1}{N}\right) + \sum_{h}^{L} \frac{W_h S_h^2}{n'}\left(\frac{1}{v_h} - 1\right)$$

where S^2 is the population variance, S_h^2 is the variance in stratum h, and $v_h = n_h/n_h'$ is the sampling fraction of stratum h.

For our study, a test subset of the 38 even-numbered trawl haul/echogram recordings taken in the POP strata in 1998, and a subset of 49 odd-numbered trawl/echogram recordings in 1999, were assumed to be taken randomly, the relative high or low stratum area sizes were assumed to be in proportion to the number of hauls classified as high or low by their echogram, and the respective population means and variances for the strata are assumed to be the means and variances

Table 6. Means, variances, and sizes of data strata categorized by echograms.

		1998 data subset		1999 data subset		
		Scientist I	Scientist II	Scientist I	Shipboard scientists	Captains
Sample size	n'	38	38	49	49	49
Proportion of pop. in stratum 1	$W_1 = n'_1/n'$	0.47	0.37	0.24	0.39	0.14
CPUE in stratum 1	$Y_1 = y_1$	4,333	5,394	4,048	3,148	7,525
CPUE in stratum 2	$Y_2 = y_2$	669	661	1,134	1,024	901
Variance of total pop	S^2	1.57E+07	1.57E+07	1.18E+07	1.18E+07	1.18E+07
Variance of pop in stratum 1	S_1^2	2.56E+07	2.79E+07	3.14E+07	2.16E+07	3.71E+07
Variance of pop in stratum 2	S_2^2	9.43E+05	8.18E+05	3.95E+06	4.21E+06	1.90E+06

estimated from the samples. Table 6 shows this information for the 1998 and 1999 data subsets.

Scientist II's echogram categorization not only classified the 1998 hauls into high or low categories more accurately, but also maximized the contrast in catch rate and variance between strata (Table 6). Likewise, the captains' categorizations performed the best in the 1999 data.

Double sampling is advantageous if the initial stage (echosounder) sample is less costly than the second stage (trawl haul) sample and more initial samples are taken. The variance equation shows that if the initial sample, n_h', is of the same size as the second sample, n_h, there is no difference between the simple random estimate variance, S^2/n', and $V(\bar{y}_{st})$. However, Table 7 shows that as n' increases, the variance is lowered, while maintaining the same number of secondary samples in each stratum. For example, in the 1998 data categorized by scientist I, the variance decreases 18% from 412,337 to 339,882, as n' increases tenfold from its original level. The improvement is even better for scientist II, decreasing variance 28% to 297,074. The classification by the captains in 1999 was even better, decreasing variance 37% from 239,831 to 151,388.

As can be seen in the variance equation, further increasing of n', the echogram samples, continues to improve the variance estimate until the variance approaches the simple stratified random sampling variance (the case where stratum sizes are known, not estimated). However, further improvement can be obtained more efficiently by reallocating the second-stage sampling effort to reduce the variance of the estimate

Table 7. Variance estimates from random sampling, 2-stage sampling with increased echosounder sampling (n'), and reallocated trawl sampling (n).

		Original n' random sampling)	n' doubled	n' 10x	n' doubled	n' 10x	Random n for equal variance
Scientist I 1998 data							
1st stage sample size (echogram)	n'	38	76	380	76	380	68
2nd stage sample size (trawl)	n	38	38	38	38	38	68
Sample size in stratum 1	n_1	18	18	18	31	31	32
Sample size in stratum 2	n_2	20	20	20	7	7	36
2nd stage sampling rate, stratum 1	v_1	1.00	0.50	0.10	0.86	0.17	1.0
2nd stage sampling rate, stratum 2	v_2	1.00	0.50	0.10	0.18	0.04	1.0
Variance estimate	$V(y)$	412,377	372,102	339,882	262,672	230,452	230,439
Scientist II 1998 data							
1st stage sample size	n'	38	76	380	76	380	87
2nd stage sample size	n	38	38	38	38	38	87
Sample size in stratum 1	n_1	14	14	14	28	29	32
Sample size in stratum 2	n_2	24	24	24	10	9	55
2nd stage sampling rate, stratum 1	v_1	1.00	0.50	0.10	1.00	0.21	1.00
2nd stage sampling rate, stratum 2	v_2	1.00	0.50	0.10	.21	0.04	1.00
Variance estimate	$V(y)$	412,377	348,320	297,074	232,007	179,719	180,110
Scientist I 1999 data							
1st stage sample size	n'	49	98	490	98	490	69
2nd stage sample size	n	49	49	49	49	49	69
Sample size in stratum 1	n_1	12	12	12	23	23	17
Sample size in stratum 2	n_2	37	37	37	26	26	52
2nd stage sampling rate, stratum 1	v_1	1.00	0.50	0.10	0.96	0.19	1.00
2nd stage sampling rate, stratum 2	v_2	1.00	0.50	0.10	0.35	0.07	1.00
Variance estimate	$V(y)$	239,831	228,705	219,804	179,506	170,605	170,312

Table 7. (Continued.)

		Original n' random sampling)	n' doubled	n' 10x	n' doubled	n' 10x	Random n for equal variance
Shipboard scientists' 1999 data							
First stage sample size	n'	49	98	490	98	490	61
2nd stage sample size	n	49	49	49	49	49	61
Sample size in stratum 1	n_1	19	19	19	29	29	24
Sample size in stratum 2	n_2	30	30	30	20	20	37
2nd stage sampling rate-stratum 1	v_1	1.00	0.50	0.10	0.76	0.15	1.00
2nd stage sampling rate-stratum 2	v_2	1.00	0.50	0.10	0.33	0.07	1.00
Variance estimate	$V(y)$	239,831	231,838	225,443	199,086	192,691	192,649
Captains' 1999 data							
First stage sample size	n'	49	98	490	98	490	123
2nd stage sample size	n	49	49	49	49	49	123
Sample size in stratum 1	n_1	7	7	7	14	21	18
Sample size in stratum 2	n_2	42	42	42	35	28	105
2nd stage sampling rate-stratum 1	v_1	1.00	0.50	0.10	1.00	0.30	1.00
2nd stage sampling rate-stratum 2	v_2	1.00	0.50	0.10	0.42	0.07	1.00
Variance estimate	$V(y)$	239,831	190,696	151,388	143,213	95,844	95,536

of total population. The potential improvement is shown in Table 7 for the cases where the first stage sampling effort is increased either two- or tenfold, by reallocating the original second-stage trawl effort to the most variable stratum. The variance is greatest in the high strata, so increasing the sampling in the high strata, and reducing the sampling in the low strata by an equal amount, reduces overall variance. For example, placing 31 of the 38 hauls in the strata defined as high by scientist I, and only 7 in the low strata, the variance was reduced to 262,672 when the initial sample was doubled, or down 44% from the original value, to 230,452 when the initial sample was increased tenfold. Likewise, for scientist II's categorization where the initial sample is doubled, variance can be reduced to 232,007 by sampling all 28 of the echogram samples in the high stratum, n'_1, and using the rest of the effort in the low stratum. If the initial sample size had been increased sufficiently, the 38 trawl hauls could have been allocated optimally, so that there were 29

in the high stratum, resulting in a decrease of 56% from the random sample variance, to 179,719 when n' is increased tenfold. The captains' classification of the 1999 data subset would have reduced variance 60% from the original value to 95,844 by increasing n' echogram samples tenfold and reallocating 49 trawl haul samples optimally.

As expected, the performance improvement obtained from double sampling increases with the ability to distinguish high and low strata in the echogram sample. To illustrate how double sampling compares with simple random trawl sampling, the last column of Table 7 shows how many random trawl hauls would be necessary to obtain the variance obtained by increasing echogram samples tenfold and allocating the original number of trawl samples optimally. For scientist I's categorization of the 1998 data, it would take a (68/38 =) 1.8-fold increase in trawl hauls, whereas for the more accurate echogram categorizations by scientist II, it would take 87 trawl hauls, a 2.3-fold increase, to equal the performance of double sampling. If one could categorize echogram signals as well as the captains did on the 1999 data, it would take a 2.5-fold increase in random trawl hauls to match the variance of double sampling.

Discussion

Applications

The echosounder sampling could be used in either an adaptive sampling approach similar to the TAPAS (Everson et al. 1996) approach or the simpler approach we used here. In the TAPAS application, certain categories of echogram sign would correspond to threshold levels of CPUE and cluster sizes could be determined efficiently before sampling the cluster with trawl hauls. Everson et al. (1996) and Thompson and Seber (1996) provide extensive explanation of the theory and application of these approaches. The approach we demonstrated in this paper does not require the concept of a cluster, but is stratified sampling with the strata sizes estimated by the echosounder sampling.

This approach could be accomplished by randomly surveying a relatively large number of sites with an echosounder and categorizing each site. If echosounder sampling can be completed before trawl sampling, (i.e., with two independent passes), then the available trawl sampling effort can be allocated according to the relative strata population sizes and expected relative fish density and variance. The effectiveness of this will diminish if the rate and magnitude of fish movement between the echosounder sampling and the trawl sampling is substantial. It is likely that cost factors will not allow separate echosounder and trawl sampling stages and the survey must be done in a single pass through the survey area, requiring a predetermined sampling rate be established for each stratum category. Expected relative density and variance, and

guesses of relative stratum sizes, can be used to estimate the sampling rate. For example, from the best guesses of stratum densities, variance, and sizes, the result may be that 10% of high echogram category sites, and 1% of low category sites, should be sampled with a trawl. Thus every 10th (either systematically, or randomly chosen) high category site would be trawl sampled, and every 100th low category would be trawl sampled.

Obviously, the initial guess at the sampling rate may result in too few hauls to fully utilize the available trawl effort or too many trawl hauls to finish the survey coverage. Predicting the number of clusters in the TAPAS approach leads to the same problem. Everson et al. (1996) suggest having the last planned background (low-density strata) stations widely placed over the survey area and skipping them randomly. This can't be done in a single pass, however, which is a consideration for the Gulf of Alaska bottom trawl surveys. Any adjustments made during the survey would have to be taken into account. Information from past surveys can provide an estimate of the proportion of high and low density hauls. Plots of survey trawl catch rates in Martin (1997) and Martin and Clausen (1995) show extensive areas of low catch rates of POP and areas where high catch rates occur. POP are not thought to be highly migratory and the locations of these areas have been relatively consistent over the last few years of the survey and should provide useful information to estimate the proportion of samples that will be high or low. Estimating the number of random samples that will be high or low should be simpler than predicting the number and size of clusters, which is necessary in planning for TAPAS or adaptive sampling.

Our results indicate that CVs of 27% and 31% obtained in a random trawl survey could be improved to 17% and 22%, respectively, with a relatively rudimentary echogram evaluation with modest ability to differentiate between high and low catches. Everson et al. (1996) demonstrated the efficiency of the TAPAS approach compared to a random survey using a simulation study. Whether Everson et al. (1996) took into account any error in the interpretation of the echogram as to the presence or absence of the target species is not clear.

Potential improvements in predictive power of categorizations

While this method should not require a great deal of echosounder expertise to apply, better understanding or expertise in hydroacoustics would enable the choosing of equipment and setting to best display the distinguishing characteristics of the target species. The authors used the available echosounder equipment and relied on the boat captain's judgment for settings. If such a method were to be applied in an actual

survey, expertise should be sought in choosing the optimal equipment and settings for the target species and expected depth.

In our study, the categorization of echograms were subject to interpretation, and the correlation between categories and trawl catch was not without error. There were cases where high catches occurred in hauls categorized as low, and low catches occurred in hauls categorized as high. Whether these occur from errors in interpretation of the echograms or by small-scale patchiness in fish distribution is not known. Reducing this error would undoubtedly increase the advantage of using the applications we described.

Applying such a method for one species in a multispecies survey could degrade the results for another species, and agency priorities would need to be considered. In the Gulf of Alaska, rockfish, particularly POP, survey precision is the lowest of the important species occupying the slope strata. Applying such an approach within the survey resources allocated to the slope habitat would have little effect on survey results for most of the other important species that tend to reside in shelf habitat.

