# Can Management of Barents Sea Capelin Be Improved by Multispecies Modeling?

**Sigurd Tjelmeland**
*Institute of Marine Research, Bergen, Norway*

## Abstract

This paper gives a model for the maturation of Barents Sea capelin and consumption of mature capelin by the Northeast Arctic stock of cod (*Gadus morhua*) during the spawning migration in January-March. The stock has traditionally been managed using a constant escapement strategy and the model is used for repeated stochastic long-term runs to investigate the effect of different levels of the target spawning stock. It is shown that the target spawning stock should be more than 0.4 million metric tons and that the management of capelin may be improved by taking into account predation from cod and the presence of herring in the Barents Sea. The maturation is modeled as a monotonically increasing function of length. The shape parameter is determined from a fit to empirical maturation data while the length at 50% maturity is determined by comparing the immature stock for one year to the total stock for the next year, assuming total spawning mortality. Based on the estimated maturation parameters, historical values of maturity ogives, natural mortality, and spawning stock are calculated and used for resampling during the long-term runs.

## Introduction

A general overview of the biology of the Barents Sea capelin is given by Gjøsæter (1997) in this volume.

The Barents Sea capelin stock has been managed using a target escapement strategy. The philosophy has been that a certain amount of spawners are needed in order to give sufficient recruitment. Furthermore, it has been assumed that the capelin die after spawning.

The restriction of the capelin fishery by quota started in 1978, following the record fisheries of almost 3 million metric tons in 1976 and 1977. The target spawning stock was set to 0.5 million metric tons, based on a "rule-of-thumb" evaluation of the then available series of spawning stock estimates and recruitment observations. Later, a sex-aggregated population model with cut-off maturation by length led to an estimation of an optimal spawning stock of 0.43 million metric tons (Hamre and Tjelmeland 1982). This analysis has since been further refined to include sex disaggregation, multispecies effect, and stochastic treatment (Tjelmeland and Bogstad 1993).

The core of the procedure was, and still is, the yearly September trawl-acoustic survey of the stock. This data series starts in 1972. From 1978, the cruise has been a joint Russian-Norwegian effort where 4-5 vessels participate over a period of 3-4 weeks in one unified operation. The data from the cruise are presented to the International Council for the Exploration of the Sea (ICES) Northern Pelagic and Blue Whiting Fisheries Working Group as tables of number of capelin by age and length. For the present study these tables have further been divided by sex using the Norwegian biological samples weighted with the mean echo integrator value from the area surrounding the trawl station.

In the period 1972-1982 the Barents Sea was practically devoid of herring. As the rich 1983 year class of herring affected the Barents Sea capelin stock, the assumptions underlying previous analyses failed. Since 1983 there have been two capelin collapses relating to the good herring recruitment in 1983 and 1990-1992. It is likely that as a rule there will be much herring in the Barents Sea at intervals comparable to the life span of the capelin. A consequence of this is that the capelin stock most probably will be extremely dynamic, with long periods of a very small stock.

It is not easy to devise a management rule in such a situation. However, underlying all management of the capelin stock will always be the necessity of calculating the spawning stock based on the September estimate of the total stock. In the Barents Sea, direct measurements of the spawning stock do not exist, so we will have to resort to modeling. The most important parts of a model predicting the spawning stock from the September data are: (1) a model for maturation, and (2) a model for natural mortality. There will be some growth also during the winter period, but the growth is considered of lesser importance in this period compared to maturation and natural mortality.

The capelin feeds in the central and northern Barents Sea (Gjøsæter 1997). During the spawning migration the capelin overlaps with the cod stock, thus being heavily preyed on (Figure 1). For a general overview of the capelin's role as source of food for the cod stock, see Bogstad and Mehl (1997).

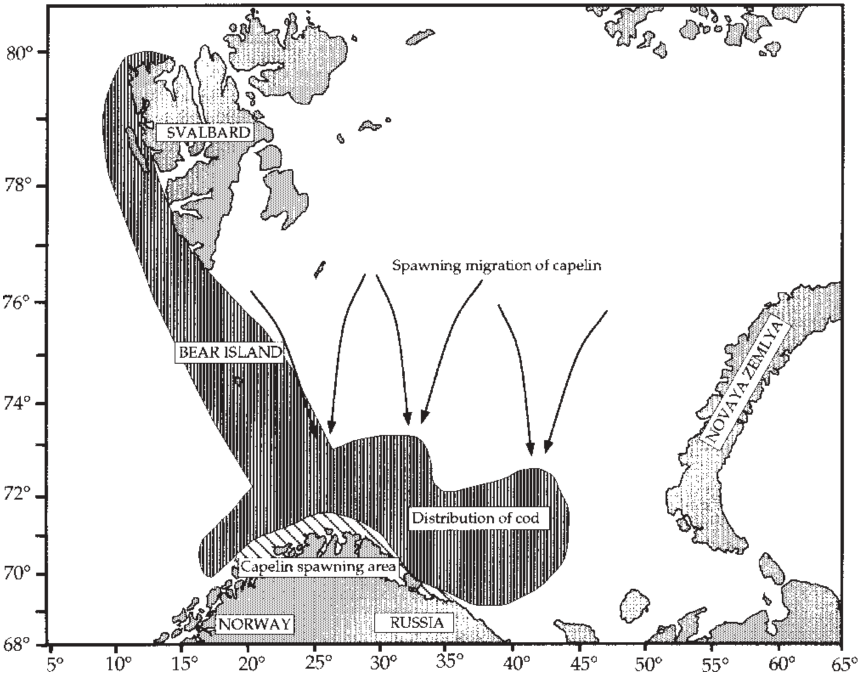

*Figure 1. Barents Sea capelin spawning migration.*

# Methods

## *Maturation Model*

The relative number of fish in each length group measured during the September cruise that will mature and spawn the next spring is modeled by:

$$m(l) = \frac{1}{1 + e^{4P_1(P_2 - l)}}$$

If the total number of fish in length group l for a given age and length is n(l), the number of maturing fish is $m(l)\ n(l)$ and the number of immature fish is $[1 - m(l)]\ n(l)$. $P_2$ is the length at 50% maturity and $P_1$ is the change of maturation with length at $P_2$.

Because the length distributions of various age groups are different, $m(l)$ affects not only the number of fish in each length group for the two maturation components, but also the age composition. The parameters will be estimated by comparing the effect of applying the above function to the total stock at the next September cruise. It is customary to assume total spawning mortality. Hence the maturation parameters determine not only the size and the age composition of the maturing component, but also the estimated yearly natural mortality and growth.

### *Estimation of empirical maturation parameters*

It is difficult to use empirical maturation data directly, since it is not known what degree of maturation corresponds to spawning the next spring. However, these data give information as to the shape of the maturation curve, i.e., $P_1$.

Two time series of maturation data from the yearly trawl-acoustic survey in September exist, both based on visual inspection of the gonads: a maturity scale based on the gonad volume (referred to in this paper as the "old" method) and a maturity scale based on the development of the eggs (referred to in this paper as the "new" method). The latter method is only applicable for female capelin. Both methods are documented in Institute of Marine Research instructions (Anon. 1996b), the latter also by Forberg (1983).

All samples are weighted with the integrator value. The empirical maturation function is calculated as the ratio of the length distribution of fish in a given maturity stage and higher maturity stages to the total length distribution. The parameters are found by minimizing least squares. The terms in the least squares function are weighted with the number of fish in each length group that actually are used for the determination of maturity. All samples from the period 1972-1995 are lumped together. The underlying assumption is that the maturation parameters are properties of the species that do not depend on endogenous or exogenous factors. This rather primitive view on maturation will later be challenged, but may at the moment serve as a basis for our understanding of the population dynamics of the Barents Sea capelin.

In Figures 2 and 3 the data are given along with the parameter estimates and the empirical maturation curves for the new and old method, respectively. The estimated maturation function fits the data remarkably well. It will later be shown that the value of $P_2$ is estimated in the range 13.5-14.5 cm, and therefore the value of $P_1$ to be taken from the empirical estimations should be selected among the values having values of $P_2$ in this range. The parameter values vary with maturity stage and age. The analysis will be centered around age 3, because at this age the total number of mature fish is most sensitive to the maturation function. At age 2 most of the fish will be immature and at age 4 most of the fish will be maturing.

There is a tendency for a negative correlation between $P_1$ and $P_2$; i.e., as the 50% length at maturity decreases, the slope increases. Thus, the values of $P_1$ used in the model should be selected at a value of $P_2$ at or close to the outcome of the estimation. It will turn out that the new maturity stage 31 for females and the old maturity stage 2 for males are best suited, giving $P_1$ values of 0.42 and 0.31, respectively. The data also

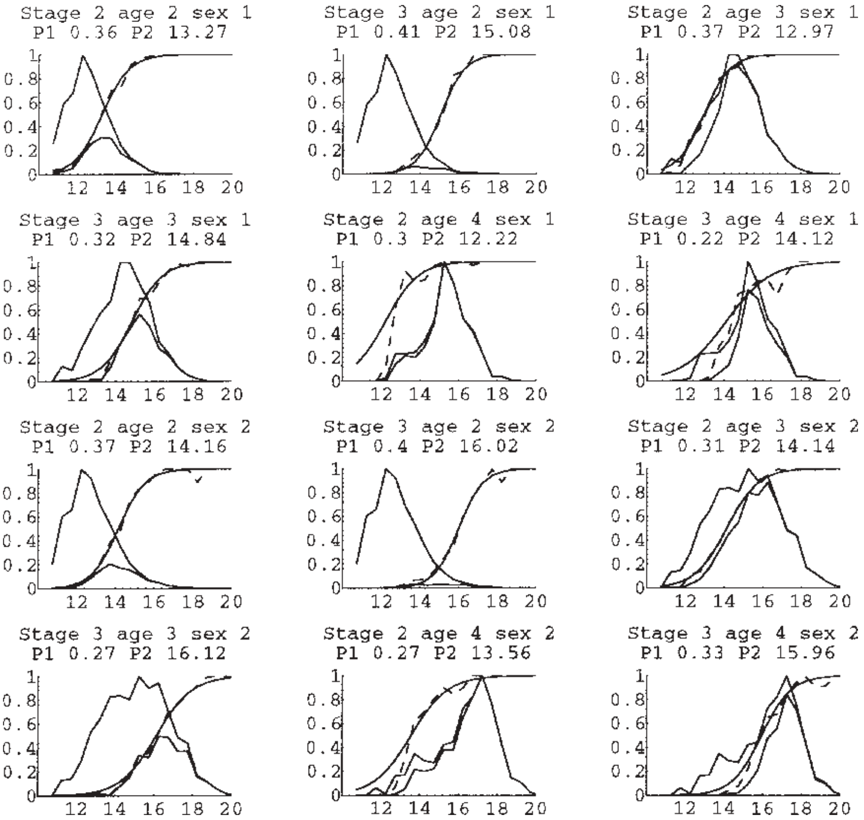

*Figure 2. Maturation using a maturation stage based on visual assessment of gonadal size. Solid lines: Total length distribution, length distribution of mature fish, and empirical maturation function. Dashed line: Fitted function.*

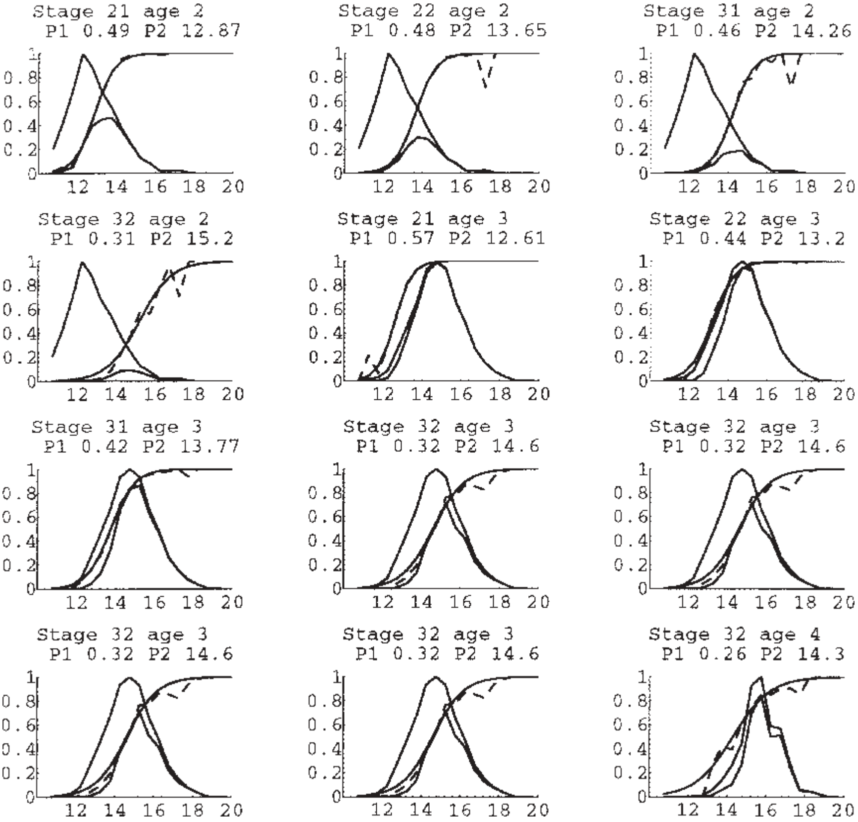

*Figure 3.* *Maturation using a maturation stage based on visual assessment of gonadal development (females). Solid lines: Total length distribution, length distribution of mature fish, and empirical maturation function. Dashed line: Fitted function.*

give evidence for 0.5 cm greater length at maturity for female 2-year-old capelin than for older female capelin, which is used in the model.

## Estimation of length at maturity

Different maturation parameters for males and females are assumed, since because there is a large difference in growth between the sexes there is no reason to assume that the maturation by length parameters are the same. Both the initial data and the data used for constructing the likelihood function are sex-disaggregated and therefore a sex-dependent estimation is possible. However, the catch is not determined by sex. This introduces some parameter correlation, so the estimation is done iteratively.

The estimated parameters will to some extent be dependent on the natural mortality because the catch is not determined by sex. The assumption of the natural mortality being constant over time seems too strong so the natural mortality cannot be entered simply as a third parameter. Rather, the natural mortality is determined by demanding that the number of simulated 3-year-old capelin equals the number of measured 3-year-old capelin. The number of simulated 3-year-old capelin is only weakly dependent on the maturation parameters, since the overall maturation of the 2-year-old capelin the autumn before is low. The natural mortality is calculated each year and applied also for older capelin.

The number of 5-year-old capelin in the autumn is generally low and the number of 3-year-old capelin in the autumn is determined by the estimated mortality. Therefore, the object function is chosen to be the sum of squared deviations of the simulated number of 4-year-old capelin to the measured number of 4-year-old capelin, weighted by the inverse of the variance.

There has not yet been any study of the variance of the September estimate taking into account the most important sources of uncertainty. In last year's cruise report the various sources of error are listed, with the aim of a later quantitative study (Anon. 1996a). In the present paper the variance from identifying echo recordings is assumed proportional to the total number of fish at low stock levels and constant at high stock levels, plus a small constant term:

$$\mathit{VarianceIdentification} = 10\ \mathit{TotalNumber} / (5 + \mathit{TotalNumber}) + 0.5$$

where the unit is billion fish. The variance of number of fish by age and sex from errors in biological sampling is supposed proportional to the measured values, which is equivalent to assuming a multinomial distribution with many bins. It should in the future be possible to arrive at better quantitative estimates of these two, and other, parts of the total variance through resampling techniques.

Figure 4 shows the value of the objective function over the investigated parameter range. The most likely values are $P_2 = 13.80$ for females

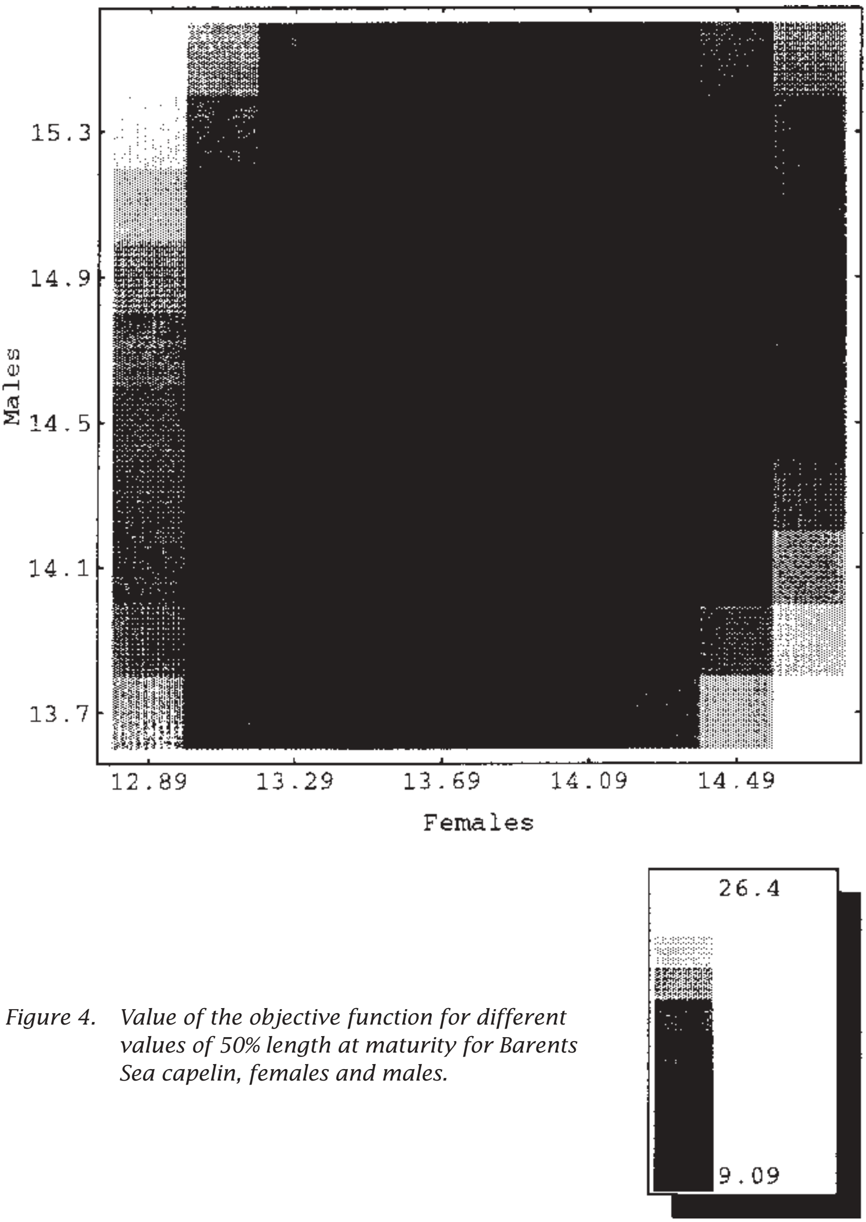

*Figure 4. Value of the objective function for different values of 50% length at maturity for Barents Sea capelin, females and males.*

and $P_2 = 14.61$ for males. The expectation values are $P_2 = 13.69$ for females and $P_2 = 14.53$ for males.

## Projecting Time of Spawning from September

During the period January-March the mature capelin migrates across the distribution area of the northeast Arctic cod stock to reach the southern coast off the Barents Sea to spawn. Following the cod-capelin submodel of the larger IMR area-distributed model for the Barents Sea, Multspec (Bogstad and Tjelmeland 1995), the predation on capelin from one age group of cod is formulated as:

$$Cons = G \frac{CapBio}{P + CapBio + OthFood} NCod \times WCod^{0.802}$$

*Cons* is consumption in kg per month, *Ncod* is number of cod in billions and *Wcod* individual weight in kg. The expression above is multiplied with a temperature effect: $\exp(0.104\,T - 0.000112\,T^3 - 1.5)$ where in this paper the temperature $T$ has been set constant to 5 degrees. The maximum consumption parameter $G$ and the predation half-value parameter $P$ are previously estimated using Multspec at 1.21 kg per month and 0.0054 metric tons per square nautical mile, respectively (Bogstad and Tjelmeland 1995). The predation half-value refers in Multspec to concentration of prey and is estimated from data having considerable contrast within one and the same year, and is thus difficult to interpret in the area-integrated context of the present paper. The biomass of capelin, *CapBio*, is converted to concentration using an effective area size determined by demanding that the sum of spawning stocks in the period 1984-1992 equals the sum of spawning stocks calculated by Multspec. The variation in the ratio of spawning stocks found using Multspec and the present model is interpreted as uncertainty induced by not taking the geographical dimension into account. The time series of these ratios for the same maturation parameters as used by Multspec is stored. During simulations one value is drawn at random with equal probability and used as a scaling factor for the spawning stock. The amount of other food, *OthFood*, is set to 0.5 million metric tons and converted to concentration by dividing by the effective area size.