In conclusion, the echogram categorizations could be improved with better hydroacoustic techniques and equipment. Standardized settings for the entire study would have improved categorization consistency and possibly precision. Calibrated scientific hydroacoustic systems can give not only an integration of signal strength, but also the frequency distribution of signal strengths. These systems should be able to provide objective criteria for categorization and perhaps further criteria for distinguishing fish sign. Accumulation of previous years' data, the echogram categories, depth and habitat categories, and the observed catch rates and their geographic distribution would allow an estimate of the probability of a site's category before sampling, which can then be updated by the new observation. In a study of rockfish in British Columbia, Richards et al. (1991) distinguished between the off-bottom distance and dispersion of rockfish schools in two categories of ocean bottom habitat.

In the future, such an approach could be evaluated using simulated scenarios of "true" stratifications with a range of stratum categorization error and sampling strategies. The effect of various within-strata distributions or relationships of hydroacoustic sign and abundance could be explored. The simulated results will show the distribution of the possible abundance estimates and possible relationships between the magnitude and precision of the abundance estimates. Such an investigation is beyond the scope of this paper.

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Localized Depletion of Three Alaska Rockfish Species

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Abstract

The distributions of some rockfish species in Alaska are clustered. Their distribution and relatively sedentary movement patterns could make localized depletion of rockfish an ecological or conservation concern. Alaska rockfish have varying and little-known genetic stock structures. Rockfish fishing seasons are short and intense and usually confined to small areas. If allowable catches are set for large management areas, the genetic, age, and size structures of the population could change if the majority of catch is harvested from small concentrated areas. In this study, we analyzed data collected by the North Pacific Observer Program from 1991 to 2004 to assess localized depletion of Pacific ocean perch (*Sebastes alutus*), northern rockfish (*S. polyspinis*), and dusky rockfish (*S. variabilis*). The data were divided into blocks with areas of approximately 10,000 km^2 and 5,000 km^2 of consistent, intense fishing. We used two different block sizes to consider the size for which localized depletion could be detected. For each year, the Leslie depletion estimator was used to determine whether catch-per-unit-effort (CPUE) values in each

block declined as a function of cumulative catch. We examined trends in CPUE over time using NMFS survey data for depleted areas. The results showed significant depletions among all species in several areas and years. Pacific ocean perch exhibited localized depletion most often, but not continuing into the next year, possibly indicating more migration than expected. Northern and dusky rockfish showed depletions less often, and occasional significant increases also occurred. Northern rockfish showed significant longer-term fishery depletion in one area. Results could be affected by hyperstability, migration, or target switching. The importance of the results depends on genetic stock structure, and importance of an area for reproductive success.

Introduction

Many deepwater rockfish (*Sebastes* spp.) in Alaska waters have a patchy or contagious distribution and are thought to move little from year to year (Love et al. 2002). This patchy distribution could be caused by several factors including a specific preference for a narrow depth range on the continental slope (Hanselman et al. 2001), the patchiness of habitats they are associated with (Krieger and Wing 2002), and oceanographic conditions that affect prey availability (Scott 1995). Species with this type of distribution may be subject to localized depletion, which is a reduction of population size over a relatively small spatial area as a result of intensive fishing.

For rockfish, localized depletion is a potential conservation issue because several species have been observed to be patchily distributed and their stock structure could occur at relatively small spatial scales. For example, Withler et al. (2001) observed two genetically distinct stocks of Pacific ocean perch (*S. alutus*) in a small area of the Queen Charlotte Islands off of British Columbia. Other genetic studies for species such as rougheye (*S. aleutianus*) and shortraker rockfish (*S. borealis*), which are relatively sedentary and associated with rugged benthic habitats indicate broadscale genetic structure similar to management areas in the Gulf of Alaska (Matala et al. 2004). However, apart from genetic information for some species, little is known about the spatial structure of Alaska rockfish populations. Local depletions could affect local spawning populations to a greater degree than the overall population.

Detectable localized depletion is dependent upon fishing intensity of sufficient strength to reduce the population size. Species that may be susceptible to localized depletions include both targeted rockfish such as Pacific ocean perch, northern rockfish (*S. polyspinis*), and dusky rockfish (*S. variabilis*) and incidentally caught rockfish such as rougheye rockfish, and shortraker rockfish. In Alaska, fisheries target only Pacific ocean perch, northern rockfish, and dusky rockfish. High catches have occurred in localized areas for some other rockfish species,

such as rougheye rockfish in the Seguam area in the Aleutian Islands. However, both the lack of a target fishery, and the relatively few hauls where rougheye dominate the catch, impede a quantitative approach to estimation of depletion. For these reasons, Pacific ocean perch in the Aleutian Islands and Pacific ocean perch, northern rockfish, and dusky rockfish in the Gulf of Alaska are the only species that have sufficient data available for an analysis of short-term localized depletion.

Typically, localized depletion is analyzed using the catch-per-unit-effort (CPUE) from directed fishing as an index of abundance. In the absence of directed fishing, changes in CPUE may not directly reflect changes in abundance (Hilborn and Walters 1992). For example, the catch of northern rockfish in the Aleutian Islands is obtained predominately in the Atka mackerel fishery, and declines in CPUE of northern rockfish could either reflect declines of northern rockfish biomass or the increased use of areas where northern rockfish incidental catch is minimized. Surveys could potentially detect localized depletion of bycatch species, but the sampling intensity of trawl surveys in Alaska is likely insufficient to detect population declines within short time periods. However, we can use trawl survey CPUEs to examine longer-term changes in CPUE for both target and non-target species.

The Leslie model was first utilized in estimating populations of rats (Leslie and Davis 1939) and was first applied to fisheries problems by DeLury (DeLury 1947, 1951). Recently, the technique was used to assess local depletion on relatively sedentary species in well-defined, heavily fished areas (Iribarne et al. 1991; Lowe and Fritz 1997; Ito 1999; Battaile 2004; P. Spencer and R. Reuter, pers. comm., 2004, Alaska Fisheries Science Center, Seattle; Fritz and Brown 2005). The purpose of this study is to assess the extent to which localized depletion has occurred for Pacific ocean perch, northern rockfish, and dusky rockfish in Alaska waters. We consider the geographic scale at which localized depletion is detectable and important. We also differentiate two types of localized depletion. Serial depletion, or depletion that persists year after year, is a conservation concern because it may reduce spawning biomass to levels that are unsustainable for a distinct stock. Conversely, ecological depletion, or depletion that only occurs during a short fishing season, is an ecological concern because it may disturb predator-prey dynamics or alter schooling behavior. In addition, we examine longer-term trends in local densities by utilizing trawl survey CPUEs.

Methods

Data selection

To identify potential areas of study, we selected trawl hauls from the rockfish fishery sampled for species composition by the North Pacific Groundfish Observer Program. Data from this program were not con-

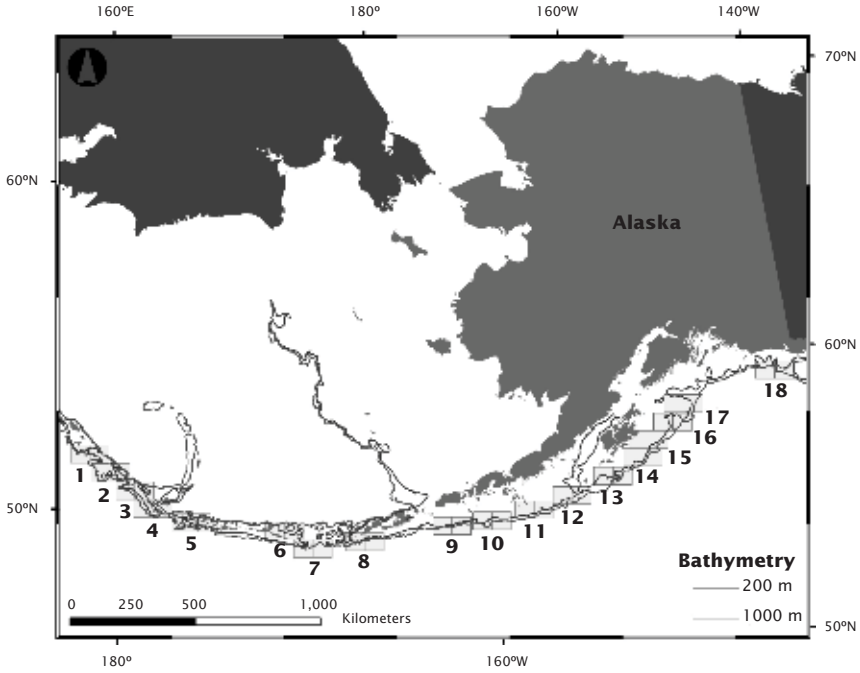


Figure 1. Map of selected blocks for Leslie depletion analysis for Alaska rockfish. The whole rectangles are the ~10,000 km² blocks while the horizontal line splits them into ~5,000 km² blocks. Smaller blocks are designated as #.1 and #.2 for the western and eastern sides respectively (e.g., area 5.1 is the western half of area 5).

sistent in sampling methodologies until 1991. We displayed retrieval positions of these data in a geographic information system (GIS) to locate areas of intense fishing from 1991 to 2004. The resulting maps indicated that 18 areas of approximately 10,000 km² (150 km × 67 km) in the Gulf of Alaska and Aleutian Islands areas had consistent rockfish targeting over a number of years (Fig. 1). Data from Southeast Alaska were not used because there was little rockfish trawl effort and it has been closed to trawling since 1998. To further analyze the concept of "local" depletion, these 18 rectangles were divided in half to create 36 squares of approximately 5,000 km² (67 × 75 km). Initially, 10,895 hauls over 14 years were available for analysis. Results from the 10,000 and 5,000 km² areas were compared to determine if there was a difference in detectability of depletion depending on the size of an area that was examined.

From a larger pool of hauls with potential for inclusion in the analysis, the number of hauls was reduced through a series of restrictions to select for hauls that targeted rockfish. The commercial rockfish fishery typically occurs in the summer months; therefore, only hauls between June 1 and September 30 were used. An individual haul was considered to be targeting rockfish if the sum of the three target species' catch was greater than 35% of the total catch (Fritz 1996). Fritz and Brown (2005) used different target percentages for Pacific cod between 20% to 60% and found that regressions generally fit better with lower percentages. Different percentages were attempted for rockfish, ranging from 20% to 60%, and 35% seemed to best identify coherent targeted fishing. The remaining 65% of the catch in the hauls near the 35% level consisted mainly of non-target rockfish such as sharpchin (*S. zacentrus*) and redstripe (*S. proriger*) rockfish or arrowtooth flounder (*Atheresthes stomias*) and skates (*Bathyraja* spp. and *Raja* spp.). Few hauls had relatively high catches of pollock (*Theragra chalcogramma*) which would likely be unintentional, while others had sablefish (*Anoplopoma fimbria*) which could represent "topping off" of valuable bycatch species. Of all included hauls, 84% contained at least 60% of the three target rockfish species.

We implemented additional restrictions on the data that accounted for specifics of the Leslie estimation procedures. In two depletion experiments, Ito (1999) and Battaile (2004) found that shortraker/rougheye rockfish and pollock were replenished after seven days. Data were considered acceptable for Leslie estimation when there were at least 10 hauls that were not separated by more than three days. Additionally, some amount of catch goes unobserved because catcher boats under 125 feet in length do not require 100% coverage. Therefore, to account for unobserved catch, cumulative catches (not CPUE) were expanded to expected catch by the percentage unobserved by year and area, to give reasonable estimates of initial biomass (Fritz and Brown 2005).

This restriction process considerably narrowed available hauls for each species (Table 1) and resulted in a total of 249 data sets to use for Leslie estimation for both block sizes. Data from the biennial groundfish surveys conducted by the National Marine Fisheries Service were selected for these same areas from 1983 to 2004 to examine areas where depletion was detected.

Statistical methods for depletion estimation

The Leslie method assesses population depletion by a fishery via a linear decline in the CPUE as a function of cumulative fish catch since the start of the fishery:

$$\frac{C_t}{f_t} = qB_0 - qK_t$$

Here, C_t and f_t are an observation of catch and effort, respectively, for a daily time period t, B_0 is the initial biomass prior to the start of the

Table 1. Number of hauls containing one of the three targeted rockfish species before filtering by year and number of hauls with each species after filtering.