For the number and weight at age of the cod stock we used the same numbers used by the ICES Arctic Fisheries Working Group in 1995 (Anon. 1996c). It should be noted, however, that prior to 1983 the weight at age used by this working group is constant. It is assumed that only immature cod preys on capelin during the period January-March, since the mature cod stock migrates to the spawning grounds during this period. The maturity ogive for the cod stock is also taken from the working group. The size-dependent suitability function in Multspec is approximated by assuming that only cod of age 3 years and older prey on mature capelin.

## Long-Term Projective Runs

Associated with each value of $P_1$ and $P_2$ there are historical series of maturity by age and natural mortality, which are stored for each box in the maturation parameter space and from which values are drawn at random during long-term simulations into the future. Also, from the historical series of spawning stocks corresponding to each value of $P_1$ and $P_2$ historical values of the recruitment half-value parameter $H$ in the Beverton-Holt recruitment function

$$R = R_{max} \frac{S}{H + S}$$

are calculated. $R$ is the recruitment as 2-year-old capelin, $S$ is the spawning stock biomass and H is a parameter that characterizes the spawning conditions. $R_{max}$ is, somewhat arbitrarily, set to 1.5 times the maximum observed recruitment. From the historical series a value of $H$ is drawn at random each year during the simulation, i.e., it is assumed that the recruitment follows a Beverton-Holt formulation within one and the same year. Later an attempt will be made to model the historical values of the half-value parameter $H$ as a function of predation and environmental variables, as previously attempted by Tjelmeland (1995) and Ulltang (1996) for northeast Arctic cod. The mature capelin is supposed to die after spawning.

The number of 2-year-old capelin will be taken for the recruits, since there is evidence of underestimation of the 1-year-old capelin in earlier years (Gjøsæter, this symposium).

During repeated runs into the future first a value of $P_2$ will be drawn using the results in Figure 3, where the probability of drawing the value in the center of each box is proportional to exp(–*obj*), where *obj* is the value of the objective function in the box. Then the corresponding historical series of natural mortality, maturation ogive, and recruitment half-values stored for this box are selected.

## Influence from Herring on the Capelin Stock

The collapses of the capelin stock coincide with inflow of rich year classes of herring into the Barents Sea. The herring hamper capelin recruitment and the highest values for the recruitment half-value occur in herring periods.

Two different scenarios are used: (A) the herring occurs as frequently in the Barents Sea as it did from 1950 to present, and (B) the herring occurs as frequently as it did from 1983 to present. Scenario A gives a probability of 0.10 and scenario B a probability of 0.30. However, no more than 3 years of herring 0-group in a row is permitted. A herring year class is assumed to hamper capelin recruitment for 3 years. The presence of herring is modeled by drawing at random one of the six highest recruitment half-values, corresponding to presence of herring in 1983-1985 and 1990-1992; 1992 is the last year for which a recruitment half-value is calculated.

### *Exploring Harvesting Strategies*

Given a long-term model, different harvesting strategies may be explored. This paper is centered around finding an optimal value of the spawning stock to be used as a target biological reference point. It distinguishes between two different situations as to the predation by cod on mature capelin: (1) the model represents the reality, of which the manager has perfect information; and (2) the model represents the reality, but the manager's model of the predation from cod is represented by one single number for the winter natural mortality.

All runs start in 1995, which is used as the last year of data. In this year the capelin stock was very low, but in all simulations it did rebuild. The simulations are run until the year 2100 and the catch from the first 20 years is dropped in order to avoid initial transients. There is only catch on the mature population during the spawning migration in the period January-March and no catch on the total stock in the autumn. Growth in the period September-March is neglected, with an exception for the comparison between the present model and Multspec. Also, variable growth of immature capelin is neglected and the weight at age for the starting year 1995 is used throughout the simulation period. There is no catch limit and it is assumed that the managers know the autumn stock with infinite precision.

## Results

Figure 5 shows the catch meaned over the simulation period and the replicates for herring scenario A. The highest long-term mean catch of about 0.75 million metric tons is found for a target spawning stock of about 0.4 million metric tons if predation from cod is taken into account. The long-term mean catch is about half of what was estimated by Hamre and Tjelmeland (1985) using data from the earlier period when there was no herring in the Barents Sea, while the optimum spawning stock is about the same. In the present paper the long-term mean catch is about the same as that estimated by Tjelmeland and Bogstad (1993) while the optimal target spawning stock is considerable higher. The latter result may be due to either the inclusion of the herring period 1990-1992 or to a different recruitment model being used in the present paper.

If a constant monthly mortality of 0.15 is used for the winter period the perceived optimum is lower and the perceived long-term mean catch is higher while the realized long-term mean catch is lower. If a constant mortality of 0.05 is used the perceived optimum is somewhat higher,

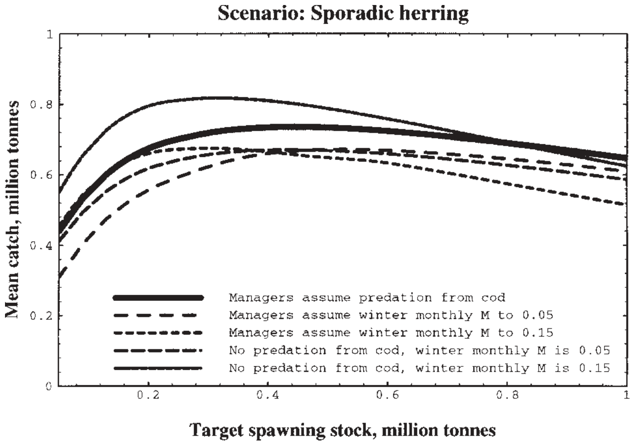

*Figure 5. Mean long-term catch for different values of the target spawning stock when herring occurs as frequently as in the period 1950-1995.*

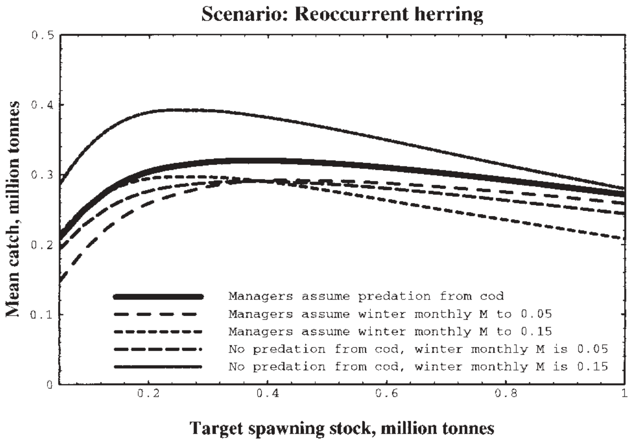

*Figure 6. Mean long-term catch for different values of the target spawning stock when herring occurs as frequently as in the period 1983-1995.*

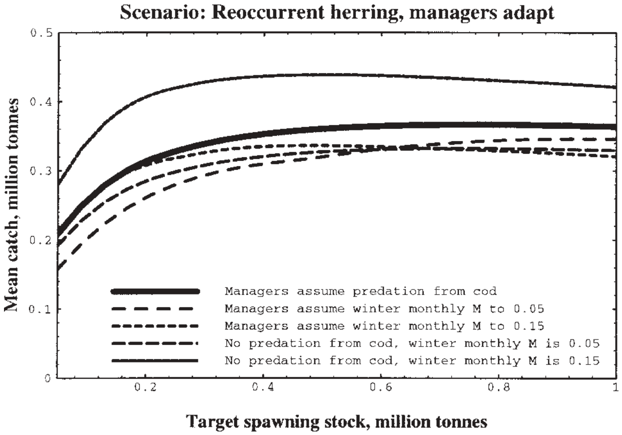

*Figure 7. Mean long-term catch for different values of the spawning stock when herring occurs as frequently as in the period 1983-1995 and when a fixed target spawning stock of 0.1 million metric tons is used when herring are present in the Barents Sea.*

while both the perceived and realized long-term mean catch is lower than when predation from cod is taken into account.

The mean long-term catch for herring scenario B (Figure 6) is about 0.3 million metric tons, more than halved with respect to scenario A. The optimum target spawning stock is the same, however, as is the difference between taking into account predation from cod and not taking into account predation from cod.

The amount of herring present in the Barents Sea is known from a cruise in August-September at the time (October-November) when the management decision is taken. Since presence of herring will hamper capelin recruitment to the extent that the recruiting year class will be poor no matter how large the spawning stock, a possible management strategy might be to aim at a low spawning stock of capelin when there is herring present in the Barents Sea and a high spawning stock when herring is not present in the Barents Sea. Figure 7 shows the result of exploring this strategy. In presence of herring the target spawning stock is set to 0.1 million metric tons and different levels of the target spawning stock are tried when herring is not present. Herring scenario B is used. This management strategy increases the mean long-term catch by about 0.5 million metric tons. The mean long-term catch increases with target spawning stock up to 0.4 million metric tons, as in the previous case. However, below 1.0 million metric tons there is in this case no decrease in catch with increasing spawning stock. Also in this case the management performs better by taking into account predation from cod.

## Discussion

The simulation results show that the management of Barents Sea capelin indeed can be improved by multispecies modeling. However, no drastic improvements can be anticipated before the recruitment dynamics is better understood, especially how herring influences recruitment. The results suggest that the target spawning stock should not be below 0.4 million metric tons, which is in agreement with the harvesting strategy that has been used since the capelin stock became regulated by total allowable catch in 1978.

Only the mean long-term catch has been investigated. However, in practical management one would also be interested in management strategies that led to as few years as possible with no catch, especially since the capelin is highly price elastic because moderate amounts of catch can be sold for consumption. Inclusion of this aspect may alter the results. Also, in the present paper no considerations are given to the value of capelin as source of food for cod, which would shift the preferred target spawning stock to higher levels.

One should be aware that the perceived optimal spawning stock when the managers do or do not take into account predation from cod are not directly comparable. What is of interest is the difference in suggested quota that these two different modeling approaches would lead to in a given situation. Using a high natural mortality instead of modeling the predation from cod will lead to a low optimal spawning stock but not necessarily to a high quota. The present paper has been limited to investigating whether taking into account multispecies effects will matter for the management of the Barents Sea capelin, and a more detailed comparison between the year-to-year performance of different modeling approaches is deferred to the future.

All parameters in the model are determined from data, with two exceptions. The assumption of total spawning mortality has poor basis in data but stems rather from biological considerations and non-quantified observations of large amounts of dead male capelin on the shores after spawning. Still one might assume that some capelin, supposedly predominantly females, will survive the spawning as has been suggested by Russian investigators (Pers. comm., T. Lebskaya, PINRO, Murmansk, Russia). However, it is likely that very few of these will survive the return migration over the cod stock. Hence a possible survival of some capelin will only to a small degree affect the present model, but might be of some significance when the capelin's significance for cod is studied. Furthermore, the assumption of the maximum possible recruitment being 1.5 times the maximum observed recruitment is rather speculative. Recent work on herring using the same recruitment model (Tjelmeland 1996) shows that the exact value of this parameter does not significantly affect conclusions about management strategy.

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# Copepod Nauplii Abundance in an Alaskan Glaciated Fjord During Spring Walleye Pollock Hatch in 1988 and 1991

**A.J. Paul, J.M. Paul, and L.A. Clayton**
*University of Alaska Fairbanks, Institute of Marine Science, Seward, Alaska*

## Abstract

Copepod nauplii were sampled in 1988 and 1991 to examine the temporal variability of their abundance along the length of a Gulf of Alaska glacial fjord during the spring hatching of walleye pollock, *Theragra chalcogramma*. During 1988 the numbers of copepod nauplii 150-350 µm long coexisting with the pollock larvae were typically 2-15/liter in April and exceeded 20/liter thereafter. After the middle of May nauplii counts >40/liter were common in 1988. Walleye pollock were abundant during 21 April to 18 May with peak abundance on 5 May in 1988 in the fjord. During most of the period when pollock larvae were present concentrations of copepod nauplii, of the size they prey on, exceeded 20/liter. The 1988 year class of pollock in the northern Gulf of Alaska was a large one, indicating high early-stage survival.

In 1991 the number of nauplii 150-350 µm long was typically <5/liter in April and 5-19/liter during May. It was not until mid-June that counts >20/liter existed. In 1991 peak abundances of pollock larvae in Resurrection Bay occurred on 16 April with a second peak on 4 June. In 1991 copepod nauplii were generally present at <10/liter when pollock larvae were most numerous. As 2-year-olds the 1991 year class was not abundant, suggesting that there was low survival of young-of-the-year fish.

In 1988 copepod nauplii were numerous and pollock larvae hatched in synchrony with the spring increase of their prey. In 1991 the pollock larvae hatched earlier than usual into a poor prey environment. The 1988 spawning gave rise to a strong year class, while the 1991 year class was weak. These contrasting conditions suggest that the match-mismatch predator-prey hypothesis was applicable for larval walleye pollock in 1988 and 1991.

# Introduction

Along the northern Gulf of Alaska coast there are numerous glaciated fjords and embayments. While European fjords have been identified as highly productive nurseries for larval fish (De Silva 1973, Lie 1978, Carmo Lopes 1979, Strickland 1983), Alaska's glaciated fjords have not been studied in much detail. Fisheries scientists believe that recruitment in planktonic fish larvae is regulated largely through variations in predation pressure and growth rates (Ware 1975). Growth rates of fish larvae are related to prey concentrations (Haldorson et al. 1989). Few studies have described the abundance of prey for larval fish in Alaska's many glaciated bays.

This survey measured the abundance of copepod nauplii along the length of a glaciated fjord, Resurrection Bay, in the northern Gulf of Alaska during spring of 1988 and 1991. Concurrently there was sampling for the larvae of walleye pollock, *Theragra chalcogramma*. Nauplii abundance is compared to published values for prey concentrations required by pollock. Pollock is the most abundant icthyoplankter in the study area (Müter 1992) and its feeding biology has been described (see Hillgruber et al. 1995). Thus, it was a fitting species by which to judge the suitability of the fjord as a nursery area for larval fish that feed on copepod nauplii.

# Methods

## *Study site*

All work was done at the head of a line of oceanographic stations of the University of Alaska's Institute of Marine Science, known as the Seward Line (Figure 1). The study area, Resurrection Bay, is a fjord estuary approximately 30 km long and 6-8 km wide, oriented in a north-south direction. Its 290-m-deep inner basin is separated from the outer reaches of the fjord by a 250-m-deep sill. The fjord opens onto the Gulf of Alaska. The seaward station R4 is influenced by the Alaska Coastal Current (Müter 1992) and R1 is near a river mouth. Previous information on the physical oceanography of the study area is included in Heggie et al. (1977) and Müter (1992). Generally there is temperature and salinity stratification in the upper water column beginning in April from summer warming, snow and glacier melt, and rain. The depth of visibility measured by a Secchi disk is typically 2-7 m during April and May. By the end of May there is a strong pycnocline at 20-25 m of depth (Heggie et al. 1977). The geology of the area protects the bay from winds, so the mixed layer depth is generally shallower than the pycnocline. Zooplankton and larval fish are subjected to advection forces that could transport them both into and out of Resurrection Bay (Müter 1992) and the copepod community consists of both deepwater Alaska Coastal Current species and neritic indigenous species.

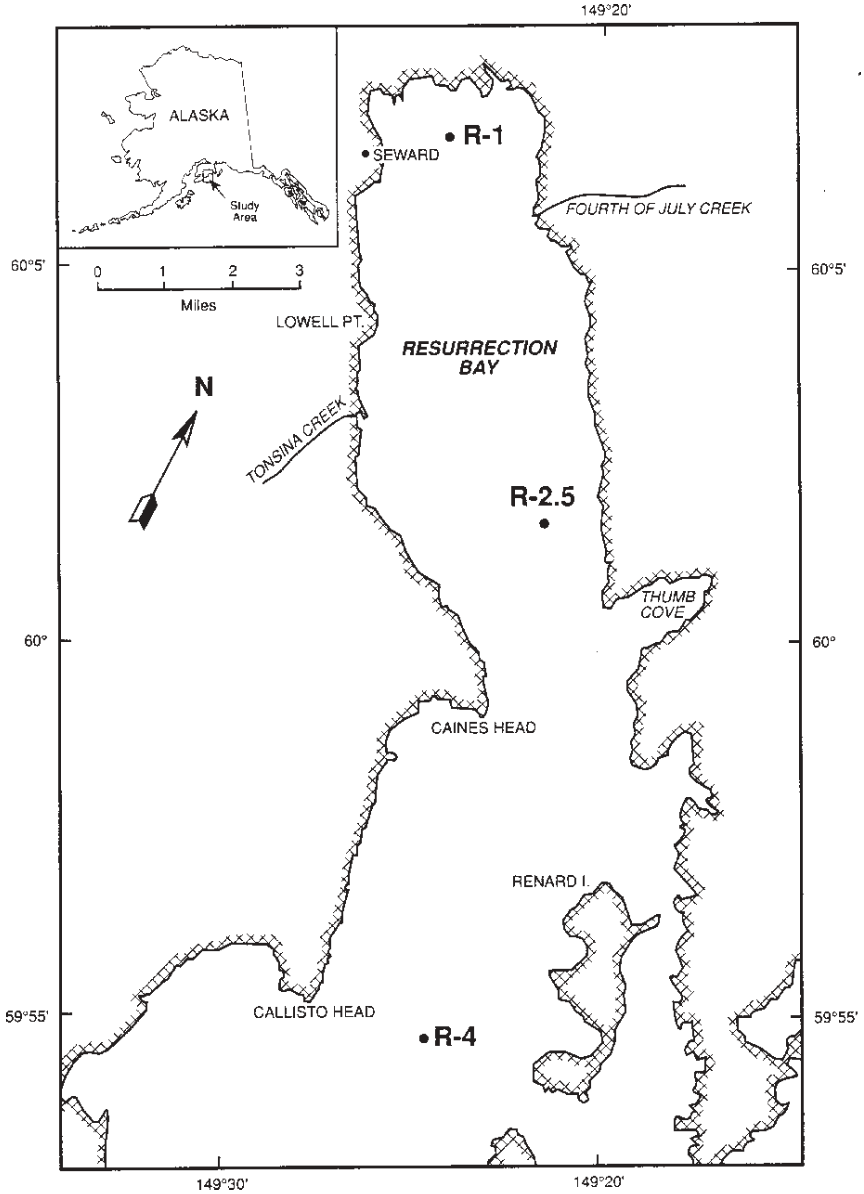


*Figure 1. Map of sampling stations for fish larvae and copepod nauplii in Resurrection Bay, Gulf of Alaska, during spring 1988 and 1991.*

### *Timing of pollock larvae*

Larval walleye pollock were sampled to determine when they were in the plankton. The larval fish sampling was not intended to be a population estimation. Larval fish were collected with a depth-gage-equipped 1-m Tucker trawl (NIO 505-µm mesh net) towed double obliquely from depth to the surface at station R1 only. In 1988 larval fish samples were collected every other week from 31 March to 20 July. During all the sampling in 1988 the tow wire was released to a depth of 35 m. The volume filtered was calculated from the flowmeter attached to the mouth of the net. In 1988 the average amount of water filtered for all the tows was 671 $m^3$ (SD = 393).

In 1989 an independent study found that in Resurrection Bay larval pollock were commonly found to a depth of 70 m (Müter 1992), so in 1991 the NIO net was towed to an average depth of 82 m (SD = 20). In 1991 the average amount of water filtered for all the tows was 156 $m^3$ (SD = 43). In 1991 larval fish were collected weekly from 2 April to 9 July. All samples were preserved in 10% formalin and populations are presented as number per cubic meter.