	Before filtering	After filtering		
Year	Total	POP	Northern	Dusky
1991	705	33	233	180
1992	420	94	41	40
1993	837	67	71	83
1994	984	33	133	133
1995	656	12	103	94
1996	1021	80	71	84
1997	394	60	25	32
1998	676	101	57	21
1999	736	117	102	88
2000	632	124	26	31
2001	793	100	38	30
2002	955	176	11	11
2003	1,061	152	55	23
2004	1,025	165	89	41
Total	10,895	1,314	1,055	891

POP = Pacific ocean perch.

fishery, q is the catchability coefficient defining the proportion of B_0 that is taken with one minute of trawling, and K_t is the cumulative total catch taken prior to period t plus one half of the catch during period t (Braaten 1969). Catchability estimates were the negative of the slope of regressions and estimates of initial biomass were the regression intercepts divided by the catchability.

Assumptions of the Leslie model include (1) the population is closed to immigration and emigration, and the period of study is short enough where natural mortality was negligible; (2) the catchability of the fishing gear remains constant; (3) changes in CPUE are directly related to abundance; (4) catch is measured with little error; and (5) the quality of fishing effort does not change over the time of fishing (Miller and Mohn 1993). These assumptions are more likely met if directed fishing occurs within a well-defined area within a relatively short time. Violations of these assumptions for rockfish might include fishing gear disaggregating schools of rockfish or vessels "targeting" rockfish, but "topping off" on valuable bycatch species such as sablefish.

Table 2. Summary results of Leslie regressions for three species of rockfishes in Alaska.

	DR-5K	DR-10K	NR-5K	NR-10K	POP-5K	POP-10K
Total regressions	28	30	39	39	52	61
Negative count	16	17	17	19	38	42
% Negative	57%	57%	44%	49%	73%	69%
Positive count	12	13	22	20	14	19
% Positive	43%	43%	56%	51%	27%	31%
Significantly negative	2	3	5	5	12	16
% Sig. negative	7%	10%	13%	13%	23%	26%
Significantly positive	2	3	0	2	0	1
% Sig. positive	7%	10%	0%	5%	0%	2%

DR = dusky rockfish, NR = northern rockfish, POP = Pacific ocean perch, 5K = 5,000 km^2 blocks, 10K = 10,000 km^2 blocks

Results

Of the 249 area, year, and size combinations analyzed, 43 produced significant depletions (negative slopes), which was many more than the approximately six negative results that would be expected by chance at the $\alpha = 0.05$ significance level. Only eight regressions had significantly positive slopes, which was approximately what was expected at the $\alpha = 0.05$ significance level (Table 2). Comparisons of estimated initial biomasses with catches in some areas with significant results showed high exploitation rates, with some catches exceeding the estimated initial biomass (Table 3). It should be recognized that the estimates of initial biomass are not very precise. One example was in area 7 for Pacific ocean perch in 1999; the point estimate was 1,053 t, but when a 95% confidence interval was calculated using methods from DeLury (1951), the range was from 791 t to 2,402 t. Confidence intervals were always asymmetrical, indicating that many of the exploitation rates over 100% may have been due to the imprecise and skewed distribution of initial biomass. Important results for each species are described below.

Pacific ocean perch

Pacific ocean perch is the dominant commercial rockfish species and had the most data available for analysis. A total of 113 regressions were performed across 14 of the 18 selected areas. In both block sizes, regression slopes were mainly negative (Table 2) and on average 24% of these negative slopes were significant for both block sizes ($p < 0.05$). Only one regression had a significant positive slope. Depletions were detectable at both scales of block sizes and significant results occurred in similar areas and years between block sizes (Table 3). Areas with the

Table 3. Significant results from Leslie depletion analysis of Pacific ocean perch for two block sizes.

Block	Year	Intercept	Slope (–q)	p-value	B_0 (t)	Catch	% Caught
5,000 km² blocks							
1.2	2003	720	–0.00028	0.011	2,589	2,289	88%
4.1	1993	331	–0.00016	0.006	2,089	1,022	49%
4.2	1991	202	–0.00031	0.009	651	447	69%
6.1	1994	276	–0.00028	0.011	984	625	64%
6.1	2002	397	–0.00039	0.016	1,032	737	71%
6.1	2004	538	–0.00032	0.011	1,675	1,236	74%
6.2	2003	597	–0.00082	0.002	730	747	102%
7.1	1993	400	–0.00047	0.003	846	756	89%
7.1	1994	303	–0.00019	0.010	1,580	1,061	67%
12.2	1997	361	–0.00027	0.039	1,361	1,073	79%
18.2	1992	191	–0.00024	0.013	809	676	83%
18.2	1996	311	–0.00100	0.002	311	301	97%
10,000 km² blocks							
1	1999	309	0.000109	0.013	–2,829	4,306	–152%
1	2003	705	–0.00025	0.011	2,779	2,414	87%
2	1998	411	–0.00017	0.043	2,447	1,436	59%
4	1993	336	–0.00017	0.004	1,957	996	51%
5	2001	307	–0.00045	0.040	680	438	64%
6	1994	276	–0.00028	0.011	984	625	64%
6	2002	300	–0.00014	0.041	2,149	1,194	56%
6	2003	437	–0.00019	0.001	2,249	2,042	91%
6	2004	514	–0.00023	0.004	2,234	1,632	73%
7	1993	382	–0.00043	0.000	887	835	94%
7	1994	303	–0.00019	0.010	1,580	1,061	67%
7	1999	1537	–0.00146	0.018	1,053	1,231	117%
7	2003	491	–0.00020	0.030	2,486	1,671	67%
12	1997	356	–0.00026	0.033	1,374	1,120	82%
16	2002	397	–0.00022	0.021	1,815	1,348	74%
18	1992	197	–0.00026	0.001	749	683	91%
18	1996	294	–0.00086	0.003	342	320	94%

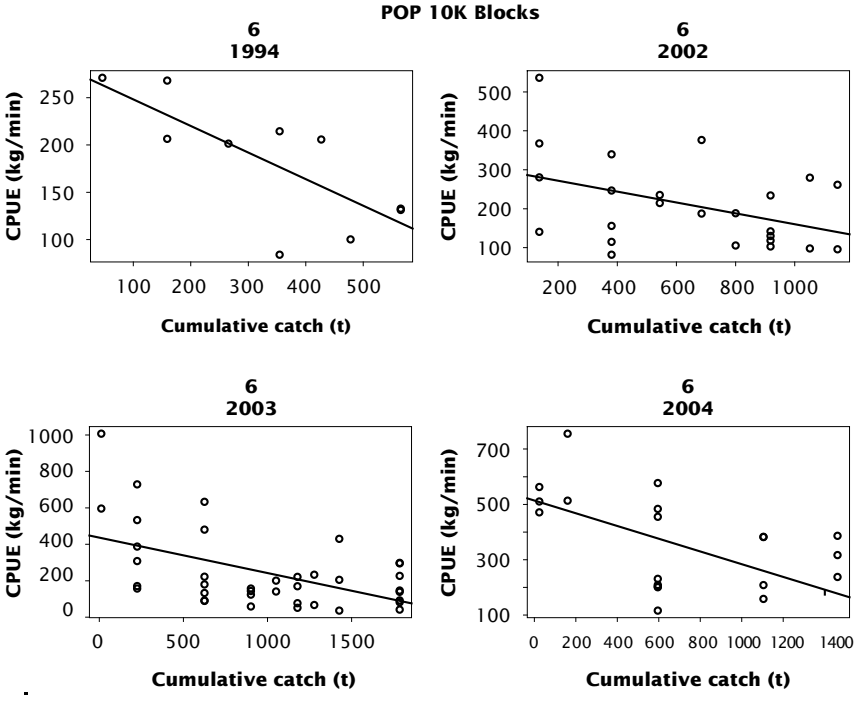


Figure 2. Four significant depletion regressions using fishery CPUE versus cumulative catch in area 6 for Pacific ocean perch.

most consistent depletion were in the eastern Aleutian Islands between Seguam Island and Yunaska Island (areas 6 and 7). Regressions in area 6 showed depletions in the last three consecutive fishing seasons (2002-2004, Fig. 2). The estimates of initial biomass suggested that much of the Pacific ocean perch biomass in area 6 was being depleted over the fishing season, but was likely replenished by the next year. Area 7 also had four significant depletions, but not in consecutive years. Several depletion events in the 1990s were found in area 18, around Yakutat; however, this area is no longer fished for rockfish, mainly due to the eastern Gulf of Alaska bottom trawling closure.

Northern rockfish

Northern rockfish are the next most abundant rockfish in Alaska waters following Pacific ocean perch. A total of 78 regressions were performed across 12 of the 18 selected areas (Table 2). Under both block sizes, 13% of the regressions had significant ($p < 0.05$) negative slopes. Only two

Table 4. Significant results from Leslie depletion analysis of northern rockfish for two block sizes.

Block	Year	Intercept	Slope (–q)	p-value	B_0 (t)	Catch	% Caught
5,000 km² blocks							
4.2	1991	7	–0.00047	0.021	15	14	94%
11.1	1994	232	–0.00038	0.000	609	432	71%
13.2	1994	267	–7.1E–05	0.001	3,731	2,236	60%
14.1	1996	213	–0.00204	0.012	104	103	98%
17.2	1999-2	211	–0.00073	0.001	288	278	96%
10,000 km² blocks							
2	1998	41	–0.00101	0.002	41	41	101%
11	1994	232	–0.00038	0.000	609	432	71%
13	1994	270	–5.5E–05	0.002	4,944	2,720	55%
14	1996	168	–0.00107	0.023	156	159	102%
16	2004	17	0.000549	0.041	–31	102	–328%
17	2001	59	0.000515	0.048	–114	303	–266%
17	1999-2	211	–0.00073	0.001	288	278	96%

1999 was split into two "seasons" because of a large break in consecutive fishing.

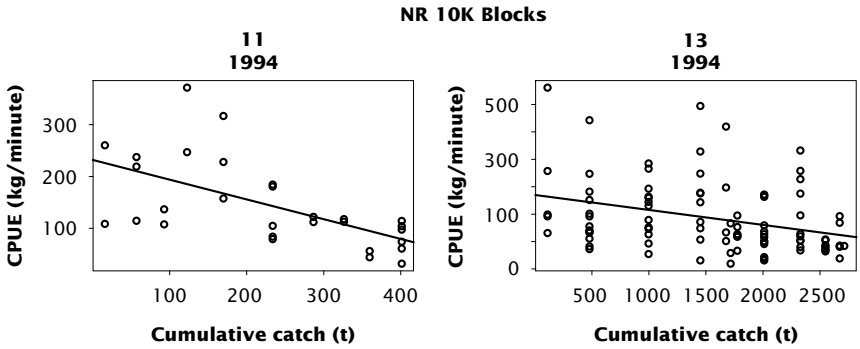


Figure 3. Two significant depletion regressions using fishery CPUE versus cumulative catch in areas 11 and 13 for northern rockfish.