### *Copepod nauplii*

During 1988 and 1991 copepod nauplii were sampled at a depth of 10 m at stations R1, R2.5, and R4 (Figure 1) during the spring and early summer. Larval pollock are visual feeders, and they have to feed near the surface where the nauplii are (Paul 1983, Haldorson et al. 1993). Each week a single 10-liter water bottle sample was taken at each of the three stations. All water bottle samples were taken at a depth of 10 m. Water from the bottle was passed through a 64-µm-mesh bag net and the concentrated sample was preserved for microscopic analysis. Walleye pollock larvae select nauplii prey with body lengths primarily 150-350 µm long (Dagg et al. 1984). In this study nauplii were measured with an ocular micrometer and those with body lengths 150-350 µm were recorded, as well as the total number of nauplii.

## Results

### *Copepod nauplii*

Temporal trends in copepod nauplii concentrations were similar to those observed in other areas of Alaska, with low abundances in early spring followed by increasing numbers as time passed. The counts of copepod nauplii of all lengths are shown in Figure 2. During April 1988 copepod nauplii 150-350 µm in length were present at concentrations of less than 10/liter during the first 3 weeks of April (Figure 3). Throughout May 1988 they were above 20/liter and periodically they were over 100/liter. Nauplii 150-350 µm long were most abundant in the 18 May samples which contained some very high nauplii counts, with mean

*Figure 2. Total number of copepod nauplii at depth of 10 m at three stations along the length of Resurrection Bay, Alaska, during 1988 (station R1 ●, station R 2.5 ■, station R4 ▲).*

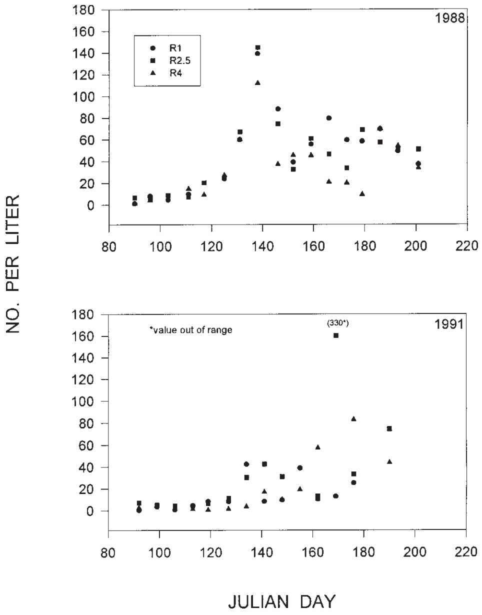
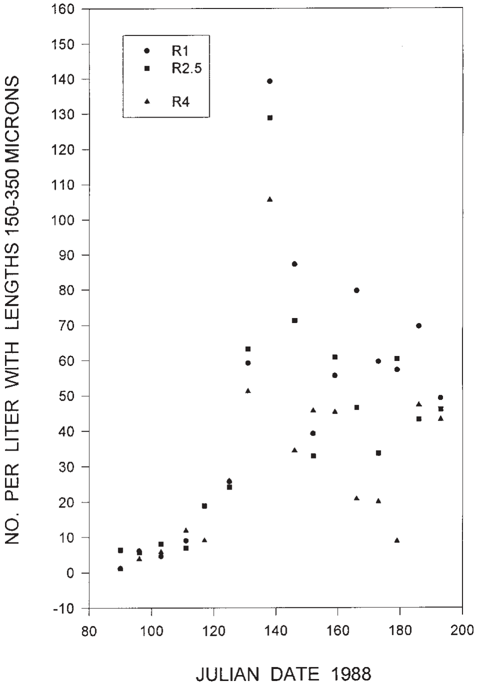


*Figure 3. Number of copepod nauplii with body lengths of 150-350 µm captured at depth of 10 m at three stations in Resurrection Bay, Alaska, during 1988 (station R1 ●, station R2.5 ■, station R4 ▲)*



concentrations of 124/liter. There was not much consistency in the station location with the most nauplii. Nearshore station R1 had the highest number of nauplii 150-350 µm long 58% of the time. Offshore station R4 had the highest number of nauplii in 13% of the samples.

In 1991 the 150-350 µm nauplii were typically <5/liter until mid-May and did not exceed 20/liter until mid-June (Figures 2, 4). After 18 June counts >40/liter were observed at the two seaward stations. During April and May nauplii counts were generally similar at the three stations, but after the last week of May the highest counts were usually seen at R4, the most seaward station. The largest concentration of 150-350-µm nauplii was 285/liter at station R4 on 18 June.

### *Timing of pollock larvae*

In 1988 pollock larvae exhibited a strong peak of abundance indicating a large synchronous spawning event (Figure 5). However, because samples were taken every 2 weeks the true peak period of spawning may have been missed. Pollock were most abundant from late April though mid-May, with a maximum count on 5 May (Julian day 125). At that time average copepod nauplii concentrations exceeded 20/liter (Figure 5). All larvae hatching after 5 May coexisted with nauplii concentrations >30/liter (Figure 5).

In 1991 pollock larvae were most abundant on 16 April (Julian day 106) and there were less than 0.2/m$^3$ for most of the rest of the sampling period. From April to mid-May, the number of nauplii coexisting with the larvae were typically under 10/liter (Figure 6). On 4 June there was another peak of pollock larvae at 42/100 m$^3$ when nauplii were slightly more abundant. During the last week of June and the first week of July nauplii exceeded 20/liter, but there were few pollock larvae to benefit from the increase in prey (Figure 6).

## Discussion

Generally it is thought that larval fish have better survival rates if they hatch during the period when copepod nauplii are most abundant. In the northern Gulf of Alaska peak abundances of pollock larvae typically occur between the third week of April and the first week of May (Müter and Norcross 1994). In 1988 pollock larvae were most abundant on 5 May and entered the first-feeding stage with nauplii >20/liter and increasing rapidly. According to previous studies (Haldorson et al. 1989), larval pollock growth rates approach maximum when nauplii concentrations exceed 20/liter. In addition, there were still pollock larvae in the samples from mid-May into early June of 1988, so some of them began feeding when their prey was even more abundant. Moreover, the temperature in the upper 70 m of the water column was about 2°C warmer than in 1991 (unpubl. data). The number of 2-year-old pollock derived from the 1988 spawning was relatively large (Figure 7), indicating good larval survival.

*Figure 4. Number of copepod nauplii with body lengths of 150-350 μm captured at depth of 10 m at three stations in Resurrection Bay, Alaska, during 1991 (station R1 ●, station R2.5 ■, station R4 ▲).*

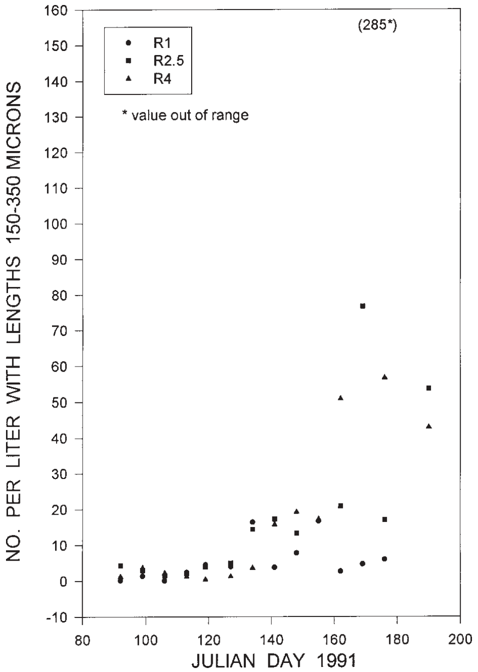


*Figure 5. Abundance of walleye pollock larvae (Theragra chalcogramma) at station R1 in Resurrection Bay, Alaska, during spring 1988 (●) and average number of copepod nauplii 150-350 μm long (■) at depth of 10 m.*

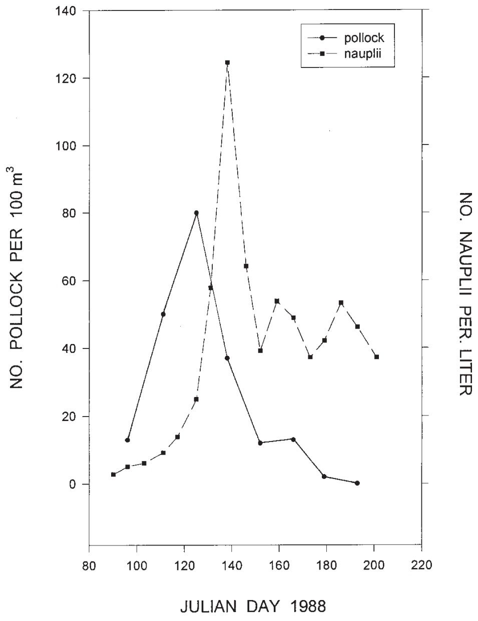


*Figure 6. Abundance of walleye pollock (Theragra chalcogramma) larvae at station R1 in Resurrection Bay, Alaska, during spring 1991 (●) and average number of copepod nauplii 150-350 µm long (■) at depth of 10 m.*

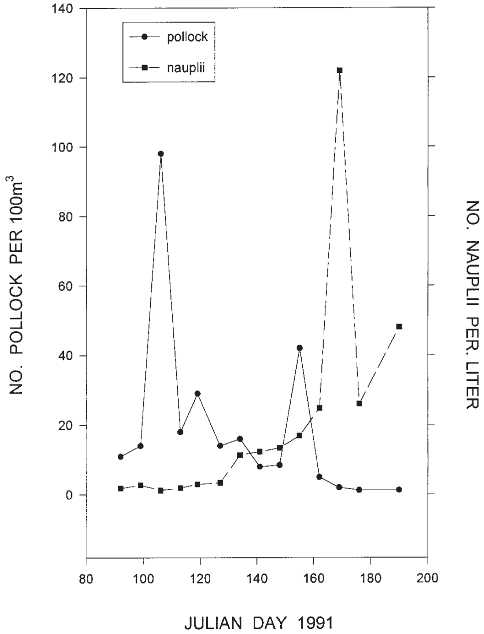
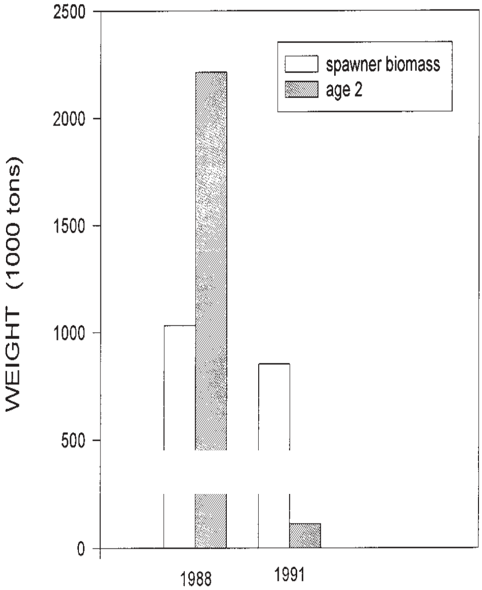


*Figure 7. Spawning biomass of walleye pollock in the northwestern Gulf of Alaska (clear bars) and the subsequent number of age-2 walleye pollock resulting from the 1988 and 1991 spawning (lined bars).*



During 1991, nauplii concentrations were often under 5/liter when pollock larvae were present. This was marginal feeding conditions for the larvae (Paul 1983) since saturation feeding probably occurs at prey densities >20/liter (Haldorson et al. 1989). In nearby Shelikof Strait, near Kodiak, 40% of pollock larvae in the 1991 year class were found to be starving (Theilacker and Porter 1994) and prey concentrations were <10/liter (Bailey et al. 1995).

In general, copepod nauplii abundances in Resurrection Bay were similar to those reported for unglaciated North Pacific pollock rearing grounds (Dagg et al. 1984, Haldorson et al. 1989, Nakatani 1991, Paul et al. 1991, Incze and Ainaire 1993, Bailey et al. 1995). The fjord probably benefits from having a resident neritic copepod population plus the transport of oceanic types into the area by the Alaska Coastal Current. This influx of oceanic copepods enriches the community of nauplii producers. The largest known concentrations of pollock larvae occur in the southeastern Bering Sea, and there nauplii (all sizes) typically occur at concentrations of 2-20/liter (Dagg et al. 1984). Competent larvae grow normally at nauplii concentrations of 20-25/liter (Paul 1983, Haldorson et al. 1989). Our observations for 1988 show that in Resurrection Bay counts of nauplii, of the sizes preferred by pollock larvae, frequently exceed 20/liter both at the head of the fjord and at its mouth. Growth rates of pollock larvae are related to nauplii abundance (Haldorson et al. 1989) and in Resurrection Bay their growth rates during 1989 were similar to those observed in other nonglacial nursery areas (Müter and Norcross 1994). In 1991, during April and May, there were far fewer nauplii than we saw in 1988. These observations suggest that in some years the glacially influenced embayments of the northern Gulf of Alaska are suitable nursery areas for walleye pollock larvae, providing them with prey concentrations high enough to insure maximal growth rates. In other years copepod nauplii prey in the fjord exist at concentrations too low for saturation feeding by pollock larvae.

Sampling at only 10 m depth precludes identifying the range of prey concentrations that coexisted with the pollock larvae, and it is probable that on some dates there were denser aggregations of nauplii at unsampled depths. However, there was consistency in abundance at the three stations showing the trends of high (1988) and low (1991) nauplii abundance. Also, the results show marked interannual variation in nauplii abundance when pollock larvae are present. In the future survival studies of specific cohorts relative to prey availability need to be done to understand the iimpact of interannual variations in nauplii standing stocks on recruitment success of walleye pollock.

## Acknowledgments

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# The Other F: Forage Considerations in Fisheries Management

**Robert L. Stephenson**
*Department of Fisheries and Oceans, Biological Station, St. Andrews, New Brunswick, Canada*

## Abstract

It is common fisheries evaluation and management practice to partition mortality into that resulting from fishing (*F*) and that from all other "natural mortality" causes (*M*). Forage considerations, or the trophic contributions made to predatory species, usually are considered part of a natural mortality rate, which most often is assumed to be a constant value. However, there has been increasing awareness, interest, and concern about the necessity to include forage considerations as a specific factor in resource evaluation of common prey species (e.g., herring), and as a quantifiable element in "ecosystem" or multispecies management. More recently there has been the call for explicit inclusion of forage considerations in management objectives and allocations. It is predicted that explicit consideration of forage issues will be required as the changing philosophy of management moves toward a precautionary approach. If so, primary forage relationships could be considered as a specific term in the partitioning of total mortality (the "other *F*"). In this paper I review some recent attempts to include forage considerations specifically in evaluation and management. The issue is complicated by a lack of information on the dynamics of noncommercial forage species, and on the degree of reliance on specific prey species by particular predators. Resolution of these issues requires both improved knowledge of the dynamics of forage species, and development of a context in which available information can be most optimally used in evaluation and management. It appears that proper consideration of the role of significant prey species as forage for other species represents an important, but as yet unarticulated, management objective.

## Introduction

By far the majority of papers contributed to the International Symposium on the Role of Forage Fishes in Marine Ecosystems dealt with biological attributes of forage fish species (e.g., distribution, population dynamics, behavior), or of the processes of foraging (e.g., predator-prey interactions). Although the increasing need to include forage fish considerations specifically in management was implicit in most papers, few gave this aspect any more than passing reference. An exception was the paper by Meyer (this volume) which discusses the treatment of forage fish considerations in environmental assessments, and makes the plea that forage fish work be made more relevant to end users and to fisheries management. In this paper I also attempt to move beyond consideration of forage itself, toward the inclusion of forage considerations in management.

Approaches to the management of fisheries, and to the care of aquatic systems generally, are changing. There is an increasing movement toward explicit consideration of the full range of impacts of management actions. With this will come more emphasis on forage issues.

Forage fishes, as defined for the purposes of this conference, are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. The forage issue should include not only the dynamics and management of these "forage species," but also management in reference to forage; for example, how these species are managed in relation to their predators and prey.

## Evidence of the Growing Forage Issue

There has been increasing public awareness of the importance of species at lower levels of the food web (including forage species), and increasing awareness of interactions and tradeoffs in management involving forage species. These have been reflected in questions from interested parties, resulting in articles in the media, and in political issues, such as: criticism of proposed development of new fisheries for species (e.g., krill) which are considered important forage species; criticism of existing fisheries on forage species (such as herring, sand lance, capelin), on the basis that fisheries are reducing forage for segments of the ecosystem such as marine mammals or birds; suggestions that fisheries on forage species (such as herring) be reduced to allow for the recovery, or maintenance, of other fish stocks (such as depleted groundfish stocks); and suggestions that management should be taking a more "ecosystem" or multispecies approach.

Stock assessment and advisory bodies face increasingly complex stock assessments, and increased requests from clients, as a result of forage considerations. Recent reports of the International Council for the Exploration of the Sea (ICES) Advisory Committee on Fisheries Management (ICES 1996a, 1997a), for example, illustrate the growing forage issue by consideration of items such as:

1. The effect of northeast Atlantic sand eel fisheries on local aggregations of sand eels in sensitive areas close to important wildlife assemblages such as seabird colonies. This request was the result of "public concern over the large-scale harvesting of fish species which constitute the prey of other fish, birds, and marine mammals" (ICES 1997b).
2. Assessments for Arctic cod, haddock, and capelin which had been revised due to progress in understanding the pivotal role of capelin abundance as a forage species for cod and haddock, and an increase in predation and cannibalism by cod in the absence of capelin (ICES 1997c; see below).
3. The recent issue of poor juvenile Atlantic salmon survival, perhaps the result of predation or of changes in available forage for juvenile salmon while at sea.
4. Changes in growth rates or maturity ogives presumed to be linked to forage, and of natural mortality of some species, resulting from multispecies VPA (MSVPA) calculations.

In the western Atlantic, there are questions regarding the impact of changing forage considerations of recovery of the 4VsW cod stock. The grey seal population has been increasing rapidly off eastern Nova Scotia. Cod is a forage species for seals, making up about 15% of the seal diet in spite of reduced cod abundance (Department of Fisheries and Oceans 1996). A model of grey seal predation on cod (Mohn and Bowen 1994) indicated that predation by seals on cod is substantial, and that it increased by about 12% in 1995 over 1994. The coincidence of an increase in predation with an apparent period of low production and reproduction for cod is considered to be increasing the ecological pressure on the cod population.

Similarly, there are questions concerning the impact of changes in community structure and forage relationships on Georges Bank off the northeast coast of the United States. Perturbations due primarily to heavy fishing pressure over the past four decades on Georges Bank are hypothesized to have resulted in a change in species composition, and energy flow (Sherman et al. 1981, Fogarty and Murawski In press). There have been major shifts in the forage fish assemblage (herring, mackerel, sand lance), and an increase in the abundance of species of low commercial value has been documented, with an apparent replacement of gadoid and flounder species by small elasmobranchs (dogfish and skates). It is hypothesized that a change in forage relationships may be further hampering stock recovery of commercially important groundfish.

It seems inevitable that future fisheries resource evaluation and management will require explicit consideration of forage and multispecies issues such as these.

## Forage Considerations . . . The Other F?

Past fisheries evaluation and management has included forage relationships along with other nonfishing or "natural" mortality. The usual approach has been to partition total mortality ($Z$) into that resulting from fishing ($F$) and that from all other "natural mortality" causes ($M$): $Z = F + M$. While forage considerations have been included in the equation, management has, of course, focused on fishing mortality. Natural mortality has most often been an assumed value (often 0.2) and has usually been assumed to be constant.

Increased consideration of forage relationships would require explicit consideration of mortality to key predators, so that total mortality would become the sum of fishing mortality, forage mortality, and other natural mortality: $Z = \text{Fishing} + \text{Forage} + M$. The creation of a specific term for forage mortality (the "other $F$") would raise the profile of this issue, and would provide the context for evaluation of the forage interactions (such as most of the studies described at this symposium). Perhaps more important, it would provide the focus for establishing management objectives which would guide decisions with respect to forage considerations.

It is anticipated that the "forage $F$" would be a composite of specific predator-prey relationships (e.g., a seal $F$, a murre $F$, a whale $F$, a cod $F$). It would probably not include all predation, but a number of specific interactions which are considered dominant or in some other way of particular importance to management. Specific consideration of these major relationships would ensure, for example, that the fishing $F$ does not compromise the forage $F$.

## Recent Attempts to Include Forage Considerations in Assessment and Management

The state of management with respect to forage issues is illustrated by the following recent examples from the north Atlantic.

### *Multispecies VPA*

The multispecies VPA (MSVPA) which dates from 1979, is one of the most successful multispecies models in fisheries (Magnusson 1995). Developed within the ICES community, it has been applied primarily in the North Sea and Baltic Sea (Sparholt 1991, ICES 1996b). In North Sea applications, it commonly includes four prey species (sprat, herring, Norway pout, and sand eel), two predators (saith and mackerel), and three species which feature both as predator and prey (cod, whiting, and haddock). MSVPA is a direct extension of single species models. It partitions total mortality ($Z$) , not only into $F$ and $M$; but $M$ into $M1$ and $M2$, where M2 is the predation mortality due to specific predators included in the model, and $M1$ is the residual natural mortality: $Z = F + M1 + M2$. $M2$ is calculated inside the model, taking into account prey availability, size , and suitability as prey for the predator.

Use of this model for the past decade has given considerable insight into the magnitude of feeding relationships. It has indicated that natural mortality rates for a number of forage species are higher than previously assumed, and are likely to be variable from year to year. These revised natural mortality estimates and knowledge of feeding relationships have been used in traditional single-species VPA assessments, but multispecies models (e.g., MSVPA) have not yet led to multispecies management (Sissenwine and Daan 1991, Magnusson 1995). This seems to be due to continued scientific uncertainties concerning complex feeding relationships, and perceived difficulties in gaining acceptance of multispecies management advice (Magnusson 1995).

The most recent report of the ICES Multispecies Assessment Working Group (ICES 1996b) describes two other models currently being developed for boreal systems: MULTSPEC (developed at the Institute of Marine Research in Bergen, Norway) which has modules to simulate many types of multispecies interactions in the Barents Sea, from primary production to marine mammals, and BORMICON (developed at the Marine Research Institute in Reykjavik, Iceland) which models cod-capelin interactions.

## *Cod, haddock, and capelin in the northeast Arctic*

Recent studies of the forage relationships in the Barents sea (e.g., papers in this volume by Tjelmeland, Bogstad and Mehl, Gjøsaeter) have indicated that a recent decline in capelin, a preferred forage species, has led to increased cannibalism by cod and increased predation by cod on juvenile haddock. Assessments have been modified to include cannibalism and predation terms based on stomach sampling to monitor this forage relationship (ICES 1997c). Advice for these species now considers the need for management of the three species in the context of their impact on one another.

## *Multispecies management off Iceland*

Multispecies biological, assessment, and harvesting models have been used to develop management strategies which include forage considerations in Icelandic waters (Stefansson et al. 1995). These have included management of cod in light of its impact on capelin and shrimp (forage) fisheries. Recent modeling studies have indicated that continued increase in whale populations will result in reduced cod production (a 10% reduction in the fishery is estimated), due to forage competition.

## Explicit Consideration of Forage Issues

Further impetus for consideration of forage issues in fisheries management comes from international agreements adopted by many countries in recent years, including the Rio Declaration on Environment and Development, the United Nations Conference on Highly Migratory Fish Stocks and Straddling Fish Stocks, and the FAO Code of Conduct for Responsible Fisheries. These agreements contain statements which can be transcribed into specific objectives regarding the need to include forage considerations in management. The Code of Conduct for Responsible Fisheries (FAO 1995a) is a good example. It states, under general principles:

> 6.5 ... should apply a precautionary approach widely to conservation, management and exploitation of living aquatic resources in order to protect them and preserve the aquatic environment, taking account of the best scientific evidence available. The absence of adequate scientific information should not be used as a reason for postponing or failing to take measures to conserve target species, associated or dependent species and nontarget species and their environment.

Further with respect to the precautionary approach, the Code states:

> 7.5.1 States should apply the precautionary approach widely to conservation, management and exploitation of living aquatic resources in order to protect them and preserve the aquatic environment. The absence of adequate scientific information should not be used as a reason for postponing or failing to take conservation and management measures.
>
> 7.5.2 In implementing the precautionary approach, States should take into account, *inter alia*, uncertainties relating to the size and productivity of the stocks, reference points, stock condition in relation to such reference points, levels and distribution of fishing mortality and the impact of fishing activities, including discards, on nontarget and associated or dependent species as well as environmental and socioeconomic conditions.

The topical move toward management based on the “precautionary approach” will require major change in the current approach to fisheries management. The precautionary approach requires use of the “best scientific evidence” and speaks of a broad consideration of impacts, and that “absence of adequate scientific information should not be used as a reason for postponing or failing to take conservation and management measures.” While forage does not appear to be mentioned explicitly in these agreements or in recent key papers on the topic (e.g., FAO

1995a,b; Garcia 1994, 1996), it is quite apparent that forage considerations are implied in this initiative which links fisheries management intimately with environmental management. The reference in the code of conduct to management of "associated or dependent species and non-target species and their environment" would seem to be a clear reference to forage considerations of the type discussed at this symposium. Further, the recent paper by Garcia (1996) resulting from a June 1995 consultation on the precautionary approach to capture fisheries, contains two particularly relevant practical guidelines: "Expand the range of fisheries models (e.g., bioeconomic, multispecies, ecosystem, and behavioral models), taking into account: (a) environmental effects, (b) species and technological interactions, and (c) fishing communities' social behavior" (guideline 14); and "develop scientific guidelines and rules for multispecies and ecosystem management as a basis for agreement on acceptable degrees of disturbance" (guideline 17).

## Context for Future Management

Multispecies management will be difficult. However, I suggest that multispecies consideration, including forage relationships, must be worked into management particularly under the precautionary approach. This can only be done if forage considerations become a part of specific objectives in management, under an appropriate management context, or framework.

A number of recent papers have pointed out the problems associated with management of fisheries generally, caused in part by the inherent complexity and variability of marine ecosystems, the unobservable nature of aspects of the natural dynamics of fish stocks, multiple and conflicting objectives, and management systems that are not responsive to required rapid change. In previous papers (Lane and Stephenson 1995, Stephenson and Lane 1995) we proposed adopting techniques developed in the field of management science to meet an urgent need to improve fisheries evaluation and management by moving toward management of multiple objectives. This calls for the merging of previously disparate disciplines of fisheries science, fisheries management, and management science into a new discipline, fisheries management science, which would involve "the rigorous application of the scientific method of problem solving in the development of strategic alternatives and their evaluation on the basis of objectives that integrate biological, economic, social, and operational factors into management decision making." This framework would facilitate the management of forage considerations which would become articulated as specific objectives, and which would be the subject of evaluation, management, and review.

Several forage species (e.g., herring, sardine, anchovy) are subject to large fluctuations and rapid change in the absence of fishing, and with fishing pressure become vulnerable to very rapid stock collapse. In these cases it is especially important not only to determine appropriate targets and thresholds, but also to use these in a management system which can react quickly (e.g., Stephenson 1997).

The major future issues concerning management with respect to forage considerations then involve both the dynamics of forage species, and the context in which forage can be considered in management. Important elements would appear to be as follows:

1. Improved biological basis for management of forage species:
    a. continued improved understanding of forage relationships and mechanisms (as demonstrated by most papers at this symposium), including better definition of preferences and prey switching;
    b. development of appropriate biological reference points for key prey (= forage) species and predators; and
    c. development of an expanded range of fisheries models (e.g., multispecies, ecosystem, and behavioral) with which to test scenarios regarding forage considerations.
2. Improved consideration of forage and multispecies consideration in management:
    a. development of management consistent with the precautionary approach,
    b. development of specific objectives which reflect forage considerations, and
    c. development of appropriate harvesting strategies which explicitly address forage issues.

## Acknowledgments

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# Role of Pacific Herring in the British Columbia Marine Ecosystem

**Jacob F. Schweigert**
*Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada*

## Abstract

Pacific herring, *Clupea pallasi*, is one of the most common forage fish species on the British Columbia coast. As for many forage species, the dogma has been that herring are critical to the growth and survival of the commercially important fish predators as well as seabirds and marine mammals. This paper addresses the hypothesis that the recruitment and survival of Pacific salmon, hake, cod, rock sole, or halibut is not dependent on Pacific herring abundance. In this study stock-recruitment modeling was used to investigate predator-prey interactions and environmental effects for the important herring stocks in northern and southern British Columbia and key predator species. Few statistically significant relationships were evident between predator recruitment and herring abundance whereas temperature was a significant determinant of herring recruitment to the southern area. In the north, a previously reported predator-prey link with cod was not evident but neither was the influence of any strong environmental forcing factor on herring recruitment. The results indicate availability of herring is important to the recruitment of a few predators but that this effect is difficult to detect statistically. Predation mortality appeared to have limited effects on herring recruitment but data on the abundance of juvenile predator stocks was not available which may be the critical determinant of prey recruitment success.

## Introduction

An understanding of the factors that determine population abundance is critical to the successful conservation and management of fisheries resources, and there has been ongoing debate about whether it is environment or some other factors which ultimately determine stock abundance (Skud 1975). For pelagic forage species it is often argued that environmental factors are the prime determinants of recruitment success (Cury and Roy 1989) and a number of studies have identified environmental variables that are related to Pacific herring recruitment in British Columbia waters (Stocker et al. 1985, Stocker and Noakes 1988, Schweigert and Noakes 1991, Ware 1991, Beamish et al. 1994, Schweigert 1995).

However, a dogma has developed over the past century that forage fish species are vital to the structure and stability of marine ecosystems because they are near the base of the food chain and are consumed at all the higher trophic levels. The underlying thesis is that biotic interactions are the prime determinants of reproductive success, yet few studies have addressed this question quantitatively at even the basic level of one predator-prey interaction (Anderson and Ursin 1977, Skud 1982, Walters et al. 1986, Collie and Spencer 1994, Ware and McFarlane 1995). The major difficulty has been in demonstrating the existence of a predator-prey relationship that has persisted over time. Pacific herring are ubiquitous throughout the British Columbia coast and provide forage for a vast array of predators throughout their life cycle spanning several levels of the food chain. As a result, quantifying any predator-prey interaction is complicated by variations in space and time of both predator and prey populations as well as in accounting for the impacts of other components of the system for which little or no information exists, e.g., other forage species, seabirds, and marine mammals.

The objective of this study was to address these questions by reexamining the predator-prey relationship postulated for Hecate Strait Pacific cod and herring by Walters et al. (1986). To do so, I included more recent data on key predator and herring abundance in Hecate Strait and in southern British Columbia and assessed prey-predator interactions for several species as well as the influence of environmental indices on these relationships.

## Methods

A major limitation of species interactions studies is the availability of estimates of stock abundance for both prey and their predators in appropriate time and space scales. Another difficulty is determining appropriate lags in interactions of predators and prey, since estimates of abundance are usually not available for all age classes, or the age-structure is not well known or estimated. To minimize confusion about time lags between spawning and recruitment, all data were standardized to the year class, the spawning biomass which produced it, and the predator or prey population which was impacting the year class (Table 1). To simplify analytical complications related to spatial resolution (since data for most species are not available at relatively small spatial scales) the British Columbia coast was divided into two areas, north and south of Vancouver Island (Figure 1).

To quantify the interrelationship of herring and potential predator species I adopted the analytical approach outlined in Walters et al. (1986). The adult stock was usually taken as the index of spawning stock each year and multiplied by an average effective fecundity (2,000 for herring and 1,000 for all other species) to provide a larval production estimate, $E_t$. An effective fecundity of 2,000 for herring represents about 10% of the average total fecundity and so accounts for some of the prehatching and early larval mortality, and as Walters et al. (1986) note precise levels of these losses are not critical to the analysis. The index of recruitment was then determined as $Z_t = \log$ (recruits/eggs) in each stock in year t. Then according to standard Ricker stock-recruitment theory, intraspecific competition should result in the linear relationship

$$Z_t = a - pE_t + W_t \qquad (1)$$

where $a$ represents an average density-independent mortality rate, $pE_t$ represents additional density-dependent mortality due to intraspecific competition or cannibalism, and $W_t$ is a random mortality component due to abiotic factors and biotic factors not related to stock size as indexed by $E_t$. A simple extension to (1) to reflect species interactions is:

$$Z_t = a - pE_t + qP_t + W_t \qquad (2)$$

where $P_t$ is the number of predators (for herring $Z_t$ calculations) or prey (for predator $Z_t$ calculations). The parameter $q$ should be negative if $P_t$ is the number of predators, and represents the fraction of the prey stock eaten by each predator prior to prey recruitment. The value of $q$ should be positive if $P_t$ is the prey stock, and is the effect of increasing prey abundance on predator fecundity or juvenile survival. The environmental variables, $W_t$, in the form of Amphitrite Point sea surface temperature in the south and Prince Rupert sea level in the north, were also investigated in these relationships. The relationship described in (2) is also the functional form found in the Anderson and Ursin (1977) model which is used to assess multispecies interactions in the North Sea. Walters et al. (1986) discussed some of the assumptions and pitfalls of the approach used here. Below is a description of the data series used in the analysis.

## Pacific herring

The herring stocks on the British Columbia coast are considered to be composed of five major migratory stocks plus a number of smaller stocks (Schweigert et al. 1996). The three northern stocks on the Queen Charlotte Islands, Prince Rupert, and Central Coast were treated as one unit following Walters et al. (1986) and are generally felt to occupy Hecate Strait during the feeding period. The Strait of Georgia and west coast of Vancouver Island stocks were combined into a southern unit

**Table 1. Summary of data sources used in the analyses. Variables are described in the text.**

| Area | Species | $R_t$ | $E_t$ | $P_t$ | Data source |
|---|---|---|---|---|---|
| South | Pacific herring | 1951-94 | 1951-94 | 1951-94 | Catch-at-age |
| | Pacific halibut | 1951-86 | 1951-86 | 1951-94 | Catch-at-age |
| | Pacific hake | 1962-93 | 1962-93 | 1960-94 | Catch-at-age |
| | Pacific cod | 1958-94 | 1958-94 | 1958-94 | Catch-at-age |
| | Chinook salmon | 1955-95 | 1955-94 | 1955-94 | Troll and sport catch |
| | Coho salmon | 1954-94 | 1954-94 | 1954-94 | Troll and sport catch |
| | Fraser R. sockeye | 1956-88 | 1956-88 | 1956-94 | Catch and escapement |
| North | P. herring | 1951-94 | 1951-94 | 1951-94 | Catch-at-age |
| | Pacific halibut | 1951-86 | 1951-86 | 1951-94 | Catch-at-age |
| | Pacific cod | 1958-94 | 1958-94 | 1958-94 | Catch-at-age |
| | Chinook salmon | 1955-94 | 1955-94 | 1955-94 | Troll catch |
| | Coho salmon | 1954-94 | 1954-94 | 1954-94 | Troll catch |
| | Rock sole | 1951-88 | 1951-88 | 1951-92 | Catch-at-age |

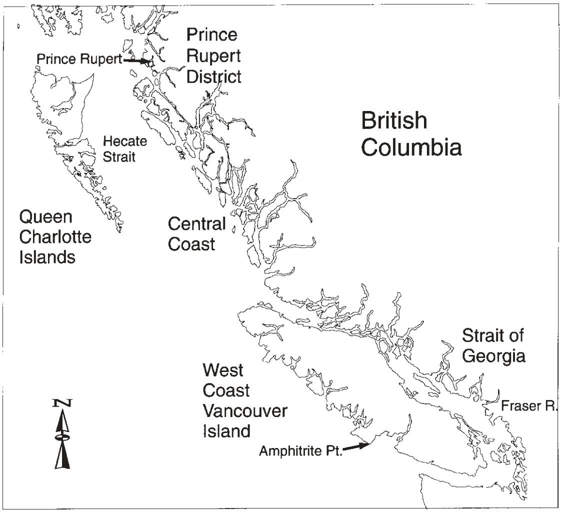

*Figure 1. The British Columbia coast detailing the study areas.*

and although this aggregation simplifies the analysis it makes the results more difficult to interpret since recruitment within these two southern stocks is not highly correlated (Schweigert 1995). Also, the Strait of Georgia stock is more than twice the size of the west coast of Vancouver Island stock, which could mask the effects of predation on recruitment to the latter. Estimates of numbers of fish at age were determined from catch-at-age analysis for 1951 through 1996 (Schweigert et al. 1996). Herring were assumed to recruit at age 3 and all fish age 3 and older contributed to the spawning population while all herring age 2 and older contributed to the prey population.

### *Halibut*

Pacific halibut range throughout much of the eastern north Pacific and they are assessed and managed by the International Pacific Halibut Commission (IPHC) who provided estimates of numbers of age 8 recruits and total abundance for their statistical areas 2a and 2b, which correspond to British Columbia waters (Pers. comm., A. Parma, IPHC). For simplicity it was assumed that all fish age 8 and older were sexually mature in determining the spawning population. While it is likely that not all fish are mature until age 12, estimates of mature numbers at age were not available in time for this analysis but this assumption should not seriously affect results.

### *Pacific hake*

Estimates of spawning and total population biomass of Pacific hake and estimated numbers of age 2 recruits were available from catch-at-age analysis from 1960 to present (Dorn 1996). No detailed breakdown of numbers and weight at age was available so the biomass estimates were converted to numbers using a mean weight of 0.82 kg per fish (Ware and McFarlane 1995). This migratory hake stock which spawns off California migrates north into Canadian waters in the spring-summer period each year and preys on herring. Ware and McFarlane (1995) demonstrated that the proportion of the stock which migrates north is related to the water temperature and that consequently this affects the degree of predation on the herring stocks. The relationship used to estimate the proportion of the total hake population in British Columbia waters was: Hake proportion = –1.135 + 0.119 sea surface temperature. It is based on the May-June mean sea surface temperature at Amphitrite Point (Pers. comm., I. Perry, Dept. of Fisheries and Oceans, Nanaimo, BC).

### *Pacific cod*

Estimates of Pacific cod are based on catch-at-age analysis, which relies on length frequency analysis of cod (Pers. comm., V. Haist, Dept. of Fisheries and Oceans, Nanaimo, BC). Estimated numbers of cod at age are available for two stocks, one in Hecate Strait and the other off the west coast of Vancouver Island. Cod are assumed to recruit to the spawning or adult population at age 3 and estimates of recruitment are available for age 2 fish. All cod age 2 and older were assumed to contribute to the predator population.

### Chinook

It was not possible to obtain total abundance estimates for chinook in either northern or southern units for this analysis due to the migratory nature of chinook and difficulty in determining the origin of fish in these areas. As a result, I included total catch of chinook in the troll and sport fisheries in the north and south as an index of abundance of chinook for the analysis. All chinook were assumed to mature and spawn at age 4 in both stock areas so catches in a given year were assumed to represent the progeny or recruitment from the year class spawned 4 years earlier. Catch data are available from 1952 to present from the Department of Fisheries and Oceans, Vancouver, B.C.

### Coho salmon

Like chinook salmon, coho salmon are migratory and no estimates of total or spawning stock abundance are available. Consequently, total catch in the troll and sport fisheries in the north and south were taken as an index of abundance of coho salmon for this analysis. All coho salmon-were assumed to mature and spawn at age 3 in both stock areas and catches in a given year were assumed to represent the progeny or recruitment from the year-class spawned 3 years earlier. Catch data are available from 1952 to present from the Department of Fisheries and Oceans, Vancouver, B.C.

### Rock sole

Estimates of numbers at age are available from catch-at-age analysis for the rock sole stocks in Hecate Strait from 1951 through 1992 (Stocker and Fargo 1995). Rock sole recruitment is estimated at age 4 and the spawning population is assumed to comprise fish age 4 and older. All fish age 4 and older were assumed to contribute to the predator population.

### Fraser River sockeye salmon

Sockeye salmon range throughout the eastern Pacific during their adult life but spend some of their first year at sea in nearshore waters where they may experience predation similar to herring. Estimates of total stock abundance are available from total catch and spawning escapement data for the 1951 through to the 1988 brood years (Pers. comm., A. Cass, Dept. of Fisheries and Oceans, Nanaimo, BC). All sockeye salmon were assumed to mature and spawn at age 4 and total returns in a given year were assumed to represent the progeny or recruitment from the year class spawned 4 years earlier. All fish in the brood year were assumed to contribute to the predator or competitor population.

# Results

The time trends in estimated abundances of herring and potential predator populations (millions of fish) provide some indications of the possible species interactions for Hecate Strait (northern) and west coast Vancouver Island (southern) stocks (Figures 2 and 3). In the northern stocks, a previously noted inverse relationship between herring and Pacific cod is still evident (Figure 2A) as is an inverse relationship between herring and coho salmon (Figure 2B) and between herring and rock sole (Figure 2C), although the latter relationship disappeared in the late 1970s. In the southern area there is no clear indication of any probable predator-prey interactions (Figure 3A-C) with the exception of Pacific cod which was inversely related to herring abundance during the 1960s and since the early 1980s but positively related to herring during the 1970s (Figure 3A).