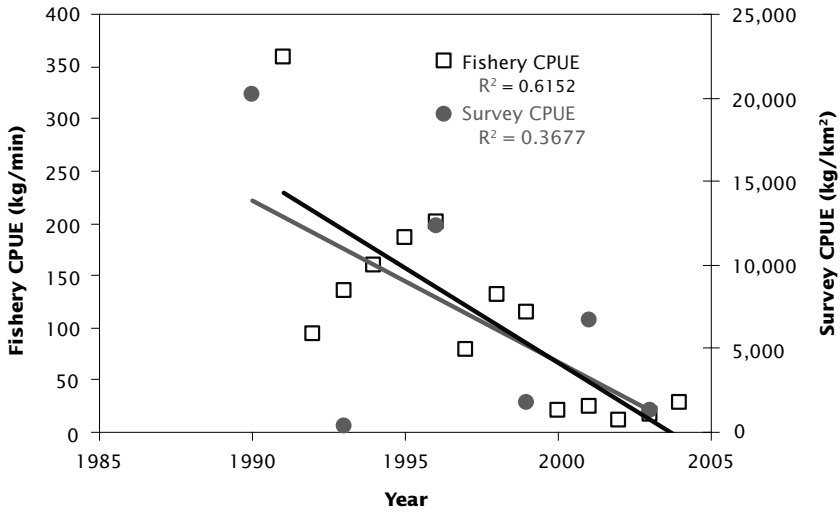


Figure 4. Fishery and survey CPUE for northern rockfish in area 13, the Albatross Bank area in the Gulf of Alaska. Solid lines are linear regressions for each data set.

regressions had significant positive slopes. Significant results were dispersed without a discernable pattern between years, areas, and block sizes (Table 4). No area had more than one significant depletion event. Areas 11 and 13 had significant depletion in 1994 over both block sizes, which may suggest the only legitimate depletions for northern rockfish (Fig. 3). Area 13 contains the "Snakehead" area, a known high intensity fishing area off of Kodiak Island, where much of the recent northern rockfish catch has been harvested. When annual CPUEs from the fishery and survey were examined for northern rockfish in area 13, there was a strong and significant downward trend for fishery CPUE ($p < 0.001$, $n = 14$) and a similar but weaker downward trend for the survey CPUE, indicating potential serial depletion (Fig. 4). Aside from area 13, estimates of initial biomass suggested that other significant results were located in areas with small populations.

Dusky rockfish

Dusky rockfish are the third most abundant rockfish in Alaska waters. A total of 58 regressions were performed across 7 of the 18 selected areas (Table 2). Approximately 10% of the regressions had significant ($p < 0.05$) negative slopes with an equal number of significant positive slopes. Significant results were only in areas 13, 17, and 18 with negative

Table 5. Significant results from Leslie depletion analysis of dusky rockfish for two block sizes.

Block	Year	Intercept	Slope (–q)	p-value	B_0 (t)	Catch	% Caught
5,000 km² blocks							
13.2	1994	33	–4.7E–05	0.019	698	418	60%
13.2	1996	85	–0.00236	0.057	36	35	98%
17.2	1996	15	9.86E–05	0.000	–153	412	–268%
10,000 km² blocks							
13	1994	34	–3.5E–05	0.041	956	502	52%
13	1996	85	–0.00238	0.034	36	36	101%
17	1996	15	0.0001	0.000	–145	412	–284%
17	1999-1	66	0.000283	0.021	–234	896	–383%
17	1999-2	206	–0.00028	0.010	736	598	81%
18	1992	7	0.000744	0.001	–9	124	–1392%

1999 was split into two "seasons" because of a large break in consecutive fishing.

results only in 13 and 17 (Table 5). Again, area 13 seemed to be the only location with results suggesting likely depletion (Fig. 5). Like northern rockfish, dusky rockfish exhibited a long-term decreasing trend in both survey and fishery CPUE in area 13 (Fig. 6). In area 17, there was a significant positive result early in the 1999 season that contrasts with a significant negative result later in that year (Fig. 5).

Discussion

Fishery depletions

When intensive fishing occurs such that the CPUE is markedly reduced over the length of the fishing season, the Leslie depletion estimator reasonably estimates catchability, initial population size, and exploitation rate. For this study, we were more interested in the ability to detect localized depletion in a targeted fish population, and at what scales depletion could be detected.

Overall, Pacific ocean perch exhibited the most significant depletions in consistent areas. Some depletions occurred over consecutive years, such as in area 6 in 2002-2004. However, these depletions did not appear to proceed where they left off in the previous year. The areas seemed to be replenished by new fish or the fishery shifted to an aggregation nearby in the same area because the CPUEs at the start of the fishery each year were similar (Fig. 2) and the estimate of initial biomass was also similar. This replenishment may indicate a higher degree of migratory behavior then previously thought. Area 7 was locally depleted

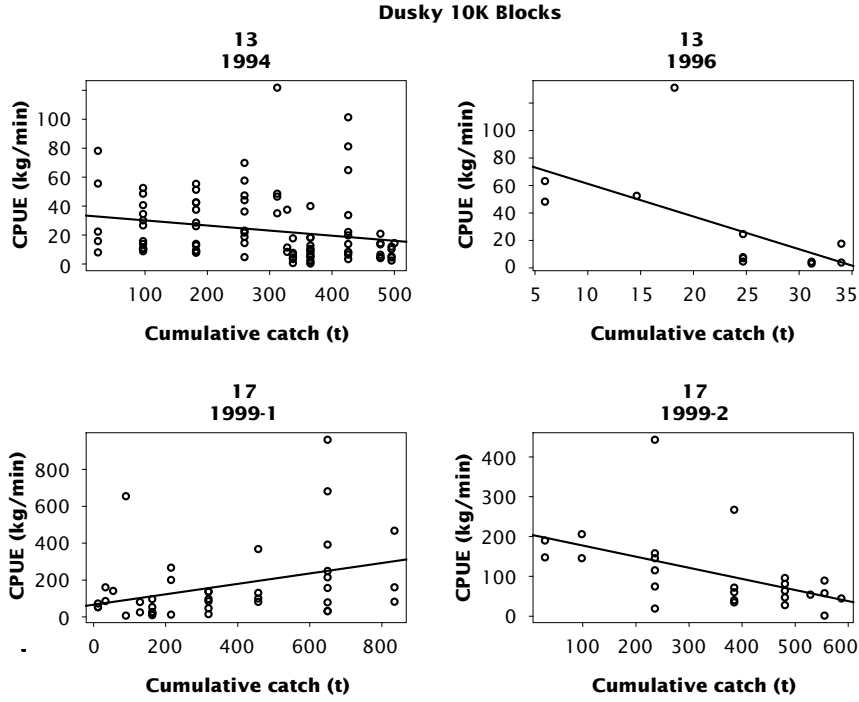


Figure 5. Four significant depletion regressions using fishery CPUE versus cumulative catch in areas 13 and 17 for dusky rockfish. 1999-1 and 1999-2 were the same year but had a large break in fishing.

in the 1990s and was lightly fished until 2003 when CPUE increased rapidly as the area was fished again. Pacific ocean perch may have shown the most depletion because this species had the most data available and was the most intensely fished in the commercial rockfish fishery.

Localized depletion in a concentration of northern rockfish only seemed to occur in one year in the "Snakehead" area of the Gulf of Alaska (area 13) in 1994. Some depletion of dusky rockfish appeared to occur in the same area and year. This area was fished heavily for northern rockfish in the1990s, but is now only lightly fished. The long-term downward trend in the fishery and survey CPUE for northern rockfish (Fig. 4) and dusky rockfish (Fig. 6) suggests the area has been slow to recover. Clausen and Heifetz (2002) also noted that 46% of the catch of northern rockfish was taken from this area during 1990-1998. However, northern rockfish and dusky rockfish did not show substantial intra-annual depletions since 1991. Several explanations of this may exist: (1) local populations may be large enough compared to the

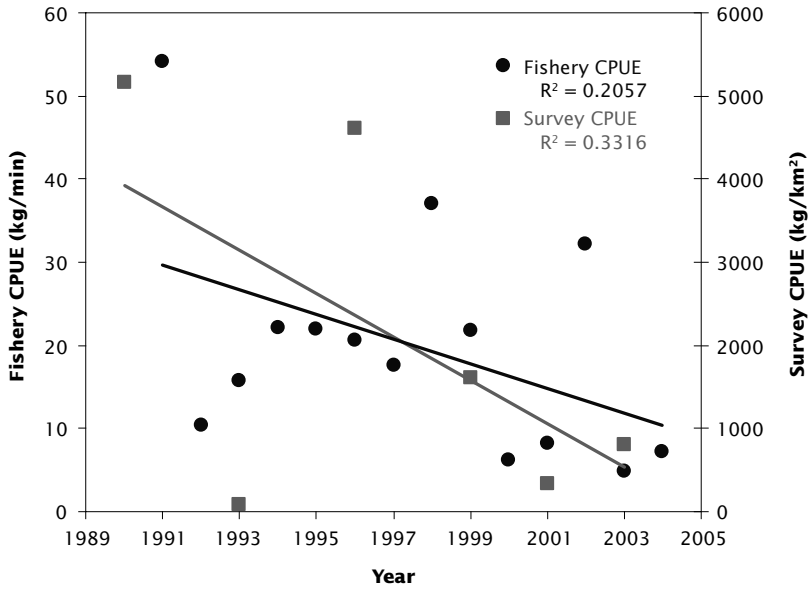


Figure 6. Survey and fishery CPUE of dusky rockfish in area 13 (the "Snakehead"). Solid lines are linear regressions for each data set.

existing catch limits that significant depletions do not occur; (2) there may be insufficient data to detect real depletions that have happened; or (3) the detectability of localized depletion may be affected by target switching. If the fishery begins targeting Pacific ocean perch until the catch limit is reached, then targets northern rockfish, and finally dusky rockfish, depletion would be exaggerated for the first target and then underestimated for the final target. This is parallel to Polovina's (1986) result showing an increase in CPUE for one of three species of snapper throughout a controlled longline experiment. As a more competitive species was removed, the CPUE of the less competitive species increased.

Scale and comparison to other studies

In this study we analyzed relatively large areas at two scales. We used two block sizes to see if localized depletion was detectable at different block sizes to help determine what "localized" means for rockfish, and at what scale there are sufficient data to perform an effective analysis. We showed that in most cases, localized depletions were detectable at

both scales. However, in a few instances, depletions were significant at one scale and not the other.

Controlled studies have demonstrated depletion on small scales for sedentary and immobile populations. Iribarne et al. (1991) conducted an intensive depletion experiment on a very small area (0.36 km^2) for scallops. In their study, they used both the Leslie (CPUE vs. cumulative catch) and the DeLury estimator (log of CPUE vs. cumulative effort) and showed a 50% decrease in CPUE over a 31-day period with similar results for each estimator. Joll and Penn (1990) also used two areas of 0.36 km^2 for scallops. They swept each experimental area three times over three nights and determined that they captured 93-96% of the scallops from their estimates of initial biomass using the Leslie estimator. Their reductions in CPUE were rapid, as scallops are sedentary and vulnerable to capture. These studies differed from our study because those studies were planned experiments with restricted areas and planned fishing effort.

Similar to this study, Lowe and Fritz (1997) used medium-sized areas (200-1,200 km^2) of observed fishery data for a depletion study on Atka mackerel. Like the rockfish analyzed in this study, Atka mackerel are highly aggregated and the fishery had been locally concentrated in space and time. In this analysis, they found that eight of nine area-year combinations yielded significant depletions of Atka mackerel. Since then, a regulatory amendment was instituted to spread the fishery out spatially and temporally (Lowe et al. 2005).

Fritz and Brown (2005) estimated depletion of Pacific cod in the southeastern Bering Sea for two larger areas (8,000 and 12,000 km^2) using trawl data from the fishery observers. Their study on the smaller of the two areas had "high observer sampling" and had a data set of 47 fishing days and a cumulative catch of over 11,000 t. Their results showed highly significant depletion and showed the strongest results when the target percentage was the lowest of three different thresholds (when catch was >20% cod). However, results were similar and nearly as strong at the other two targeting thresholds (40% and 60%). They also examined data from the longline fishery, which also showed strong and significant depletion over a 27 day study period.

Several specific and small areas (1,000 km^2) in the Aleutian Islands were analyzed for Pacific ocean perch depletions in an unpublished manuscript presented to the North Pacific Fishery Management Council (P. Spencer and R. Reuter, pers. comm., 2004, Alaska Fisheries Science Center, Seattle). Significant depletion was detected in the Northwest Buldir reef area in 2003, which was located inside of area 1 in this study. Data were more limited for that study at the smaller spatial scale.

From these four studies, it appears that depletion may be detectable with targeted fishery data at a number of different spatial scales and targeting thresholds. Large changes in CPUE appear to suppress noisy

data and reveal actual depletions. Rockfish and Atka mackerel fishery data resulted from fairly short and intense localized fisheries. In the Pacific cod study, the fishing was more spread out temporally, but was quite locally intense with 11,000 tons of fish being removed from one small block. Other fisheries such as sablefish that are more spread out over the year, or have higher migration rates, would be less likely to exhibit signals of localized depletion. The appropriate spatial and temporal scale at which localized depletion becomes important for rockfish is a subject for future research.