To investigate the possible interactions between predator and prey populations the Ricker stock-recruitment and stock-recruitment interaction functions (equations 1 and 2) were applied to all combinations of available time series of data in both the northern and southern areas and the results are presented in Tables 2-4 and Figures 3-7. The statistical fits to the Ricker stock-recruitment function (model 1) are all highly significant ($P < 0.001$) in the northern area (Table 2). An estimate of the average density-dependent mortality ($\overline{pE}$) is obtained from the slope of the regression line at the mean level of predator or prey, and while differing between species is not affected by the presence of environmental factors. This estimate is highest for rocksole, herring, and hake, which may be expected for strongly schooling species.

In the southern area the statistical fit of the stock recruitment model is significant at least at the 0.05 level for all species except Pacific hake where the model accounts for less than 10% of the observed hake recruitment variation (Table 2). The addition of the environmental predictor, $W_t$, in the form of Prince Rupert average annual sea level improves the fit to the recruitment data marginally for all stocks in the northern area but only for Pacific herring does the additional parameter border on significance ($P = 0.09$). In the south, the addition of the environmental factor, mean annual sea surface temperature, to the basic model is statistically significant for herring and coho, and nearly so for Pacific cod ($P = 0.12$). The term $\overline{pE}$ in the southern area is the same order of magnitude as in the northern area but interestingly for species found in both areas the mean density-dependent mortality estimates are lower in the southern area.

The analysis to assess the importance of herring to the recruitment of major predator or competitor species consisted of including herring in the stock recruitment function described by equation 2. In the northern area, addition of estimates of herring abundance to equation 2 provides a significantly better fit to the recruitment time series for Pacific

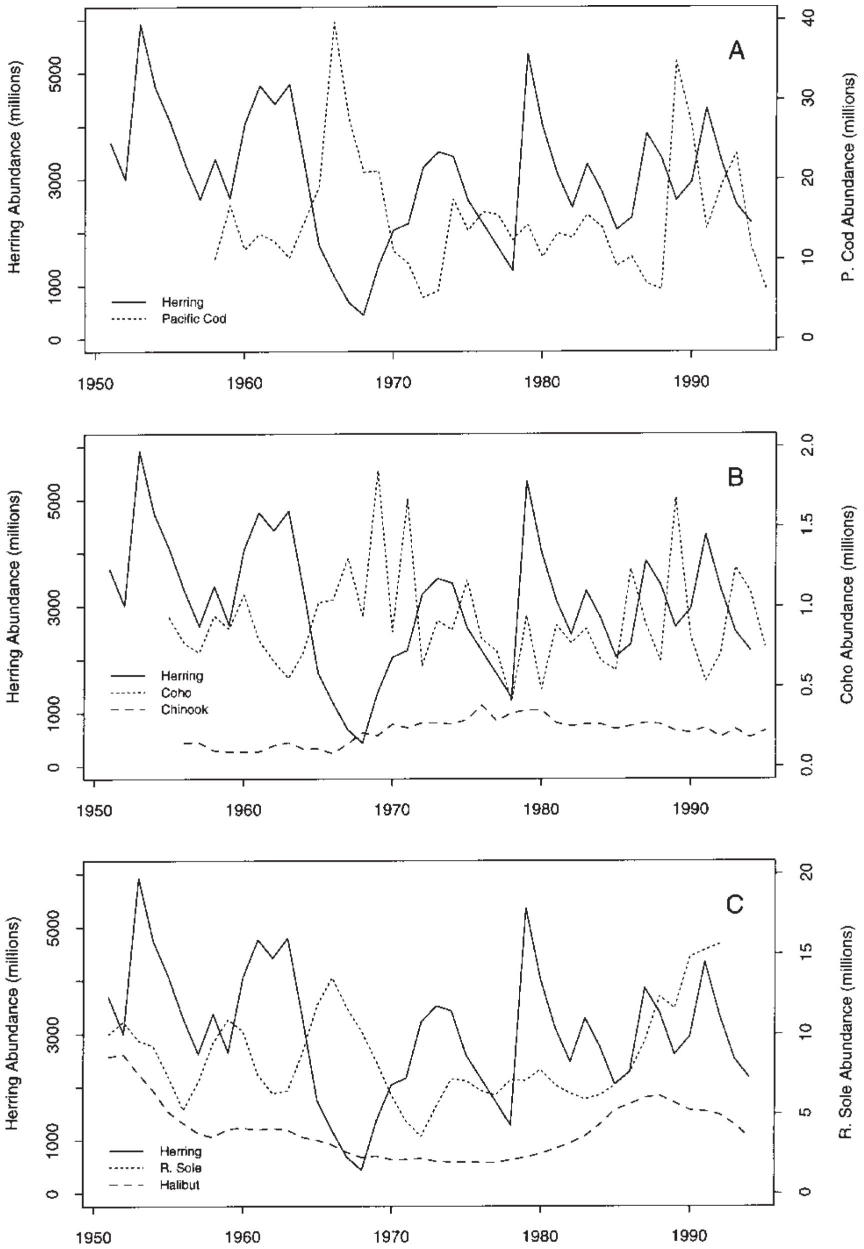

*Figure 2. Time trends in the abundances of Pacific herring and some of its important predators in the northern area.*

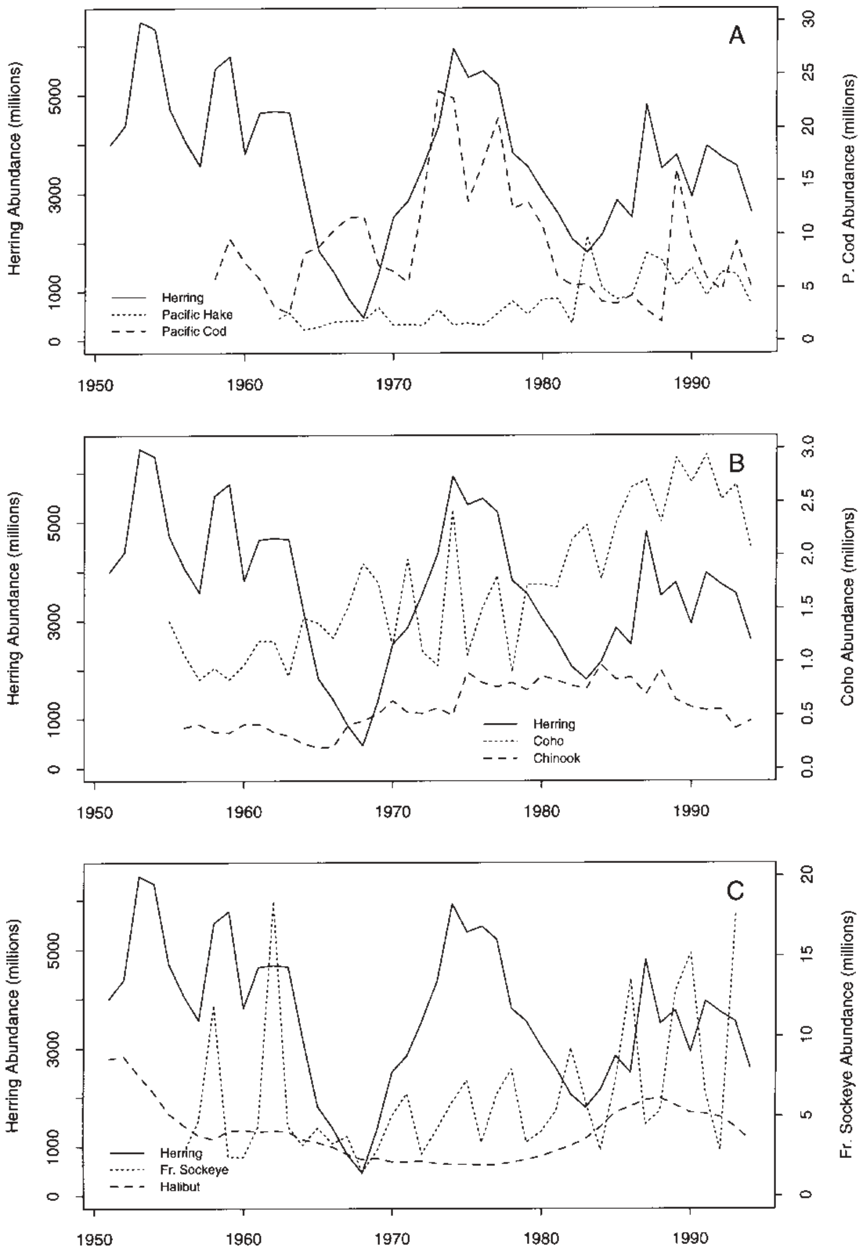

*Figure 3. Time trends in the abundances of Pacific herring and some of its important predators in the southern area.*

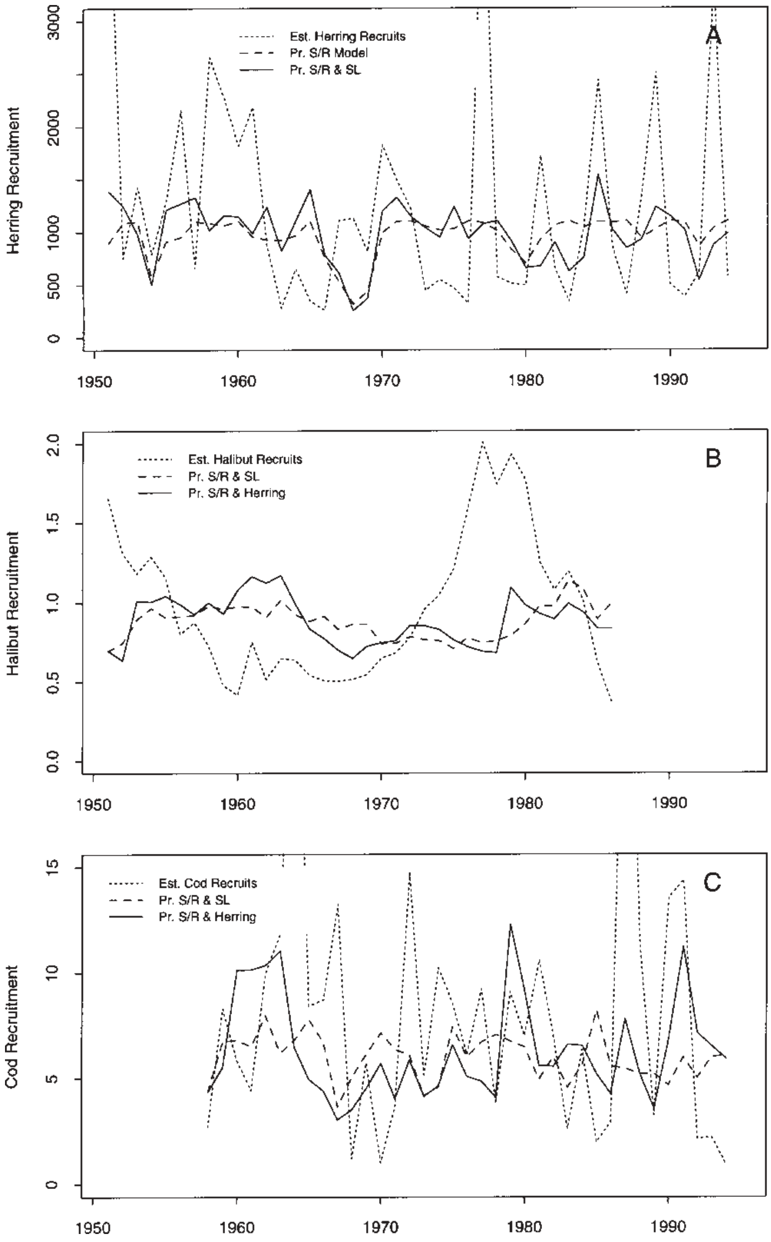

*Figure 4A-C. Observed recruitment for herring and key predators in the northern area and that predicted from stock recruitment functions including either herring or sea level.*

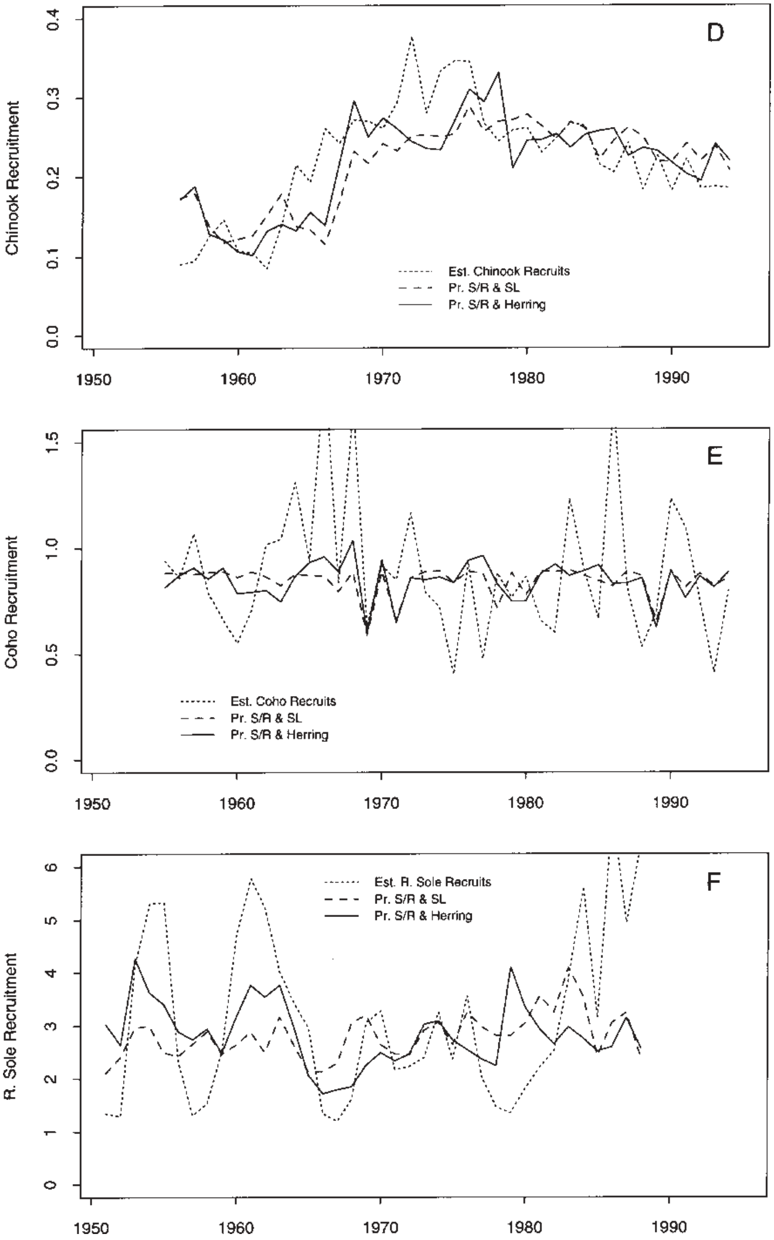

*Figure 4D-F. Observed recruitment for herring and key predators in the northern area and that predicted from stock recruitment functions including either herring or sea level.*

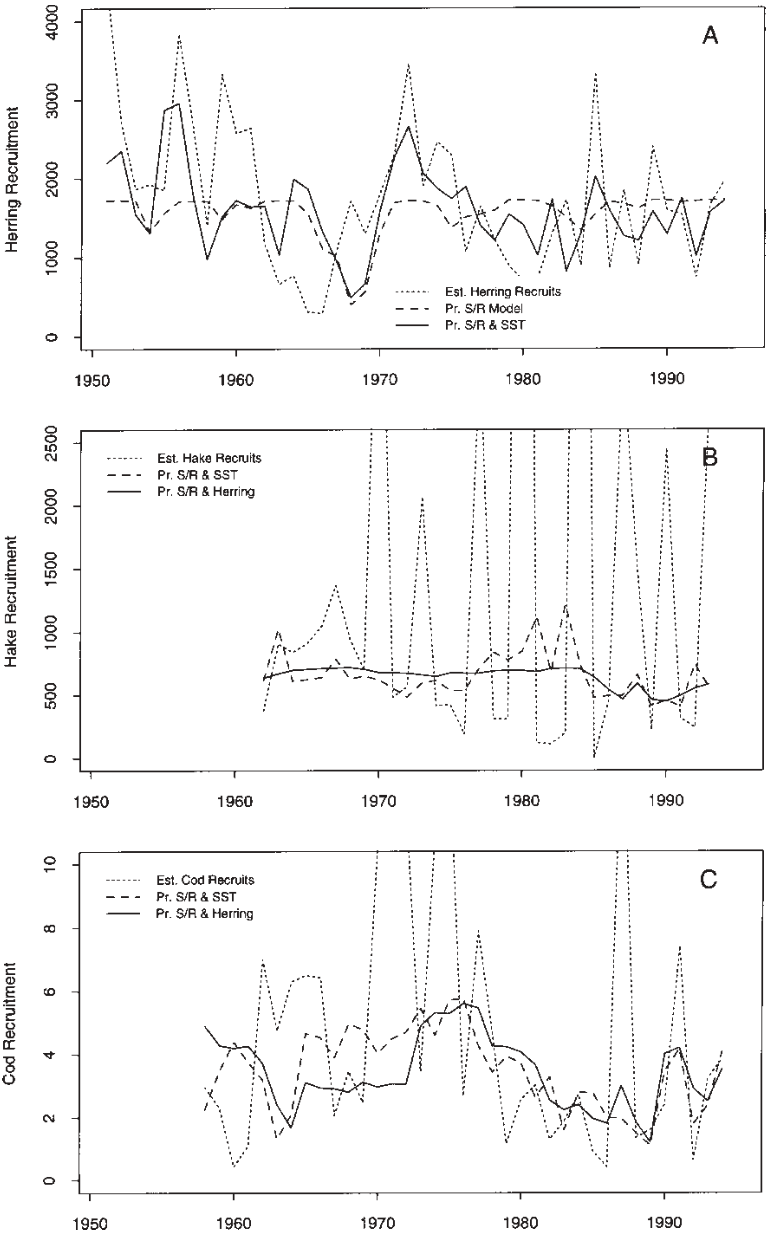

*Figure 5A-C. Observed recruitment for herring and key predators in the southern area and that predicted from stock recruitment functions including either herring or sea surface temperature.*

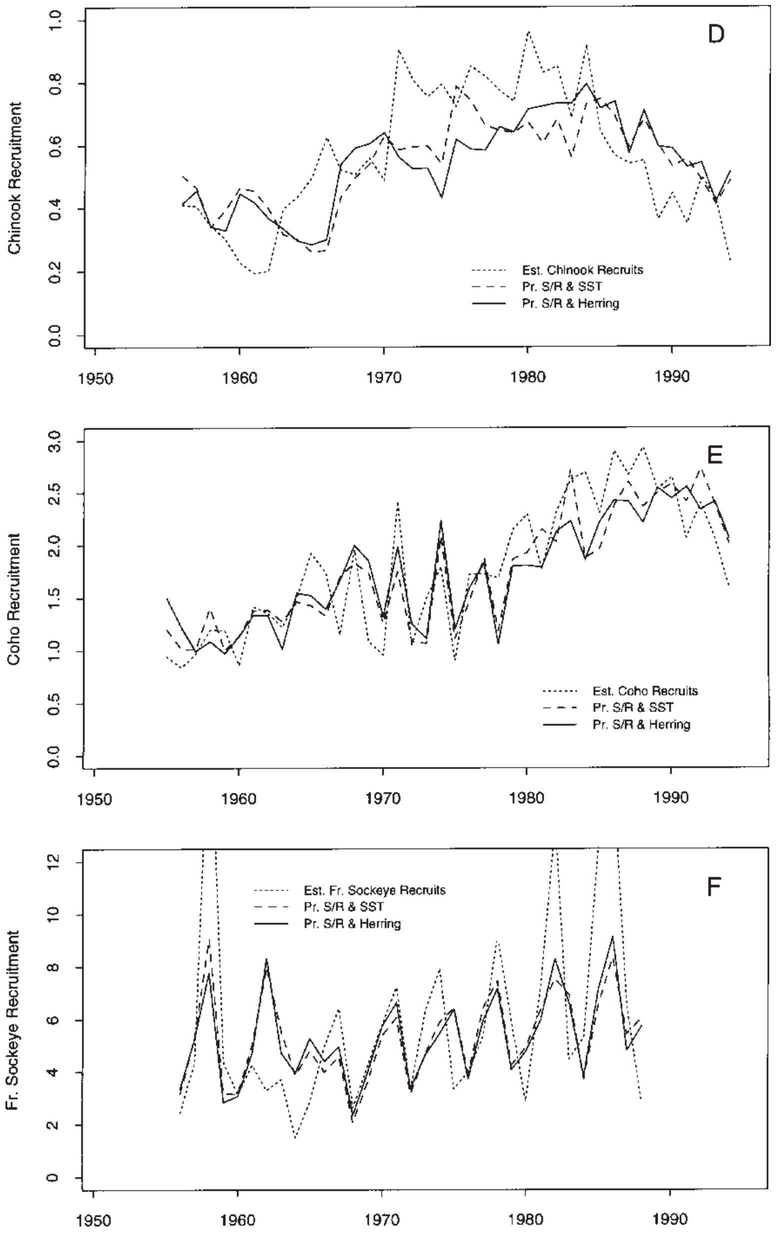

*Figure 5D-F. Observed recruitment for herring and key predators in the southern area and that predicted from stock recruitment functions including either herring or sea surface temperature.*

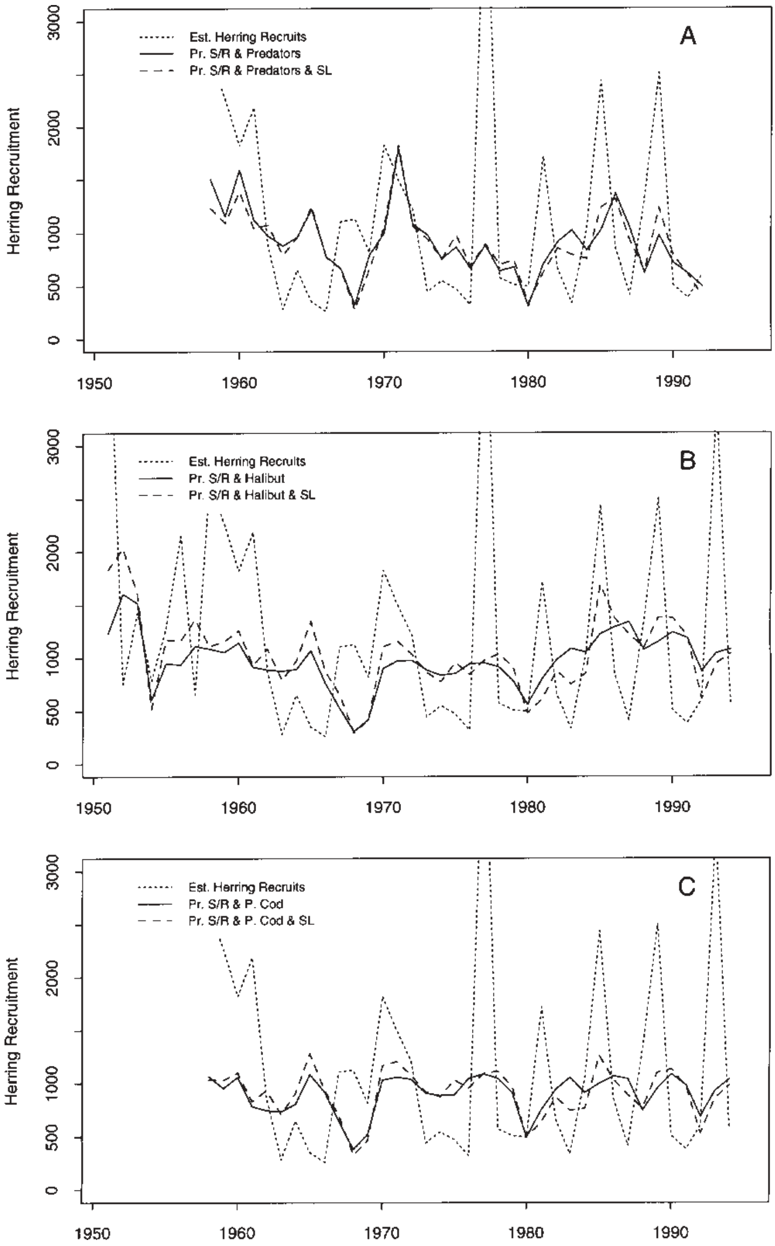

*Figure 6A-C. Observed herring recruitment in the northern area and that predicted from stock recruitment functions incorporating (A) all key predators and sea level and (B-F) individual key predators and sea level.*

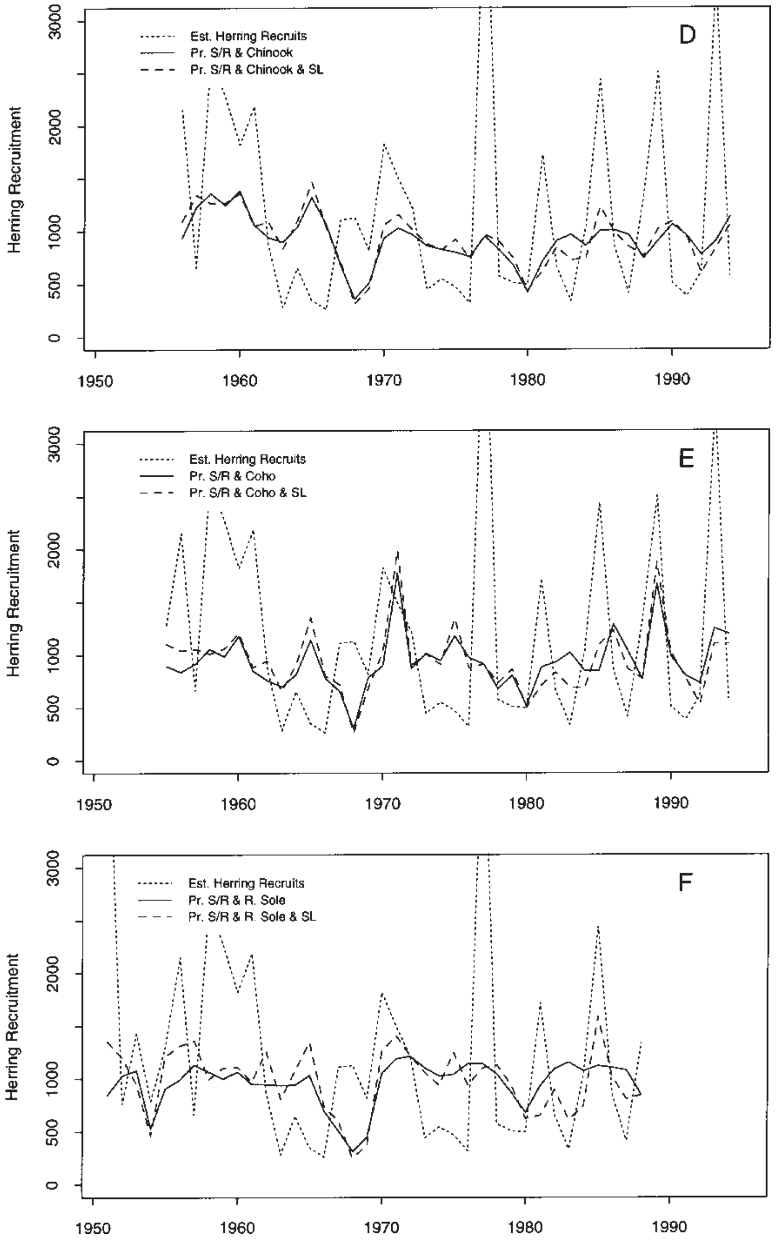

*Figure 6D-F. Observed herring recruitment in the northern area and that predicted from stock recruitment functions incorporating (A) all key predators and sea level and (B-F) individual key predators and sea level.*

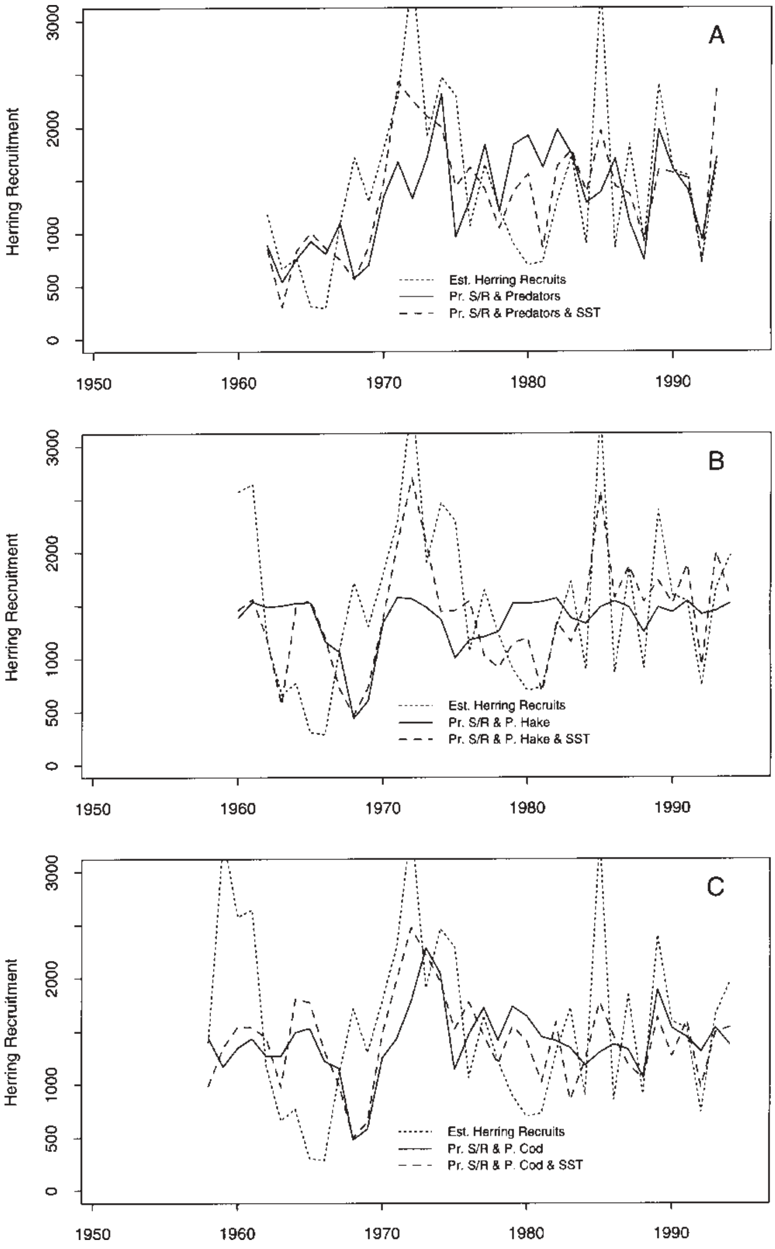

*Figure 7A-C. Observed herring recruitment in the southern area and that predicted from stock recruitment functions incorporating (A) all key predators and sea surface temperature and (B-F) individual key predators and sea surface temperature.*

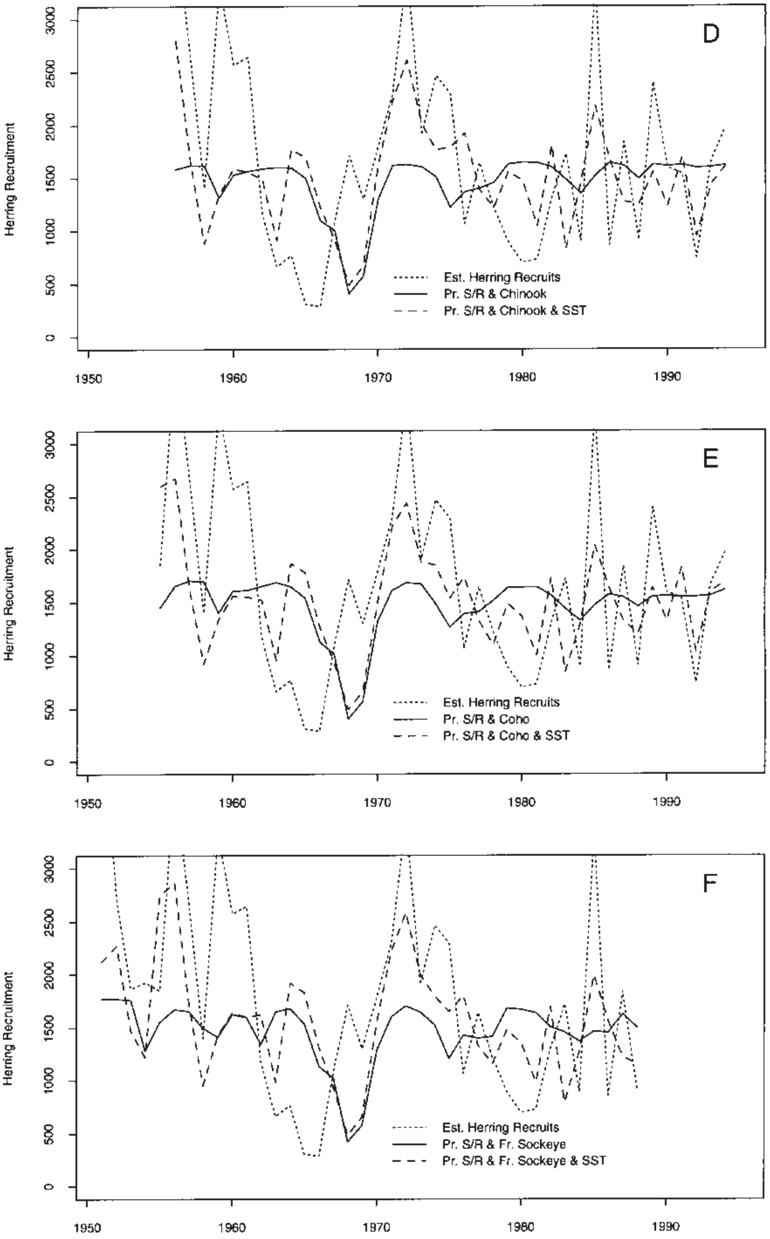

*Figure 7D-F. Observed herring recruitment in the southern area and that predicted from stock recruitment functions incorporating (A) all key predators and sea surface temperature and (B-F) individual key predators and sea surface temperature.*

**Table 2. Stock-recruitment models for herring and their predators, estimated by multiple regression from the data described in Table 1**

| Species | | Ricker stock-Recruitment models | $\overline{pE}$ | $R^2$, significance level |
|---|---|---|---|---|
| North | Herring | $R_t = E_t \exp\{-6.91 - 3.309e^{-7} E_t\}$ | −1.19 | 31.1, $P = <0.001$ |
| | | $R_t = E_t \exp\{12.52 - 3.321e^{-7} E_t - 5.038 W_t\}$ | −1.20 | 35.8, $P = <0.001$, $W_t$ ($P = 0.09$) |
| | Halibut | $R_t = E_t \exp\{-7.43 - 2.234e^{-4} E_t\}$ | −0.88 | 36.6, $P = <0.001$ |
| | | $R_t = E_t \exp\{-13.07 - 2.158e^{-4} E_t + 1.458 W_t\}$ | −0.85 | 37.4, $P = <0.001$, $W_t$ ns |
| | Pacific cod | $R_t = E_t \exp\{-6.00 - 1.362e^{-4} E_t\}$ | −0.91 | 23.0, $P = 0.003$ |
| | | $R_t = E_t \exp\{5.41 - 1.398e^{-4} E_t - 2.948 W_t\}$ | −0.94 | 24.4, $P = 0.009$, $W_t$ ns |
| | Chinook salmon | $R_t = E_t \exp\{-6.43 - 0.00199 E_t\}$ | −0.43 | 22.2, $P = 0.002$ |
| | | $R_t = E_t \exp\{-9.32 - 0.00209 E_t + 0.754 W_t\}$ | −0.45 | 23.0, $P = 0.009$, $W_t$ ns |
| | Coho salmon | $R_t = E_t \exp\{-5.85 - 0.00119 E_t\}$ | −1.07 | 54.0, $P = <0.001$ |
| | | $R_t = E_t \exp\{-6.04 - 0.00119 E_t + 0.048 W_t\}$ | −1.07 | 54.0, $P = <0.001$, $W_t$ ns |
| | Rock sole | $R_t = E_t \exp\{-6.71 - 1.518e^{-4} E_t\}$ | −1.30 | 31.7, $P = <0.001$ |
| | | $R_t = E_t \exp\{-18.13 - 1.478e^{-4} E_t + 2.954 W_t\}$ | −1.27 | 35.5, $P = <0.001$, $W_t$ ns |
| South | Herring | $R_t = E_t \exp\{-6.69 - 2.657e^{-7} E_t)$ | −0.98 | 29.2, $P = <0.001$ |
| | | $R_t = E_t \exp\{-0.24 - 2.870e^{-7} E_t - 0.610 W_t\}$ | −1.06 | 42.6, $P = <0.001$, $W_t$ ($P = 0.003$) |
| | Halibut | $R_t = E_t \exp\{-7.43 - 2.234e^{-4} E_t\}$ | −0.88 | 36.6, $P = <0.001$ |
| | | $R_t = E_t \exp\{-7.60 - 2.229e^{-4} E_t + 0.017 W_t\}$ | −0.91 | 36.6, $P = <0.001$, $W_t$ ns |
| | Pacific hake | $R_t = E_t \exp\{-6.46 - 8.251e^{-7} E_t)$ | −1.25 | 7.7, $P = 0.12$ ns |
| | | $R_t = E_t \exp\{-11.81 - 9.638e^{-7} E_t + 0.529 W_t\}$ | −1.46 | 9.2, $P = 0.25$, $W_t$ ns |
| | Pacific cod | $R_t = E_t \exp\{-6.44 - 1.285e^{-4} E_t)$ | −0.53 | 10.6, $P = 0.05$ |
| | | $R_t = E_t \exp\{-0.30 - 1.44e^{-4} E_t - 0.577 W_t\}$ | −0.60 | 16.6, $P = 0.05$, $W_t$ ($P = 0.12$) |
| | Chinook salmon | $R_t = E_t \exp\{-6.49 - 7.228e^{-4} E_t)$ | −0.41 | 14.4, $P = 0.02$ |
| | | $R_t = E_t \exp\{-4.84 - 6.66e^{-4} E_t + -0.161 W_t\}$ | −0.38 | 17.3, $P = 0.03$, $W_t$ ns |
| | Coho salmon | $R_t = E_t \exp\{-6.61 - 1.451e^{-4} E_t)$ | −0.25 | 13.7, $P = 0.02$ |
| | | $R_t = E_t \exp\{-8.94 - 1.882e^{-4} E_t + 0.229 W_t\}$ | −0.32 | 30.9, $P = 0.001$, $W_t$ ($P = 0.004$) |
| | Fraser R. sockeye | $R_t = E_t \exp\{-6.48 - 6.613e^{-5} E_t)$ | −0.41 | 21.4, $P = 0.01$ |
| | | $R_t = E_t \exp\{-7.71 - 7.007e^{-5} E_t + 0.120 W_t\}$ | −0.43 | 22.5, $P = 0.02$, $W_t$ ns |

($R_t$ = Recruitment index adjusted to year class; $E_t$ = effective egg deposition; $P_t$ = estimated predator or prey stock; $W_t$ = environmental factors).