Conclusions and management implications

Several caveats to this study exist. First, it is well known that CPUE is not necessarily proportional to abundance (Harley et al. 2001). The CPUE for fish species that have contagious distributions like rockfish often exhibits "hyperstability" (Hilborn and Walters 1992). This means that CPUE decreases slower than abundance, because fishers are able to locate dense schools until there are too few schools to target. One way to compensate for this characteristic of the fishery is to record search time between hauls. Search time is currently not recorded on vessels targeting Alaska groundfish. Hyperstability could result in an underestimate of total depletion events in Alaska rockfish. Another result of a hyperstable distribution is an overestimate of the initial biomass of the area examined. Conversely, if hauls are included at the end of the time series that have low CPUE because they are not actually target hauls, then initial biomass would be underestimated. Additionally, downward changes in catchability throughout the study period due to behavioral changes in rockfish schools or other factors would result in underestimates of initial biomass (Miller and Mohn 1993). Confidence intervals around initial biomass estimates were highly imprecise and skewed. These reasons may help explain some exploitation estimates that were over 100% (Table 3).

The extent to which localized fishing becomes problematic for rockfish is dependent upon the ability of rockfish to replenish fished areas such that local spawning populations are not eliminated. Pacific ocean perch have not been shown to have fine-scale stock structure in Alaska, but have shown fine-scale structure in British Columbia. Pacific ocean perch showed depletions that would be important on an ecological scale. That is, if they were an important prey item for another species during the time the population was being depleted, this would be a potential concern. Additionally, removing a large quantity of fish during a specific time may allow another competitive species to thrive. Northern rockfish have not yet been shown to have much stock structure, which would imply that depletions will eventually be replenished by migration. However, in one area we found a serial decline in fishery CPUE, perhaps indicating little movement. Little is known about dusky rockfish stock

structure. If either of these two species was shown to have fine-scale stock structure or area 13 was shown to be an important source of reproductive capabilities, then this type of type of longer-term depletion would be a conservation concern.

Considerations regarding localized depletion for rockfish should reflect the spatial scale characterizing fish movement within a year and the location and spatial extent of spawning populations. As more information becomes known about these characteristics of rockfish, Leslie depletion estimation will be a useful tool to identify areas where problems may arise. Future work on localized depletion might use variograms or other spatial analyses in a GIS environment to identify the exact scale and location of depletion events.

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The Effect of Maternal Age of Spawning on Estimation of F_{msy} for Alaska Pacific Ocean Perch

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Abstract

Recent laboratory research suggests that rockfish larval survival rates increase with the age of the spawner, thus potentially necessitating more conservative harvest policies that explicitly consider the age structure of the spawning stock biomass. In this study, we use simple deterministic population dynamic equations to examine the effect of reduced survival of larvae from younger females on commonly used fishing rate reference points such as F_{msy} and $F_{xx\%}$, the fishing rates corresponding to the maximum sustained yield and conservation of *xx%* of the reproductive potential per recruit relative to an unfished population, respectively. Reduced survival of larvae from younger females results in reduced reproductive potential per recruit for a given level of fishing mortality and also increased estimated resiliency, which results from the estimated recruitments being associated with a reduced measure of reproductive potential. For Bering Sea/Aleutian Islands and Gulf of Alaska Pacific ocean perch, these two effects nearly counteract each other, producing F_{msy} estimates that were relatively insensitive but decreased slightly as maternal effects were considered. Estimates of $F_{xx\%}$ rates that correspond to F_{msy} proxies are more conservative (i.e., cor-

respond to reduced fishing intensity) when uncertainty in the degree to which maternal age affects reproductive potential is considered, as compared to analyses using spawning stock biomass as reproductive potential. These results indicate that estimated stock resiliency is not necessarily independent of the life-history parameters describing production of reproductive potential.

Introduction

Declines in rockfish populations off the U.S. West Coast (California, Oregon, and Washington) have occurred during the past two decades, resulting in the development of rebuilding plans for several species and the declaration of the U.S. West Coast fishery as a "failure" by the U.S. Secretary of Commerce (Parker et al. 2000, Dorn 2002). The collapse of several West Coast rockfish populations has drawn increased attention to rockfish fishery management policies, which, historically, were based on the principle of conserving 40% of the estimated spawning stock biomass per recruit (SPR) obtained from an unfished population. The fishing mortality reference point of $F_{40\%}$ which conserves this level of SPR originated from Clark (1993), who used stochastic simulations to show that $F_{40\%}$ produces a large fraction of the equilibrium maximum sustainable yield (MSY) and reduces the likelihood of low biomass for stocks described with a plausible range of stock-recruitment curves and levels of recruitment autocorrelation. Based on these results, Alaska groundfish are managed by using $F_{35\%}$ as limiting harvest rate and proxy to F_{msy} (the harvest rate associated with MSY) in cases where MSY cannot be reasonably estimated, and $F_{40\%}$ is used as a target harvest rate. Criticisms of the $F_{40\%}$ policy have primarily focused on two issues: (1) stock-recruitment curves typical for rockfish may be less productive than the range considered by Clark (1993), suggesting that policies that conserve more than 40% of the unfished SPR may be appropriate; and (2) harvest policies for rockfish must recognize the reduction of reproductive potential (defined as the output of the spawning process (e.g., eggs or larvae) which provides the basis for stock replacement) associated with the truncated age compositions of exploited populations (Leaman 1991, Berkeley et al. 2004b).

For West Coast rockfish, analyses of stock-recruitment data suggest that fishing mortality rates more conservative than $F_{40\%}$ are appropriate. Dorn (2002) conducted a Bayesian meta-analysis of rockfish stock-recruitment data and found West Coast rockfish stocks to be generally less productive than stocks considered by Clark (1993), and suggested that a risk-neutral harvest rate policy of $F_{50\%}$ is appropriate for these stocks. Additionally, Clark (2002) recommended that for stocks with low resiliency, SPR rates of $F_{50\%}$ or $F_{60\%}$ may be required to maintain an adequate balance of maximizing yield while preserving stock size.

Research on the reproductive biology of rockfish suggests that the reproductive potential of the stock may be a function of the age structure, in particular the proportion of old fish in the population. Leaman (1987, 1991) noted that rockfish are long-lived with little somatic growth in older fish, allowing older fish to allocate a large proportion of available energy to reproduction. The removal of older females by fishing thus disproportionately reduces spawning output such that reproductive value (the lifetime expected number of offspring from a female of a particular age in a stable age distribution) is highly sensitive to increases in fishing mortality. Additionally, Berkeley et al. (2004a) found in laboratory studies that older black rockfish (*Sebastes melanops*) produced larvae with increased survival rates; thus, exploitation can be expected to disproportionately remove the most effective spawners. The implication from these studies is that simply conserving spawning biomass is not sufficient, and managers should aim to preserve spawning biomass with a desirable age structure.

Given the collapse of several West Coast rockfish species, considerable interest exists in determining whether management policies for Alaska rockfish are sufficiently conservative. A panel charged with evaluating the $F_{40\%}$ policy for Alaska groundfish (Goodman et al. 2002) suggested that the currently used $F_{40\%}$ policy may not provide sufficient conservation for Alaska rockfish. Dorn's (2002) meta-analysis is the only study that simultaneously considered the productivity of both West Coast and Alaska rockfish, evaluating eight West Coast stocks, one British Columbia Pacific ocean perch (POP) stock, and three Alaska POP stocks (at that time, Bering Sea and Aleutian Islands POP were assessed as separate stocks). The Alaska POP stocks show greater resiliency (increased slope of the stock-recruitment curve at the origin) than the West Coast stocks, with MSY occurring at SPR rates of approximately $F_{30\%}$. The finding of observed greater resiliency in the Bering Sea/Aleutian Islands (BSAI) POP and Gulf of Alaska (GOA) POP has been repeated in recent stock-recruitment analyses, which have found that estimated F_{msy} reference points are greater than the proxies of $F_{40\%}$ (i.e., $F_{msy} > F_{40\%}$; Spencer and Dorn 2003, Hanselman et al. 2004). However, these studies did not consider how changes in age structure may affect estimates of stock productivity and estimation of harvest reference points such as F_{msy}. For example, the analyses of Clark (1991,1993) evaluate the correspondence of F_{msy} and $F_{xx\%}$ (the fishing rate corresponding to conservation of *xx%* of the reproductive potential per recruit relative to an unfished population) when spawning stock biomass (SSB) is used as a measure of stock reproductive potential. How would expressing reproductive potential in units that reflect differential spawning effectiveness between age groups change the results of Clark's (1991,1993) analyses, and what would be the effect on the estimate of F_{msy} for a particular stock?

The purpose of this study is to consider the effect of the maternal age of spawning on F_{msy} and proxies to F_{msy}. The analysis consists of converting measurements of reproductive potential from spawning stock biomass to "viable larvae," the per-unit production of which is a function of spawner age. First, we consider under what conditions this redefinition may be expected to affect estimates of fishing reference points. Second, we use deterministic population dynamics equations to illustrate the effect on estimation of F_{msy}, assuming that stock-recruitment parameters are well estimated. Third, we estimate F_{msy} for BSAI and GOA POP using a variety of measures of reproductive potential, and compare these estimates to currently used fishing mortality reference points. Finally, we illustrate how common fishing rate proxies to F_{msy} that aim to conserve a specified proportion of the reproductive potential per recruit are affected by maternal effects on larval viability.

Methods

Standard population dynamics equations were used to estimate yield-per-recruit and spawning biomass-per-recruit as a function of fishing mortality for a population with life history characteristics equivalent to those estimated for BSAI POP. These life history parameters describe a stock with relatively low natural mortality ($M = 0.05$), moderate von Bertalanffy K parameter ($K = 0.17$), and age at 50% selection in the fishery less than age at 50% maturity (Fig. 1a), and are viewed as broadly representing common life-history characteristics of exploited rockfish in the North Pacific. Little information is available regarding fecundity of Alaska POP, although studies in other areas indicate that larger females attain fecundities of 305,000 (Hart 1973) and 350,000 (Leaman 1991). A fecundity-at-age relationship for Alaska POP was obtained from fitting an asymptotic curve to Vancouver Island POP data (Dr. Bruce Leaman, International Pacific Halibut Commission, pers. comm.).

Viable larvae are introduced as a measure of reproductive potential that discounts the output from younger spawners via a larval survival curve. Viable larvae were estimated as

$$\text{Viable larvae} = \sum_a s_a f_a m_a p_a N \qquad (1)$$

where N is total number of female fish, p_a is the proportion at age, m_a is the proportion mature at age, f_a is fecundity at age, and s_a is proportion of larvae surviving to two weeks.

Two separate larval survival curves were considered: (1) a proxy curve adapted from the black rockfish laboratory data of Berkeley et al. (2004a); and (2) a knife-edged curve in which no larvae produced from a female younger than 20 years would survive. Berkeley et al. (2004a) develop an asymptotically increasing relationship between maternal age and the time required for 50% mortality of black rockfish larvae, and

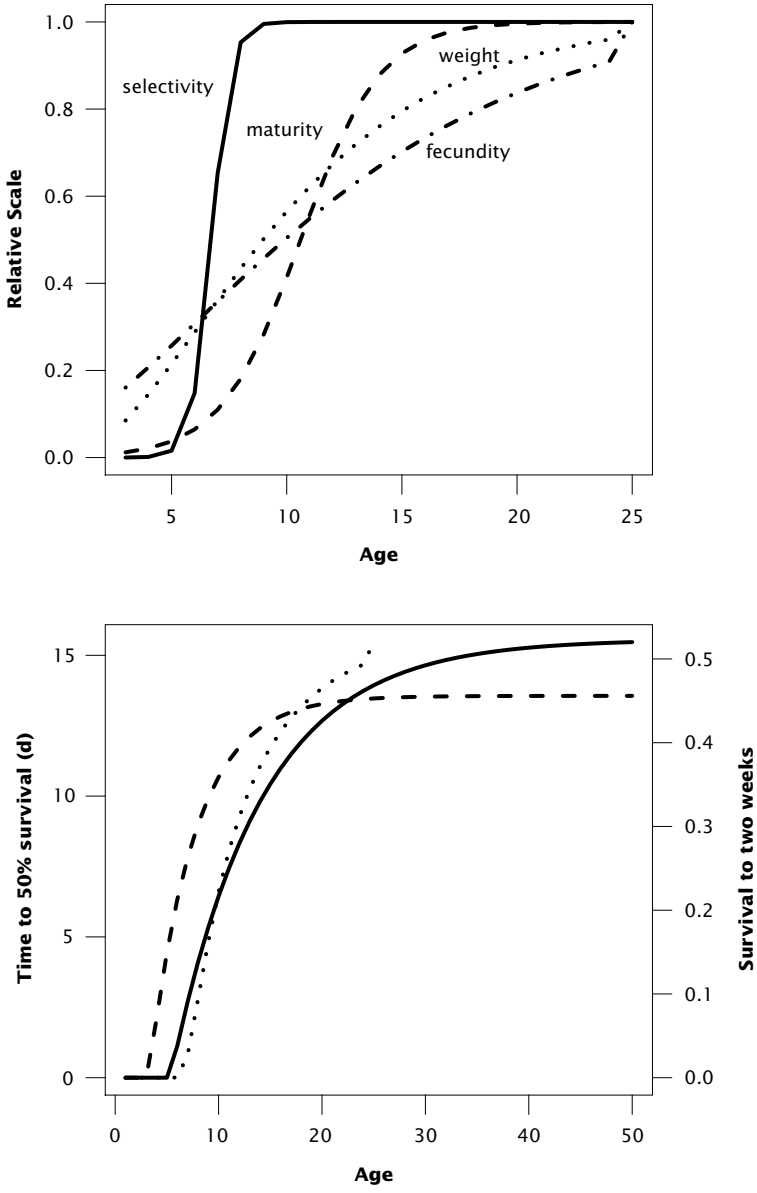


Figure 1. (a) Selectivity, maturity, weight, and fecundity at age used to model BSAI POP, all shown on a relative scale. (b) Days to 50% survival for black rockfish larvae (dashed line; from Berkeley et al. 2004a) as a function of spawner age, and modified curve used for POP (solid line); the estimated proportion of POP surviving to two weeks (shown for ages 3-25+) is shown in the dotted line.

this relationship was modified to model larval mortality rate for POP (Fig. 1b). Relative to black rockfish, POP have both a longer generation time and older age at maturity. The curve describing time to 50% larval mortality for POP thus had a higher x-intercept and lower slope to reflect these considerations and was used to calculate the proportion of larvae surviving two weeks, a period arbitrarily chosen to provide some contrast in the larval survival rates by age. The knife-edged survival curve provides a scenario of extreme maternal effects on reproductive potential, thus creating contrast between measures of reproductive potential that consider intermediate and no effects on larval survival, represented by the larvae produced with the proxy curve and SSB, respectively.

A Beverton-Holt recruitment curve was used for computation of equilibrium yield and was re-parameterized using R_0, the expected recruitment consistent with the reproductive potential of an unfished stock S_0, and a parameter that measures the resiliency of the stock, h, defined as the proportion of R_0 that recruits when the reproductive potential of the stock is reduced to 20% of S_0 (i.e., the steepness parameter of Mace and Doonan 1988). The reparameterized Beverton-Holt curve is given by

$$R = \frac{0.8\, R_0\, h\, S}{0.2\varphi_0\, R_0(1-h) + (h-0.2)S}, \qquad (2)$$

where S is reproductive potential (either SSB or viable larvae), φ is either SSB or viable larvae-per-recruit (defined as SPR and LPR, respectively), and $S_0 = \varphi_0 R_0$ for an unfished stock. Steepness ranges between 0.2 (recruits related linearly to reproductive potential) to 1.0 (recruits independent of reproductive potential). Equilibrium recruitment and yield were obtained for a sequence of harvest rates where LPR and SPR is reduced to a fraction p of unfished LPR or SPR (p = 1.00,0.99, . . .,0.01), and F_{MSY} was estimated as the instantaneous fishing mortality rate associated with the level of p at which equilibrium yield is maximized.

Application to Alaska POP

Estimates of F_{msy} for GOA and BSAI POP using larvae (produced with either the proxy or knife-edged survival curve) and SSB as measures of reproductive potential were made with a Bayesian estimation procedure. Time series of numbers at age, including recruits, for each stock were obtained from age-structured stock assessments (Spencer et al. 2004, Hanselman et al. 2003), and estimates of viable larvae were made from Eq. 1 using the appropriate life-history parameters from each region. There are three parameters for which priors need to be developed, h, R_0, and σ^2, the variance of expected recruitment. The prior for steepness was modeled by assuming that β, the logit of h, was normally distributed (after rescaling h into the interval (0,1), $(h-0.2)/0.8$, and simplifying),

$$\beta = \log\left(\frac{h-0.2}{1-h}\right),\ \beta \sim \mathrm{N}(\mu,\xi^2). \qquad (3)$$

For h in the interval (0.2,1.0) the logit β ranges from $-\infty$ to $+\infty$, allowing straightforward specification of a mean and variance. A normal prior was used for R_0, and a locally uniform prior for σ on a log scale was used. The log joint posterior distribution is the sum of the log-likelihood and the log prior, and the mode of the joint posterior distribution was obtained using the AD Model Builder nonlinear optimization software (Otter Research 1996).

The prior for β was based on levels of reproductive success (defined as R/S at the origin divided by R_0/S_0) considered plausible for rockfish. Dorn et al. (2003) generated a prior distribution by using a level of reproductive success of 8 ($\beta = 0.34$) as the midpoint of the distribution (corresponding to the middle of the range of stock-recruitment curves considered by Clark 1991), and set the prior variance so that reproductive success values of 4 and 16 were located at the 10th and 90th percentiles of the distribution. For Alaska POP, the same variance was used but the midpoint of the distribution was lowered to reflect a level of reproductive success of 4 ($\beta = -0.51$), thus reflecting the perceived lower productivity of rockfish relative to the values considered by Clark (1991). The midpoint of this distribution corresponds to a steepness of 0.50, closer to the value of 0.39 found for five rockfish stocks in a meta-analysis by Myers et al. (1999). Prior estimates of R_0 were derived from estimates of recruits consistent with the stock size in the first year of the age-structured stock assessment model, and a relatively large coefficient of variation of 0.22 was assigned.

Estimation of fishing rate proxies to F_{msy}

The relationship between equilibrium yield and fishing mortality requires knowledge of the stock-recruitment parameters h and R_0, and for cases where these parameters are unknown Clark (1991, 1993) proposed examining yield curves for a range of potential stock-recruitment relationships in which the level of reproductive success ranged from 4 to 16. The "maximin" criteria, defined as the maximum of the minimum equilibrium yield for each level of fishing mortality, was used to identify the optimal fishing rate, expressed as $F_{xx\%}$, to be used as a proxy to F_{msy}. In this study, the same methodology is applied to examine how the index of reproductive potential may affect the harvest rate proxies. Consistent with Clark (1991,1993), yield curves corresponding to the levels of reproductive success of 4 and 16 (corresponding to steepness values of 0.5 and 0.8, respectively) were produced for each of the three measures of reproductive potential (intermediate levels of reproductive success did not affect the maximin fishing mortality rate), and the optimal fishing rate proxy was then identified explicitly considering

uncertainty not only in stock-recruitment relationships, but also the degree to which spawner age affects larval viability.

Results

Spawning stock biomass is commonly used as a proxy for reproductive potential (i.e., eggs produced) in stock-recruitment analyses, and under the assumption of a linear (density-independent) relationship this substitution does not affect the stock-recruitment analyses (Rothschild and Fogarty 1989). Similarly, recasting reproductive potential from SSB to viable larvae will not change the stock-recruitment analysis unless there is a nonlinear relationship between these measures, and this can be evaluated by examining whether the ratio of viable larvae to SSB changes with stock size. Spawning stock biomass can be expressed as the sum over all ages of the product of numbers at age, weight at age, and maturity at age, and the ratio of viable larvae (Eq. 1) to SSB is

$$\frac{Larvae}{SSB} = \frac{\sum_a s_a f_a m_a p_a}{\sum_a w_a m_a p_a} \qquad (4)$$

where w_a is the weight at age. Although density-dependent changes in fecundity, proportion mature at age, and growth may occur for rockfish (Leaman 1991, Gunderson 1997), attention on the production of viable larvae has largely focused on the reduction of the age structure associated with exploited populations (Berkeley et al. 2004b). Thus, the major factor expected to affect the per unit production of viable larvae in the presence of age-dependent maternal effects is p_a, and Eq. 3 provides a framework for assessing how several factors may affect the ratio of viable larvae to SSB.

The relationships between SSB, viable larvae (produced with the proxy curve) and mean age for an equilibrium population with constant recruitment are shown in Fig. 2a. As fishing mortality increases the mean age decreases, resulting in the production of viable larvae decreasing at a greater rate than SSB due to the age-dependant maternal influence on larval survival. Thus, the proportion of viable larvae per recruit conserved, relative to an unfished stock, at any given fishing mortality rate is lower than the proportion of SSB conserved. For example, a fishing rate of 0.049 would conserve 40% of the SSB but only 35% of the viable larvae per recruit (proxy survival curve), and 27% of the viable larvae per recruit (knife-edged survival curve).

Conversely, a reduction in mean age combined with defining reproductive potential as viable larvae rather than SSB results in increased estimated steepness in the stock-recruitment curve. This occurs because although reproductive potential is reduced, the definition of recruits has not been altered. Thus, an identical level of recruits would be associated

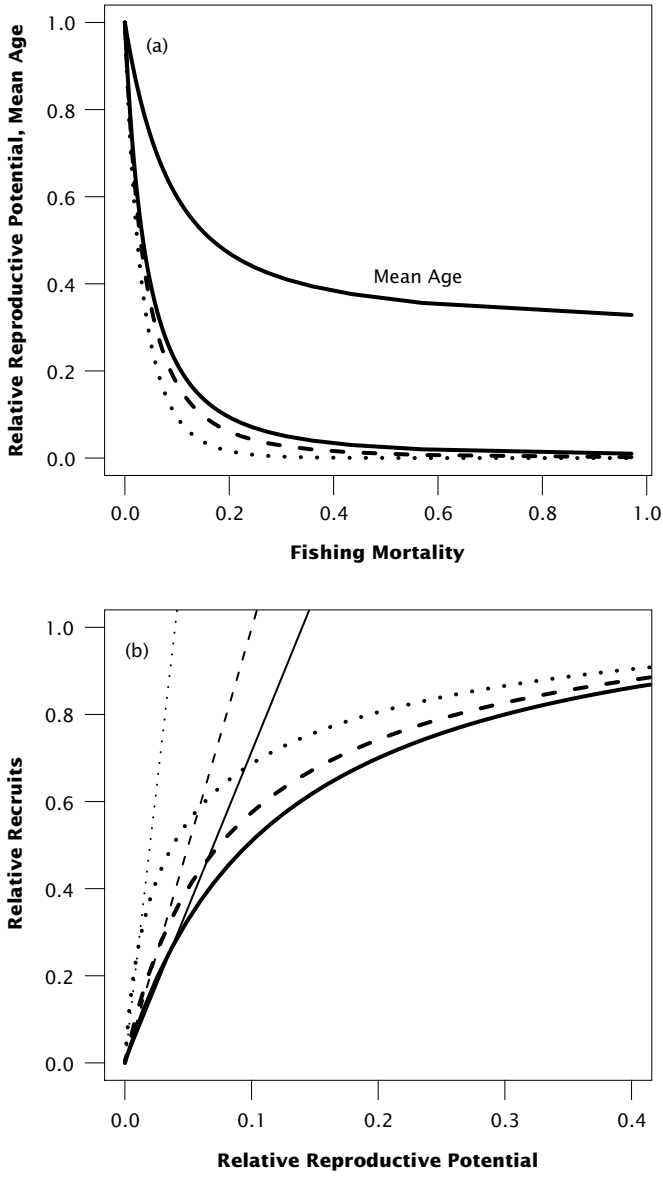


Figure 2. (a) The proportion of SSB per recruit (lower solid line) and larvae per recruit produced with the proxy (dashed line) and knife-edged (dotted line) survival curves, relative to an unfished stock, with increasing fishing mortality; the relative mean age is shown with the upper solid line. (b) Stock-recruitment curves and replacement lines for three measures of reproductive potential, plotted on relative scales: SSB (solid lines), larvae from proxy survival curve (dashed lines), and larvae from knife-edged survival curve (dotted lines). The replacement lines correspond to an *F* of 0.145.

with diminished reproductive potential, resulting in an interpretation of increased steepness h and resiliency. Consider a case where the number of recruits is defined as a function of SSB via the Beverton-Holt curve with a steepness parameter h of 0.7, and increased fishing results in reduced equilibrium SSB and the truncated equilibrium age structure as in Fig. 2a. Relating the number of equilibrium recruits derived from this curve to equilibrium viable larvae (as produced from the proxy curve) results in an estimated steepness of 0.75, whereas relating the same recruits to equilibrium viable larvae (as produced from the knife-edged curve) results in an estimated steepness of 0.85 (Fig. 2b).