**Table 3. Stock-recruitment interaction models of herring effects on their predators, estimated by multiple regression from the data described in Table 1.**

| Species | Interaction models | $\overline{pE}$ | $\overline{qP}$ | $R^2$, significance level |
|---|---|---|---|---|
| North | | | | |
| Halibut–herring | $R_t = E_t \exp\{-7.63 - 2.545e^{-4} E_t + 1.070e^{-4} P_t\}$ | –1.01 | 0.32 | 40.2, $P = 0.001$, $P_t$ ns |
| Pacific cod–herring | $R_t = E_t \exp\{-7.10 - 9.609e^{-5} E_t + 2.929e^{-4} P_t\}$ | –0.64 | 0.88 | 32.4, $P = 0.001$, $P_t$ ($P = 0.04$) |
| Chinook salmon–herring | $R_t = E_t \exp\{-6.11 - 0.002 E_t - 1.131e^{-4} P_t\}$ | –0.43 | –0.34 | 36.5, $P = 0.001$, $P_t$ ($P = 0.007$) |
| Coho salmon–herring | $R_t = E_t \exp\{-5.59 - 0.001 E_t - 6.554e^{-5} P_t\}$ | –1.15 | –0.20 | 55.8, $P = 0.001$, $P_t$ ns |
| Rock sole–herring | $R_t = E_t \exp\{-7.26 - 1.396e^{-4} E_t - 1.488e^{-4} P_t\}$ | –1.20 | –0.45 | 40.7, $P = 0.001$, $P_t$ ($P = 0.03$) |
| South | | | | |
| Halibut–herring | $R_t = E_t \exp\{-7.79 - 2.542e^{-4} E_t + 1.307e^{-4} P_t\}$ | –1.01 | 0.48 | 45.5, $P = 0.001$, $P_t$ ($P = 0.03$) |
| Pacific hake–herring | $R_t = E_t \exp\{-6.43 - 8.183e^{-7} E_t - 1.303e^{-5} P_t\}$ | –1.24 | –0.05 | 7.7, $P = 0.31$, ns; $P_{t,}$ ns |
| Pacific cod–herring | $R_t = E_t \exp\{-6.84 - 1.456e^{-4} E_t + 1.371e^{-4} P_t\}$ | –0.60 | 0.50 | 14.1, $P = 0.07$, $P_{t,}$ ns |
| Chinook salmon–herring | $R_t = E_t \exp\{-6.26 - 7.159e^{-4} E_t - 7.093e^{-5} P_t\}$ | –0.41 | –0.26 | 19.9, $P = 0.02$, $P_t$ ($P = 0.12$) |
| Coho salmon–herring | $R_t = E_t \exp\{-6.57 - 1.487e^{-4} E_t - 8.532e^{-6} P_t\}$ | –0.25 | –0.03 | 14.0, $P = 0.06$, $P_{t,}$ ns |
| Sockeye salmon–herring | $R_t = E_t \exp\{-6.35 - 6.228e^{-5} E_t - 4.438e^{-5} P_t\}$ | –0.39 | –0.16 | 23.0, $P = 0.02$,ns; $P_{t,}$ ns |

($R_t$ = recruitment index adjusted to year class; $E_t$ = effective egg deposition; $P_t$ = estimated predator or prey stock; $W_t$ = environmental factors)

**Table 4. Stock-recruitment interaction models for herring and their predators, estimated by multiple regression from the data described in Table 1.**

| Species | Stock-recruitment interaction models | $\overline{pE}$ | $\overline{qP}$ | $R^2$, significance level |
|---|---|---|---|---|
| North | | | | |
| Herring–halibut | $R_t = E_t \exp\{-7.12 - 3.641e^{-7} E_t + 0.083 P_t\}$ | –1.31 | 0.33 | 33.0, $P = <0.001$, $P_t$ ns |
| | $R_t = E_t \exp\{7.41 - 3.992e^{-7} E_t + 0.103 P_t - 3.744 W_t\}$ | –1.44 | 0.41 | 44.0, $P = <0.001$, $P_t$, $W_t$ ns |
| Herring–Pacific cod | $R_t = E_t \exp\{-6.78 - 4.078e^{-7} E_t + 0.008 P_t\}$ | –1.47 | 0.12 | 38.4, $P = <0.001$, $P_t$ ns |
| | $R_t = E_t \exp\{-5.59 - 3.869e^{-7} E_t + 0.004 P_t - 3.210 W_t\}$ | –1.44 | 0.06 | 39.9, $P = <0.001$, $P_t$,$W_t$ ns |
| Herring–chinook salmon | $R_t = E_t \exp\{-6.34 - 3.869e^{-7} E_t - 2.000 P_t\}$ | –1.39 | –0.43 | 37.9, $P = <0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{4.42 - 3.819e^{-7} E_t - 1.639 P_t - 2.813 W_t\}$ | –1.37 | –0.35 | 39.1, $P = <0.001$, $P_{t,}W_t$ ns |
| Herring–coho salmon | $R_t = E_t \exp\{-7.60 - 3.246e^{-7} E_t + 0.689 P_t\}$ | –1.17 | 0.62 | 38.9, $P = <0.001$, $P_t$ ($P = 0.12$) |
| | $R_t = E_t \exp\{6.27 - 3.248e^{-7} E_t + 0.656 P_t - 3.588 W_t\}$ | –1.17 | 0.59 | 41.2, $P = <0.001$, $P_{t,}$ ($P = 0.14$),$W_t$ ns |
| Herring–rock sole | $R_t = E_t \exp\{-6.72 - 3.417e^{-7} E_t - 0.020 P_t\}$ | –1.23 | –0.17 | 34.1, $P = <0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{14.16 - 3.433e^{-7} E_t - 0.014 P_t - 5.427 W_t\}$ | –1.24 | –0.17 | 39.6, $P = <0.001$, $P_{t,}$ ns, $W_t$ ($P = 0.07$) |
| South | | | | |
| Herring–halibut | $R_t = E_t \exp\{-6.83 - 2.710e^{-7} E_t + 0.041 P_t\}$ | –1.00 | 0.16 | 30.0, $P = <0.001$, $P_t$ ns |
| | $R_t = E_t \exp\{-0.34 - 2.932e^{-7} E_t + 0.046 P_t - 0.616 W_t\}$ | –1.08 | 0.18 | 43.8, $P = <0.001$, $P_t$,ns $W_t$ ($P = <0.001$) |
| Herring–Pacific hake | $R_t = E_t \exp\{-6.56 - 3.278e^{-7} E_t - 4.241e^{-5} P_t\}$ | –1.21 | –0.12 | 37.3, $P = <0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{4.54 - 3.239e^{-7} E_t + 6.378e^{-4} P_t - 1.106 W_t\}$ | –1.19 | 0.48 | 53.2, $P = <0.001$, $P_t$ ($P = 0.04$), $W_t$ ($P = 0.003$) |
| Herring–Pacific cod | $R_t = E_t \exp\{-6.82 - 3.282e^{-7} E_t + 0.029 P_t\}$ | –1.21 | 0.26 | 36.3, $P = <0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{-1.37 - 3.098e^{-7} E_t + 0.012 P_t - 0.509 W_t\}$ | –1.14 | 0.11 | 42.5, $P = <0.001$, $P_{t,}$ ns, $W_t$ ($P = 0.07$) |
| Herring–chinook salmon | $R_t = E_t \exp\{-6.68 - 2.884e^{-7} E_t + 0.033 P_t\}$ | –1.06 | 0.02 | 30.4, $P = 0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{-0.05 - 3.019e^{-7} E_t + 0.267 P_t - 0.640 W_t\}$ | –1.11 | 0.15 | 43.2, $P = <0.001$, $W_t$ ($P = 0.008$) |
| Herring–coho salmon | $R_t = E_t \exp\{-6.60 - 2.843e^{-7} E_t - 0.042 P_t\}$ | –1.05 | –0.07 | 30.6, $P = <0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{-0.54 - 2.983e^{-7} E_t + 0.063 P_t - 0.591 W_t\}$ | –1.10 | 0.11 | 42.6, $P = <0.001$, $P_{t,}$ ns, $W_t$ ($P = 0.009$) |
| Herring–sockeye salmon | $R_t = E_t \exp\{-6.60 - 2.817e^{-7} E_t - 0.014 P_t\}$ | –1.04 | –0.09 | 31.1, $P = <0.001$, $P_{t,}$ ns |
| | $R_t = E_t \exp\{-0.14 - 2.955e^{-7} E_t + 0.002 P_t - 0.620 W_t\}$ | –1.09 | 0.01 | 42.8, $P = <0.001$, $P_{t,}$ ns, $W_t$ ($P = 0.01$) |

($R_t$ = recruitment index adjusted to year class; $E_t$ = effective egg deposition; $P_t$ = estimated predator or prey stock; $W_t$ = environmental factors) cod, chinook salmon, and rock sole with parameters significant at $P < 0.04$ (Table 3). However, the addition of herring to the stock recruitment models only accounts for an additional few percent of the total recruitment variation and prediction of the observed recruitment is not significantly improved (Figure 4B-F). The addition of either herring or sea level to the model provides predictions of recruitment that generally follow the observed trends for each species but neither model is able to account for the very large or small recruitment events in any of the northern stocks except Pacific cod. The addition of sea level to the model to predict Pacific herring recruitment (Figure 4A) while statistically significant does not substantially improve predictions of observed herring recruitments. In this instance, the parameters of the model fits can be used to assess the impact of herring on predator stocks whereby the terms $\overline{pE}$ and $\overline{qP}$ provide estimates of the density-dependent and predation or interaction mortality, respectively. For all species except cod the density-dependent mortality estimate is comparable to that for a model without herring (Tables 2 and 3). The interaction term $\overline{qP}$ is expected to be positive for a prey species such as herring but this occurs only for halibut and cod, although there are significant negative fits for chinook salmon and rock sole, suggesting that mortality for these species and coho salmon actually increases in the presence of abundant herring stocks.

In the southern area, addition of estimates of herring abundance to equation 2 provides a significant model fit for all species except hake but only for halibut is this additional parameter significant (Table 3). Overall, predictions of recruitment in the southern area are better than in the north but they are still relatively poor at predicting the large and small year classes with the exception of coho and sockeye salmon (Figure 5B-F). Sea surface temperature substantially improves the recruitment predictions for herring (Figure 5A) but does not significantly improve predictions for the other species over those resulting from the addition of herring or the stock recruitment function alone. Estimates of the interaction term yield similar results to the northern area with only halibut and cod exhibiting a positive relationship with herring abundance. The other four species apparently exhibit higher average mortality in the presence of abundant herring stocks although the estimates are lower than in the north and approximate zero for all but chinook salmon, suggesting that herring abundance probably does not affect their recruitment at all (Table 3). For halibut and cod the presence of herring appears to reduce their mortality substantially, ranging from a third to half of the density-dependent mortality for halibut and equal to or greater than this for cod.

The analysis to assess the effects of predator abundance on herring recruitment consisted of including estimates of the predator or competitor population abundance in the stock-recruitment interaction function described by equation 2. The results are shown in Table 4 and Figures 6 and 7. In the northern area, all model fits were significant ($P < 0.001$), but only for coho salmon does the parameter for the interaction term verge on significance (Table 4). Similarly, for model 2 with both interaction and environment terms, neither parameter was significant except for sea level in the herring-rock sole interaction model. The predictions for these models are shown in Figure 6B-F and indicate relatively poor estimation of the observed herring recruitment. Coho salmon provide the closest predictions to the observed herring recruitments while the fits for the other species merely follow the general trend. Figure 6A shows the fit to the herring recruitment including all five predators but the fit is dominated by the coho salmon data. The addition of sea level to that model does little to improve the fit. In this analysis the interaction term $\overline{qP}$ should be negative if a predator is significantly impacting herring recruitment through a predator-prey relationship. Interestingly, only for chinook salmon and rock sole is this the case, and coho salmon abundance appears to positively affect herring recruitment (Table 4).

In the southern area, all model fits were significant ($P = 0.0$) but in no case was the parameter for the interaction term significant (Table 4). However, in every case when both the interaction and environment terms were included into equation 2 the parameter for the environmental effect was significant at less than $P = 0.07$. For hake, coho salmon, and sockeye salmon the interaction parameters were negative, as expected for a predator interaction, but not statistically significant. The predictions for these models are shown in Figure 7B-F and indicate reasonably good estimation of the observed herring recruitment when both interaction and environment terms are included in the models. Figure 7A presents the predictions of herring recruitment including all six predator species as well as sea surface temperature. Both models provide a reasonably good fit to the data although the addition of the environmental factor provides for the best overall fit. The estimates of the interaction terms $\overline{pE}$ and $\overline{qP}$ indicate a similar density-dependent mortality for all species and only small interactions with coho and sockeye salmon which disappear after the environmental factor is added to the model (Table 4). Since the predation effects are quite small in the absence of temperature and sea surface temperature is highly correlated with herring recruitment it appears to mask any predation effects which may be involved.

# Discussion

A series of research studies off the British Columbia coast during the past century have examined the diets of most commercial fish species and have shown a preponderance of Pacific herring in their stomachs (Pritchard and Tester 1944, Prakash 1962, Westrheim and Harling 1983, Best and St. Pierre 1986, Tanasichuk et al. 1991, Ware and McFarlane 1995). These findings led to speculation that herring are critical to the well-being of various predator species and the ecosystem as a whole. However, it is also known that the Pacific sardine was an important component of the British Columbia and California ecosystems earlier this century (Schweigert 1988, Ware and McFarlane 1995) and was common in the diets of salmon and other species (Pritchard and Tester 1944). Therefore, while herring are currently important prey items for many species, changing environmental conditions can alter the form and intensity of species interactions as Skud (1982) has shown for herring and mackerel in the western north Atlantic where temperature changes appear to alter the dominance or relative abundance of prey species and, presumably, their predators.

These complicating factors make an understanding of the importance of herring to predator populations more difficult and only Walters et al. (1986) have been successful in quantifying the possible influence of herring on Pacific cod recruitment in Hecate Strait. In this study, using similar methodology the earlier findings for cod were confirmed as was a similar result for halibut in southern British Columbia. A finding of an inverse relationship between herring availability and chinook salmon recruitment for both study areas appears to be a spurious correlation, or more likely indicates the inappropriateness of using chinook salmon catch data as an index of stock abundance. It is difficult to understand how lower herring abundance would enhance chinook salmon recruitment. Another complicating factor in describing a statistical link between prey availability and predator recruitment results from the variable lag in these effects for different species. For example, if herring are particularly abundant in a given year they may increase fecundity and survival of a predator population during the coming spawning season or perhaps result in residual effects that affect the predator population for several years. Depending on the maturation process and timing of spawning this effect will vary among species. There is no clear evidence for such an effect in Figures 4 and 5 but Walters et al. (1986) examined the impacts of a series of herring year classes on cod recruitment and achieved an improved fit to the cod recruitment times series supporting the possibility of such lag effects.

The prey components of the marine ecosystem and of the predator-prey interaction have received more study than the predators. For example, Zheng (1996) has shown that herring recruitment is not well described by spawning stock alone and that other biotic and abiotic factors must be involved. Collie and Spencer (1994) adopted a biomass dynamics model to investigate the impact of hake predators on herring stocks off the west coast of Vancouver Island. Their model suggests that hake predation can result in two equilibria between predator and prey depending on how environmental conditions affect the predation intensity. Ware and McFarlane (1986, 1995) used a trophodynamics approach to assess the impacts of hake and other predators on herring recruitment to the west coast of Vancouver Island stock but did not assess the effects of herring availability on predator stocks. They demonstrated that Pacific hake was the most significant predator determining recruitment success for the west coast of Vancouver Island herring stock although a number of other species also consumed significant numbers of herring. Pacific hake accounted for about 12% of the variation in recruitment to this stock. Unfortunately, combining the two southern herring stocks into a single unit in this study made it impossible to detect the predation effects of hake on either of the individual herring stocks or verify these earlier results. It is also unclear how well the temperature data predicts hake abundance in British Columbia waters so that estimates of hake predator biomass may be biased and mask their true impact.

Walters et al. (1986) reported a significant impact of cod predation on herring recruitment in Hecate Strait. However, in the current study this interaction was no longer statistically detectable. In fact, no significant effects of predators on herring recruitment were observed in either the northern or southern areas. The absence of any detectable impact of predators on herring recruitment is not entirely surprising since there are many predators in the ecosystem which have not been accounted for in the analysis but are nevertheless impacting herring stocks, e.g., dogfish, lingcod, Pacific mackerel, marine birds, and mammals. It is quite likely that no single predator species, except perhaps hake, is numerically abundant and voracious enough to produce a detectable impact on herring recruitment, even the combination of all the key predators in this study did not provide good predictions of herring recruitment (Figures 6A and 7A). Another possibility is that while many of the predator stocks examined here target on adult and some juvenile herring, it may be that the important determinant of herring recruitment is predation during the first year of life in the very nearshore waters by the more abundant juvenile component of the predator populations which was not investigated here. As a result the true impact of these species on herring recruitment may be greatly underestimated. As noted earlier, a major difficulty in studying predator-prey interactions has been in obtaining data on the appropriate spatial and temporal scales and that what is required are estimates of relative abundance of predators and prey during their first few years of life rather than at recruitment to the spawning stocks, data which are not generally available for most species.

Pacific herring stocks in British Columbia suffered a huge collapse in the late 1960s with a coincident decline in recruitment which was not captured by any of the models examined here. Given such a substantial contrast in herring abundance some response in the predator populations should be evident if indeed there is a critical link between predator and prey. That such a response was not observed suggests either that alternate prey were readily available to fill the void left by herring and that they are clearly not critical factors in predator survival and recruitment, or that environmental factors are more important than food supply in the reproductive success of the predator stocks. Although an exhaustive search for environmental factors that could explain recruitment of both predator and prey was not conducted, sea surface temperature is a significant factor in explaining recruitment for some predator species in the southern area (Table 2), and requires further investigation.

In conclusion, no evidence of a classical predator-prey interaction was found for Pacific herring and its key predators off the British Columbia coast. Some herring stocks are significantly affected by climatic factors that could reflect biotic interactions not detected at the spatial or temporal scale of the data available for this study. Some predators appear to benefit from abundant herring stocks but others may be responding at lag times not readily detectable in this study.

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# Long- and Short-Term Responses of Seabirds in the Norwegian and Barents Seas to Changes in Stocks of Prey Fish

**Tycho Anker-Nilssen**
*Norwegian Institute for Nature Research, Trondheim, Norway*

**Robert T. Barrett**
*University of Tromsø, Tromsø Museum, Tromsø, Norway*

**Juri V. Krasnov**
*Kandalaksha State Nature Reserve, Kandalaksha, Murmanskaja, Russia*

## Abstract

About 3 million pairs of seabirds breed in North Norway and along the Kola Peninsula in some of the largest seabird colonies in the North Atlantic. The most numerous species are Atlantic puffins (*Fratercula arctica*), kittiwakes (*Rissa tridactyla*), and common murres (*Uria aalge*), and their main prey consists of capelin (*Mallotus villosus*), herring (*Clupea harengus*), and sand lance (*Ammodytes* spp.).

The numbers of puffins, kittiwakes, and murres have changed dramatically over the last 30-40 years. While some local populations of the kittiwake west of the North Cape have increased or been fairly stable, those of the puffin and murres have decreased. For example, the puffin population at Røst, Lofoten Islands, decreased from about 1.4 million pairs in 1979 to only 500,000-600,000 pairs during the last few years. At Røst, the decrease in the puffin population and in part that of the common murre was due to long-term failures in chick production through starvation. For puffins this was caused by the collapse in the Norwegian herring stock in the late 1960s.

East of the North Cape, the kittiwake and common murre populations have increased since about 1960, probably as a result of an increased availability of capelin. Murre numbers continue to increase today but experienced a collapse of about 80% in their numbers in 1985-1987. This collapse was the result of an extraordinarily high adult mortality during the winter which was associated with the collapse of the Barents Sea capelin stock. The capelin stock is now low and kittiwake numbers are showing signs of a decrease.

Short-term responses on Røst and colonies in East Finnmark and the Kola Peninsula are documented by close correlations between choice of chick food and/or breeding success and indices of the abundance of the main prey fish. This paper presents details of these and other seabird-fish interactions in these waters.

## Introduction

Seabirds are among the top predators in the marine ecosystem. They are very numerous and, because they are extremely sociable at feeding grounds or breeding colonies, very conspicuous. Although their choice of prey is large and variable (both in space and time, and from species to species) many species concentrate their feeding on small, pelagic shoaling fish. This is especially applicable during the breeding season when their foraging range is restricted, and demands for energy-rich food by fast-growing chicks are high. In the northeast North Atlantic, important prey species during the breeding season include all age classes of capelin (*Mallotus villosus*), sand lance (*Ammodytes* spp.), and Arctic cod (*Boreogadus saida*), as well as the youngest age classes (age 0-1) of herring (*Clupea harengus*) (Belpol'skii 1957, Barrett and Krasnov 1996, Anker-Nilssen et al. In press).

Because of the foraging restrictions associated with the need to protect eggs and chicks, seabirds are particularly sensitive to changes in the availability of fish during the summer. As a result, their responses to food availability are often manifested through short-term changes in breeding parameters such as the timing of breeding, chick food and/or growth rates, and breeding success, and rarely through longer-term changes in population numbers. Due to the life-history characteristics of seabirds (high adult survival rates, slow maturation, and low reproductive rates), the latter generally only occurs when changes in food supply are extreme (Cairns 1987).