The effect of using viable larvae as a measure of reproductive potential on F_{msy} will involve a tradeoff between the greater conservatism implied by the reduced reproductive potential per recruit and the greater resiliency implied by an increased steepness in the stock-recruitment curve. Thus, while the slope of the spawner-recruit curve at the origin becomes steeper with maternal effects, the replacement lines (the recruits per unit of reproductive output) also become steeper for a given level of fishing mortality, and the effect on equilibrium recruitment, yield, and F_{msy} depends on the relative relationship of these two lines. For example, for the stock-recruitment curve with viable larvae (knife-edged curve) the rate of fishing producing equilibrium recruitment of zero (F_{crash}) was 0.145, whereas applying the same F to the stock-recruitment curves for the other two measures of reproductive output produces positive equilibrium recruitment. The estimated F_{msy} also increases from 0.057 to 0.06 when reproductive potential changes from SSB to viable larvae with the knife-edged curve (Fig. 3).

Application to the BSAI and GOA POP data provided contrasting results in which the estimates of F_{msy} decreased slightly as maternal effects are considered. Changes in the definition of reproductive potential noticeably changes the scatterplot of stock-recruitment data; the individual data points are shifted by varying degrees to the left as the recruitment data are associated with diminished measures of reproductive potential (Fig. 4). The stock-recruitment curves derived from these data are shown in Fig. 5, along with the replacement lines corresponding to extinction when reproductive potential is measured as viable larvae with the knife-edged survival curve. The fishing rate associated with this replacement line leads to positive sustained yields when reproductive output is measured as viable larvae (proxy survival curve) or SSB. For the BSAI POP, the estimates of steepness ranged from 0.86 (SSB) to 0.91 (larvae with knife-edged survival curve), whereas the estimates of $F_{40\%}$ decreased from 0.049 (SSB) to 0.033 (larvae with knife-edged survival curve) (Table 1, Fig. 5). Estimated F_{msy} decreased from 0.087 (SSB) to 0.070 (larvae with knife-edged survival curve), and F_{crash} decreased dramatically from 0.35 (SSB) to 0.17 (larvae with knife-edged survival curve) (Table 1, Fig. 6). A similar pattern was seen for

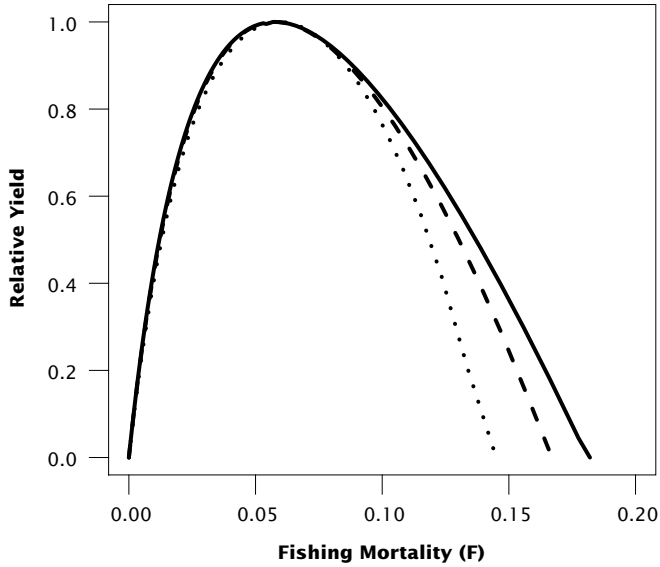


Figure 3. Relative yield as a function of fishing mortality for the stock-recruitment curves presented in Fig. 2b, with reproductive potential defined as SSB (solid line), larvae (proxy survival curve; dashed line), and larvae (knife-edged survival curve; dotted line).

the GOA POP, where steepness increased across the three measures of reproductive potential from 0.81 to 0.93, $F_{40\%}$ decreased from 0.060 to 0.036, F_{msy} decreased slightly from 0.11 to 0.09, and F_{crash} decreased from 0.37 to 0.20.

Incorporation of uncertainty in the degree to which spawner age affects larval survival resulted in estimated proxy fishing mortality reference points being more conservative than those attained from consideration of stock-recruitment uncertainty alone. The yield curves for each of the three measures of reproductive potential are shown in Fig. 7(a-c), and correspond to stock recruitment curves with levels of reproductive success of 4 or 16, spanning the range considered by Clark (1991). With reproductive potential measured in SSB, the proxy fishing mortality rate resulting from the maximin criterion occurs at an F_{spr} rate of $F_{43\%}$, identical to the results of Clark (2002) for Beverton-Holt curves. With reproductive potential defined as larvae (either from the proxy or knife-edged survival curves), the proxy fishing reference points would conserve a similar amount of the reproductive potential, but the fishing mortality reference point would decrease from 0.044 (SSB) to 0.032 (lar-

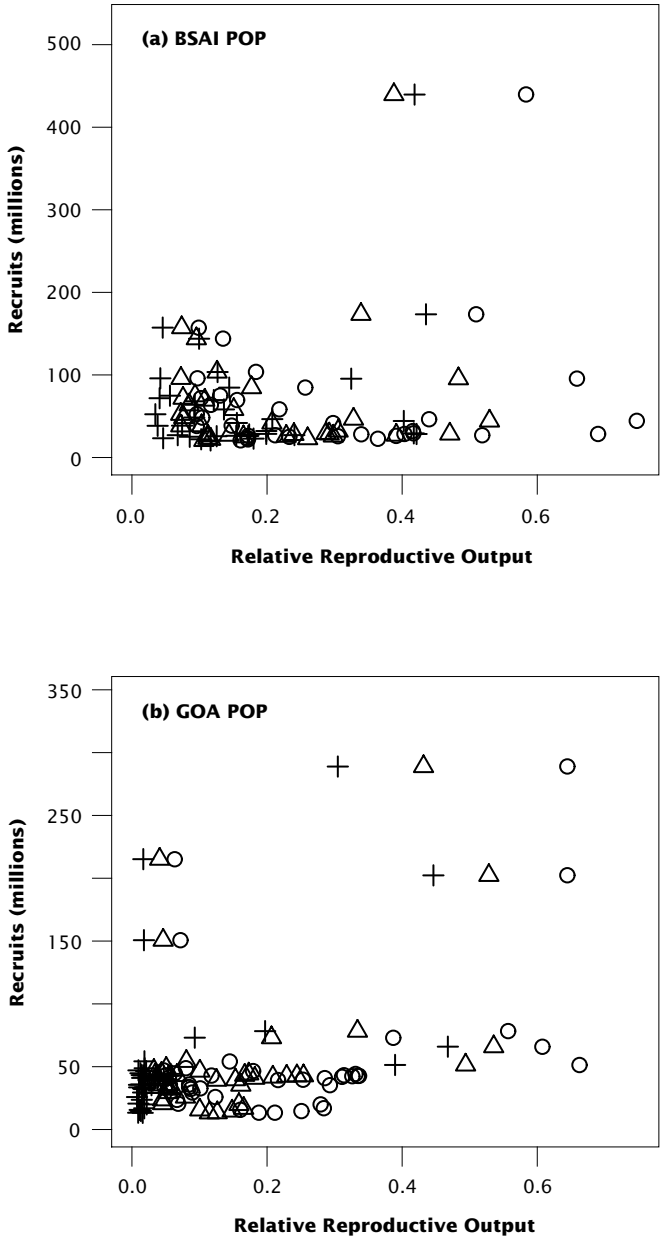


Figure 4. Stock recruitment data for (a) BSAI POP and (b) GOA POP with scaled reproductive potential measured as SSB (circles), larvae from proxy survival curve (triangles), and larvae from knife-edged survival curve (crosses).

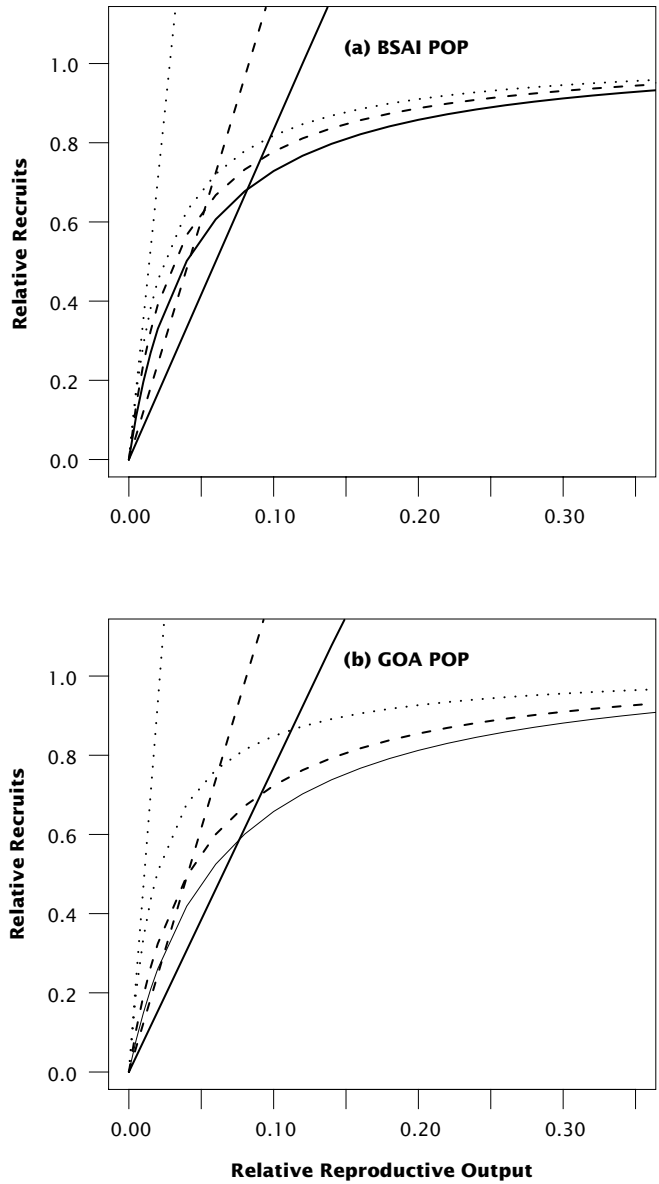


Figure 5. Estimated stock-recruitment curves for (a) BSAI POP and (b) GOA POP with scaled reproductive potential measured as SSB (solid lines), larvae from proxy survival curve (dashed lines), and larvae from knife-edged survival curve (dotted lines). The replacement lines correspond to *F* levels of 0.17 and 0.20 for BSAI and GOA POP, respectively.

Table 1. Estimates of steepness, $F_{40\%}$, F_{msy}, F_{crash}, and proportion unfished SSB or larvae at F_{msy} for BSAI POP and GOA POP with three units of reproductive potential.

Stock	Units of reproductive potential	Steepness	$F_{40\%}$	Proportion unfished SSB or larvae at F_{msy}	F_{msy}	F_{crash}
BSAI POP	SSB	0.86	0.049	0.25	0.087	0.35
	Larvae (proxy mortality)	0.89	0.042	0.21	0.084	0.29
	Larvae (knife-edged mortality)	0.91	0.033	0.17	0.070	0.17
GOA POP	SSB	0.81	0.060	0.24	0.111	0.37
	Larvae (proxy mortality)	0.85	0.049	0.2	0.101	0.29
	Larvae (knife-edged mortality)	0.93	0.036	0.12	0.095	0.20

vae with the knife-edged curve). The yield curves for all three measures of reproductive potential are plotted against F in Fig. 7d, as incorporation of uncertainty in the degree of maternal effects on larval survival in precludes presenting yield curves in terms of relative reproductive potential per recruit. Here, the identified proxy fishing mortality is $F = 0.035$, more conservative than the value of 0.044 that only considers reproductive potential as SSB.

Discussion

Effective reproductive potential of rockfish may be expected to decline at a greater rate than SSB with increased fishing due to a reduced mean age and age-dependent spawner effectiveness (Berkeley et al. 2004a). However, in order to incorporate this observation in operational management advice, it becomes necessary to examine its effect on commonly used reference points such as F_{msy}. It is important to note that although the reproductive potential may be diminished, relative to SSB, the measure of recruits has not been altered. Ideally, one would obtain recruitment estimates from juvenile surveys, although in practice they are typically obtained from stock assessment models utilizing age-composition data from fisheries and surveys. In either case, recruits are simply defined as the number of young fish entering the population. Thus, relating an identical number of recruits with a diminished measure of reproductive potential implies greater estimated resilience, and illustrates that our perception of resilience and stock productivity are not independent of the life-history parameters governing reproductive potential (Morgan and Brattey 2005). The extent to which this estimated increased resilience affects F_{msy} depends on the relative

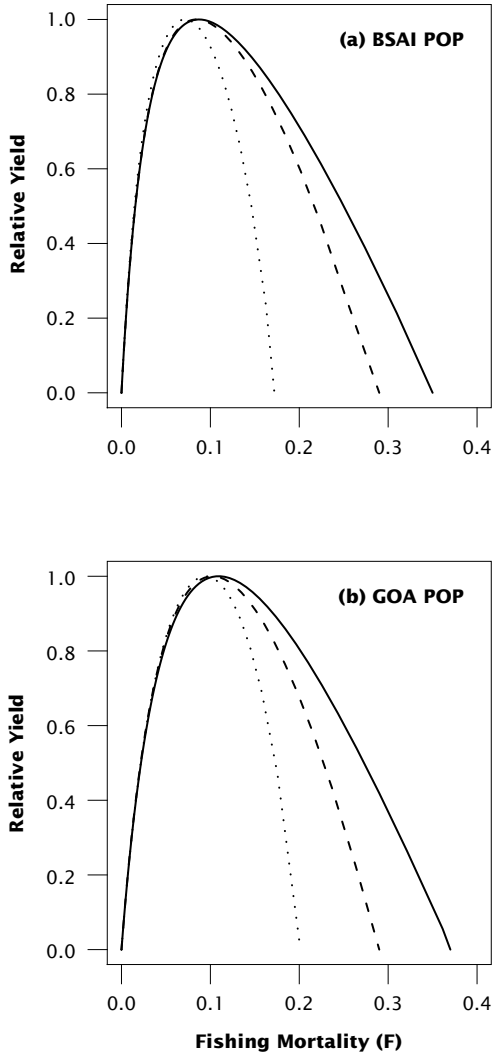


Figure 6. Relative yield as a function of fishing mortality for (a) BSAI POP and (b) GOA POP with reproductive potential defined as SSB (solid line), larvae (proxy survival curve; dashed line), and larvae (knife-edged survival curve; dotted line).

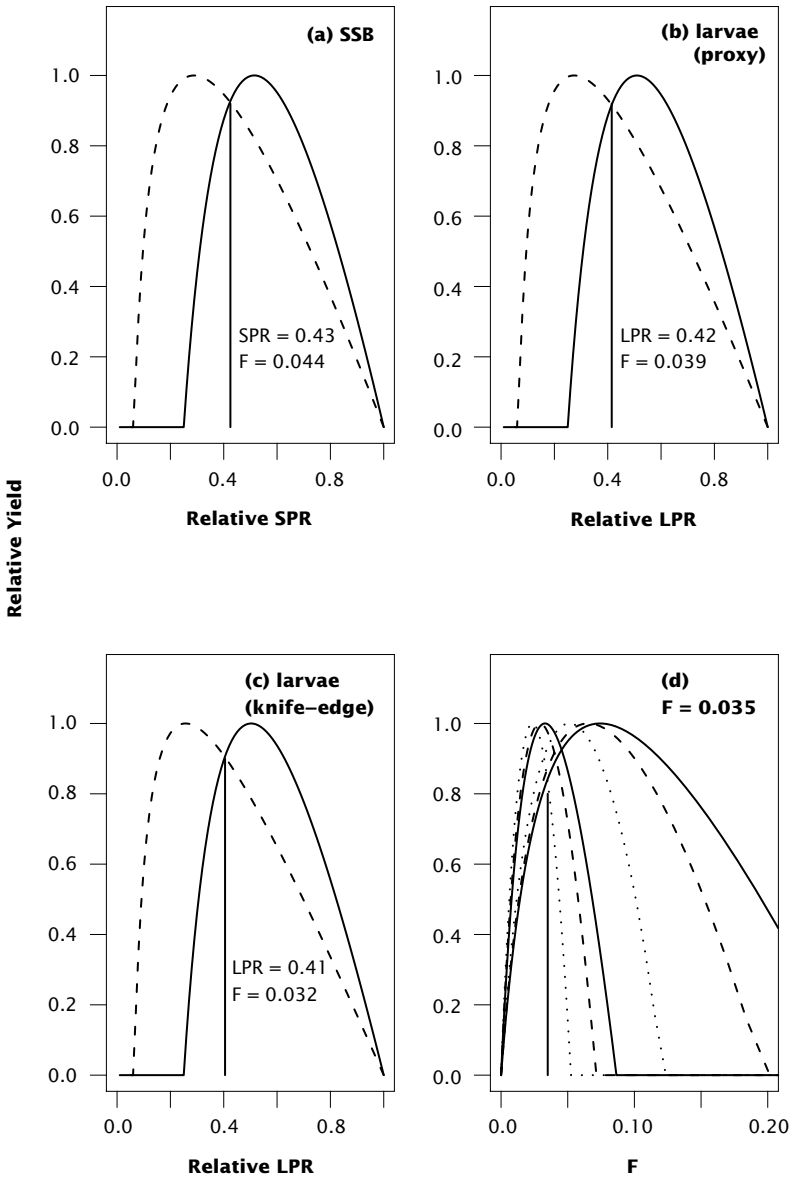


Figure 7. (a-c) Relative yield as a function of either relative spawner per recruit or larvae per recruit for three measures of reproductive potential with reproductive success of 4 (dashed line) and 16 (solid line); the maximin F_{spr} or F_{lpr} are denoted by the vertical lines. (d) Relative yield for all three measures of reproductive potential and two levels of reproductive success plotted against *F*.

relationship between the stock-recruitment curve and the replacement lines, which are a direct function of the reproductive output per recruit; thus, age-dependent maternal effects on spawning effectiveness may either increase or decrease F_{msy}. For the theoretical example presented here, the estimated increased resilience was the dominant effect and produced increased F_{msy} with maternal effects. However, for Alaska POP the two opposing processes nearly compensated each other and produced F_{msy} estimates that were relatively insensitive but decreased slightly with maternal effects, whereas F_{crash} decreased sharply. These results are similar to those found for Georges Bank Atlantic cod by Murawski et al. (2001), who found that F_{med} (based on the median level of recruits/spawner) decreased slightly from 0.61 to 0.57 as reproductive potential was converted from SSB to viable larvae, whereas F_{crash} decreased from 1.4 to 0.88.

Consideration of uncertainty in stock-recruitment relationships led to the development of $F_{35\%}$ as a proxy for F_{msy}, and additional uncertainty regarding the extent to which spawner age structure affects reproductive potential would produce more conservative proxy reference points. Similar to the results found by Clark (2002) for Beverton-Holt recruitment curves, the results presented here indicate that conserving approximately 40% of the reproductive potential per recruit is desirable even if the definition of reproductive potential changes from SSB to viable larvae (produced with either the proxy or knife-edged mortality curves). However, the level of fishing mortality associated with these reference points decreases as reproductive potential changes from SSB to viable larvae (produced with the knife-edged curve). For example, if viable larvae (produced from the knife-edged mortality curve) rather than SSB was known to be the appropriate measure of reproductive potential, the F rate used as a proxy for F_{msy} would decrease substantially in this example from 0.044 to 0.032. In practice, there is likely to be uncertainty in the extent to which spawner size/age affects larval viability in addition to the stock-recruitment parameters. Because expressing reproductive potential as SSB represents one bound where these maternal effects are assumed to not occur, any consideration of the maternal effects on reproductive potential were found to produce relatively more conservative harvest rate proxies (Fig. 7).

Given the uncertainty in stock-recruitment relationships for Alaska POP, perhaps the best use of F_{msy} estimates is as a qualitative indicator to assess the need for any directional changes in current harvest rate proxies. The currently used $F_{40\%}$ estimates for BSAI and GOA POP (0.048 and 0.062, respectively) are more conservative than estimates of F_{msy} based on any of the three measures of reproductive potential, suggesting that the current harvest policy is not unduly aggressive given available data on stock productivity. As with much stock-recruitment data, it can be difficult to parse out how much of the recruitment signal

is attributable to spawner output and how much is attributable to environmental conditions. The estimates of high resiliency for Alaska POP derive from a few strong recruitments during favorable environmental conditions in the 1980s, and these results may not be repeated in different environmental conditions. Similarly, much of what we perceive as the low productivity of rockfish recruitment derives from West Coast data collected during a period of unproductive environmental conditions (McGowen et al. 1998), and this interaction between environmental and stock effects, in part, prompted Dorn (2002) to advise cautious interpretation of his meta-analysis results. What is desired is knowledge of how species with rockfish life-history characteristics respond to a variety of environmental regimes, and development of robust management strategies appropriate for this range of environmental variation. For example, low-frequency trends in recruitment can affect the mean age of the stock and thus the indices of reproductive potential and estimation of F_{msy}. Additionally, recruitment variability may be related to longevity (Longhurst 2002), and stochastic simulations can allow examination of the effects of truncated age classes for stocks showing episodic recruitment patterns. Management strategy evaluations (Stokes et al. 1999) appear to be one promising approach for addressing these questions and will be pursued in future research.

Field and laboratory research aimed at documenting the reproductive biology of specific rockfish stocks will greatly assist the interpretation of management importance of maternal effects. Even basic information such as fecundity is absent for many Alaska rockfish stocks, and shows differences between areas for those species where data are available. Although one may never expect to obtain complete knowledge of the influence of spawner age on larval mortality rates in situ, laboratory and field studies that document, for example, the relationship between larval oil globule volume and spawner age can reduce uncertainty for specific stocks and provide a more realistic range of potential maternal effects. A realistic range of the potential influence of maternal effects on larval viability is desired for fisheries management, as this will have a large influence on the harvest rate proxies that will be obtained.

The declines in reproductive potential when maternal age affects larvae viability have also been noted by many other researchers (Scott et al. 1999, Murawski et al. 2001), prompting Berkeley et al. (2004b) to emphasize the importance of older fish in the replenishment of fish stocks and concluding that standard management practices generally do not adequately conserve older fish. However, a complete evaluation of the role of older fish in stock replenishment must not only look at the indices of reproductive potential (i.e., the x-axis of the stock-recruitment plot), but also estimates of stock productivity and management implications resulting from these improved estimates of reproductive potential.

The results of this study are consistent with those of Morgan and Brattey (2005), who found that different measures of reproductive potential can markedly affect perceived stock productivity for Atlantic cod, and demonstrate how information on maternal effects could be addressed within an F_{spr} framework. For future studies, more refined information on rockfish reproductive biology of the type conducted by Berkeley et al. (2004a) would greatly refine our estimates of reproductive potential and the resulting implications for stock productivity.

Acknowledgments

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