This paper reviews three marked responses by North Norwegian and Russian seabirds to changes in stocks of two preferred prey species in the Norwegian and Barents seas. The first change was a fisheries-induced collapse in the Norwegian spring-spawning herring stock in the late 1960s, a collapse from which it is still struggling to recover (Figure 1). The second was due to huge fluctuations in the Barents Sea capelin stock, with a steady decline in the early 1980s to a minimum in 1986-1987 and a short-lived recovery around 1990. There are no comparable data concerning sand lance stocks which have no commercial interest north of the North Sea. The observed responses by seabirds differed greatly in their timing and scale, and they clearly illustrated the different mechanisms through which these responses can be manifested. Fur-

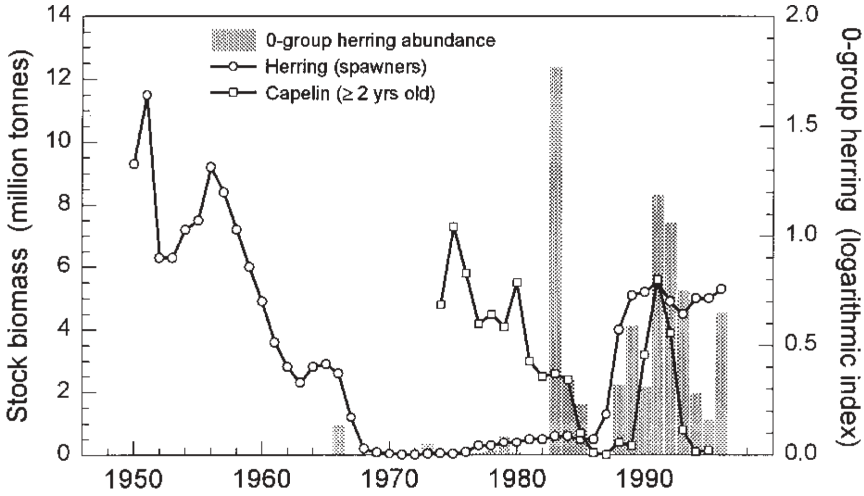

*Figure 1. Estimated stock sizes of Norwegian spring-spawning herring (Clupea harengus) (after Anon. 1996b) and Barents Sea capelin (Mallotus villosus) (≥2 years old, after Aglen 1996), and abundance indices for age-0 herring in the Barents Sea and adjacent waters in August-September (after Anon. 1996a).*

thermore, a documentation of different response types within a limited geographical region is rare.

# Results

## *Short-term changes in chick food*

Large numbers of seabirds breed in the southern Barents Sea and, since 1980, two colonies have been monitored regularly: Hornøy in East Finnmark and Kharlov off the Kola Peninsula (Figure 2). Counts have been made of numbers of selected species breeding on the colony (kittiwake, Atlantic puffin, and common murre) nearly every year, and samples of food brought to their chicks have been collected (Krasnov and Barrett 1995, Barrett and Krasnov 1996).

In the early 1980s, capelin and sand lance dominated nearly all the food samples, the breeding success of all the species on the islands was high, and populations were either stable or increasing (Barrett 1983, Furness and Barrett 1985, Krasnov and Barrett 1995). Capelin and sand lance were then abundant both in the Barents Sea and in the waters around the islands every summer, and the birds were expending little energy in collecting them and other food items (Furness and Barrett

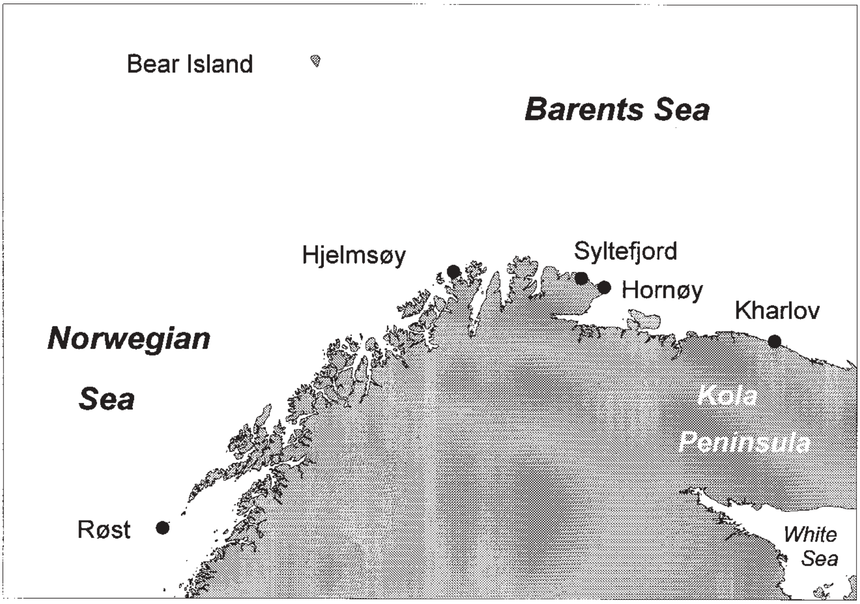

*Figure 2. Map showing the geographic positions of the North Norwegian and Russian seabird colonies mentioned in the text.*

1985). At Hornøy, the overlap in choice of food between species was generally high (Morisita's index, >0.71 in 13 of 21 cases), and diet diversity was low (Shannon-Weaver index, <0.3 in six of seven species; Barrett and Furness 1990). In 1986-1987 there was a near total collapse in the capelin stock (from 2.4 million metric tons in 1984 to 20,000 metric tons in 1987, Figure 1, Gjøsæter 1996), and a general breeding failure among many seabirds throughout North Norway in 1987 (Vader et al. 1987). However, in 1988 and 1989, when the capelin stock was still low (400,000 and 300,000 metric tons, respectively), seabirds on both colonies continued to thrive. Chick growth studies in 1988 (Figure 3) and a detailed survey of diets on Hornøy in 1989 showed that food was still plentiful, and that instead of an expected decrease in the utilization of capelin by any of the species on the island, there was an actual increase in the amount of capelin caught (Barrett and Furness 1990). Five of the seven species studied fed their chicks a diet of >70% capelin, and chick production remained high (Pers. obs., R.T.B.). This even applied to the surface-feeding kittiwakes, one of the first species one would expect to have been affected (Furness and Ainley 1984).

Whereas there was no apparent change in diet in response to the changes in the capelin stock, seabirds at Hornøy and Kharlov have sub-

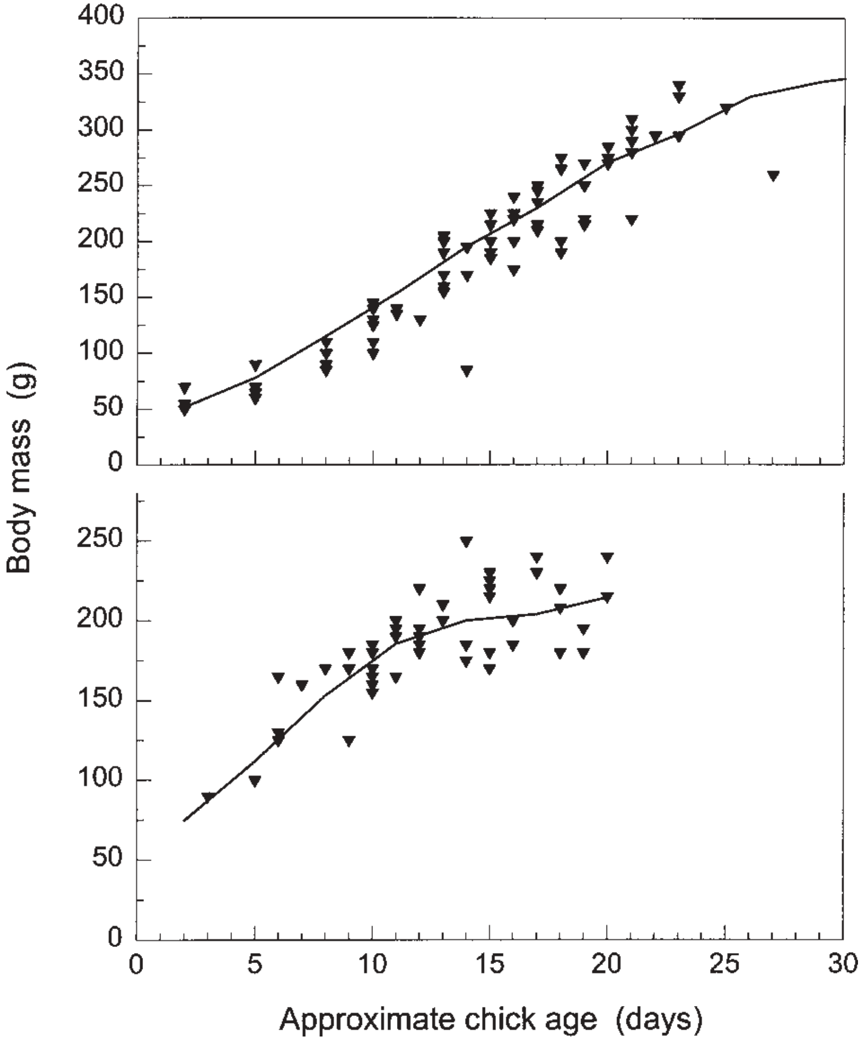

*Figure 3. Growth of Atlantic puffin (Fratercula arctica) and razorbill (Alca torda) chicks in 1988 compared to "normal" curves (data from 1980) at Hornøy, North Norway.*

sequently responded directly to the recent increase in the herring stock and the first significant production of the youngest age classes since the collapse in the stock in the late 1960s. Age-1 herring first appeared in kittiwake food samples in 1985 and since became a very significant constituent of the chick food in some years (>90% in 1993 and 1994). Similarly among common murres and Atlantic puffins, age-1 herring made up much of the chick diet after 1990 and there was a clear, significant correlation between the percentage of herring in the chick diets of all three species and the strength of the age-0 cohort in the previous year (Barrett and Krasnov 1996). At the same time, there was an increase in the diversity of prey caught by the auks, an increase in the number of prey items being carried by puffins, and a decrease in the dietary overlap between the kittiwakes, common murres, and Atlantic puffins (Barrett and Krasnov 1996). Furthermore, there was a clear negative relationship between the breeding success of kittiwakes and the amount of herring in their diet (Figure 4). These all suggest that foraging conditions for kittiwakes and Atlantic puffins deteriorated in the southern Barents Sea after herring returned to the Barents Sea ecosystem. The present hypothesis is that kittiwakes (and possibly other species) benefitted from the increase in abundance of capelin in the 1960s and 1970s in the absence of herring, capelin's main competitor, but then started to suffer as herring, a prey which seems to be less accessible than capelin, took over as the main plankton consumer in the Barents Sea (Barrett and Krasnov 1996). A longer data series is needed to test this hypothesis, but there are already signs that kittiwake chick production is dropping ($r^2 = 0.364$, $n = 13$, $p < 0.05$; data from Figure 4 supplemented by breeding success in 1982, 1991, and 1996) and that the population in the southern Barents Sea, after a general increase in the 1960s and 1970s, is now decreasing (Krasnov and Barrett 1995). Until that series is produced, this case can only be regarded as a clear example of the short-term responses of seabirds to changes in prey stocks.

### Long-term breeding failure and subsequent population decline

At Røst, at the tip of the Lofoten Islands (Figure 2), long-term population studies of Atlantic puffins (Anker-Nilssen 1992, Anker-Nilssen and Øyan 1995) have documented a rare example of how changes in prey stocks can cause changes in seabird populations through their influence on chick diet, growth, and survival. These studies have also repeatedly documented short-term responses manifested by parallel changes in chick growth and the composition of their diet within single seasons (Lid 1981, Anker-Nilssen 1987, Barrett et al. 1987, Anker-Nilssen and Lorentsen 1990, Anker-Nilssen and Øyan 1995).

With a present day estimate of 500,000-600,000 pairs, the colonies at Røst contain one of the largest Atlantic puffin breeding populations in the world (Anker-Nilssen and Øyan 1995). Successful breeding at Røst

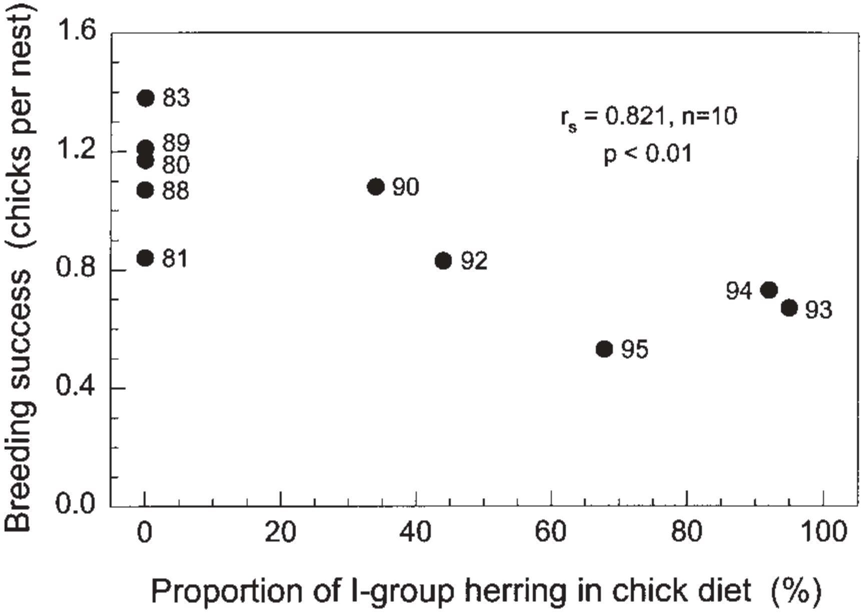

*Figure 4. The relationship between the proportion of herring (by mass) in kittiwake (Rissa tridactyla) chick diet and the breeding success of kittiwakes (no. of chicks per nest) at Hornøy, North Norway.*

is based nearly solely on the successful spring production of age-0 herring which drift past the colonies at a time and size ideally suited for puffin chicks (Anker-Nilssen 1992). Because of the near absence of alternative prey, breeding success in the colonies has proved to be exceptionally sensitive to changes in the availability of herring. This came to light after the collapse in the herring stock in the late 1960s which had a dramatic effect on the supply of food to the puffin chicks. During the 19 years when the herring stock was at its minimum (1969-1987, Figure 1), fledging success of chicks was less than 50% in all but three seasons (1974, 1983, and 1985) and most years were complete failures (Lid 1981, Anker-Nilssen 1987). After a long fishing moratorium, the herring stock finally began to show signs of improvement in 1988, and the puffins immediately responded through an improvement in their breeding success with four successful seasons in 1989-1992. It failed again, however, often nearly completely, in 1993-1996 (Figure 5).

The breeding failures were documented as direct results of adults failing to find enough food of sufficient quality to ensure chick survival, and in many seasons chicks lost mass and died in the nest within 10-20 days of hatching (Anker-Nilssen 1987). When herring was available,

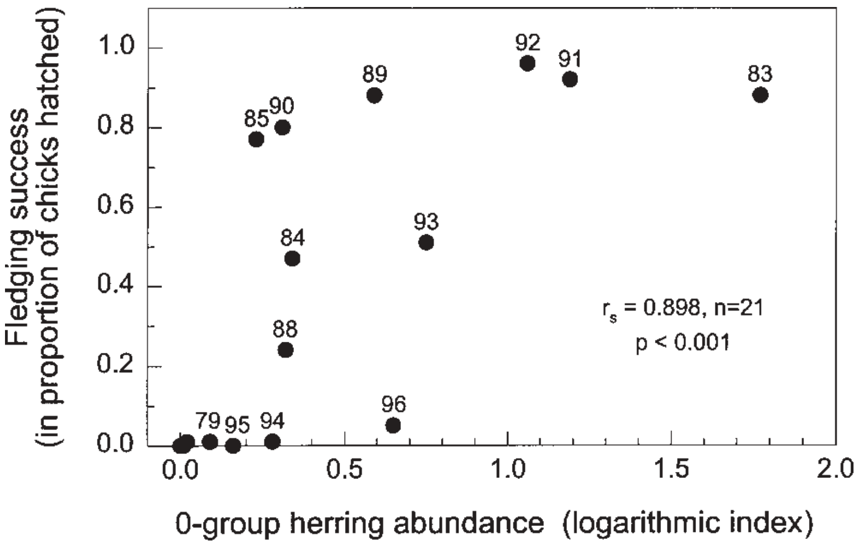

*Figure 5. The relationship between the abundance indices of age-0 herring in the Barents Sea and adjacent waters in early autumn (cf. Figure 1) and the fledging success of Atlantic puffins (Fratercula arctica) at Røst in 1975-1996 (data from all years except 1976). Eight points are situated close to the origin.*

chick growth improved and there was a very strong correlation between the puffin breeding success and independent (Institute of Marine Research, Bergen) estimations of the strength of the age-0 herring cohort the same year (Figure 5). But even in a season which started successfully, there was often a sudden cessation/reduction in chick food provisioning, the timing of which varied from early in the chick-growth period (e.g., in 1993-1994) to late in the period (e.g., 1981-1985) (Anker-Nilssen and Øyan 1995). This resulted, not only in considerable annual variations in the mean fledging mass of chicks in the period 1983-1993 (measured 1-2 days prior to fledging: range = 197-330 g, n = 8 years), but also in seasonal variations with those fledging early weighing much more than those fledging late. Even in 1989-1992, when the fledging success was high, the mass of chicks leaving the nest dropped from 300-350 g to less than 200 g two to three weeks later (Anker-Nilssen and Øyan 1995). Although Harris and Rothery (1985) failed to find any relationship between fledging mass and post-fledge survival, their data were collected in seasons when chick growth and breeding success were good. Preliminary data from Røst, where many fledglings were seriously underweight, strongly indicate that the lightest chicks have a higher mortality rate than those that fledge heavy (Anker-Nilssen and Øyan 1995).

There was also a strong positive correlation between the breeding success of the Røst puffins and the recorded changes in their population size 5-7 years later (Anker-Nilssen and Øyan 1995), the normal age of first-time breeders (Harris and Wanless 1991). Furthermore, the rate of decline between 1983 and 1987 (13.7% per year) was considered to be equivalent to the current rate of adult mortality (Anker-Nilssen and Røstad 1993). Both facts suggested that there was little immigration or emigration to and from the colonies; i.e., they were self-recruiting. Because there have been so many successive breeding failures, there has been a marked decline in the population at Røst, which dropped by 64% between 1979 and 1988. After that there was a slight increase until 1990 and a second decline until the latest counts made in 1996, when the population was only 35% of that when monitoring started in 1979 (Anker-Nilssen et al. 1996; Pers. obs., T.A.N.).

It should be added that, based on resightings of individually color-ringed birds, adult survival rates were estimated to be very high (about 95% per year) during 1990-1994, but then dropped to 85.5% between the two poor seasons, 1994 and 1995 (Unpubl., T.A.N.). Thus, it is likely that increased adult mortality in periods of very poor food supply (e.g. in the early 1980s) has contributed significantly to the population decline.

The kittiwakes at Røst also seem to depend on a good supply of young herring in order to secure high breeding success (Figure 6). However, probably due to less profitable prey being readily available, their breeding has never failed completely, and no significant decrease in their population size has been recorded after monitoring was initiated in 1980 (Anker-Nilssen et al. 1996). The results may suggest that both puffins and kittiwakes respond to certain threshold levels in herring abundance, above which breeding success is consistently high, and that the threshold for kittiwakes is somewhat higher than that for puffins (Figures 5 and 6). Considering the very different foraging behavior of the two species, such a difference could be expected, as herring is likely to be more available for a diving than a surface-feeding predator.

## *Acute adult mortality and subsequent population decline*

The most dramatic event, both in its brevity and scale of response, recently documented in North Norway was the collapse of the common murre population in 1985-1987. During the two previous decades, numbers on several colonies west of the North Cape had been declining at a steady rate of about 5% per year (Bakken 1989), but to the east they had been either stable (Syltefjord) or increasing (Hornøy, Kharlov) at a similar rate (Vader et al. 1990a, Krasnov and Barrett 1995). Causes of the decline to the west had not been directly documented, but recruitment

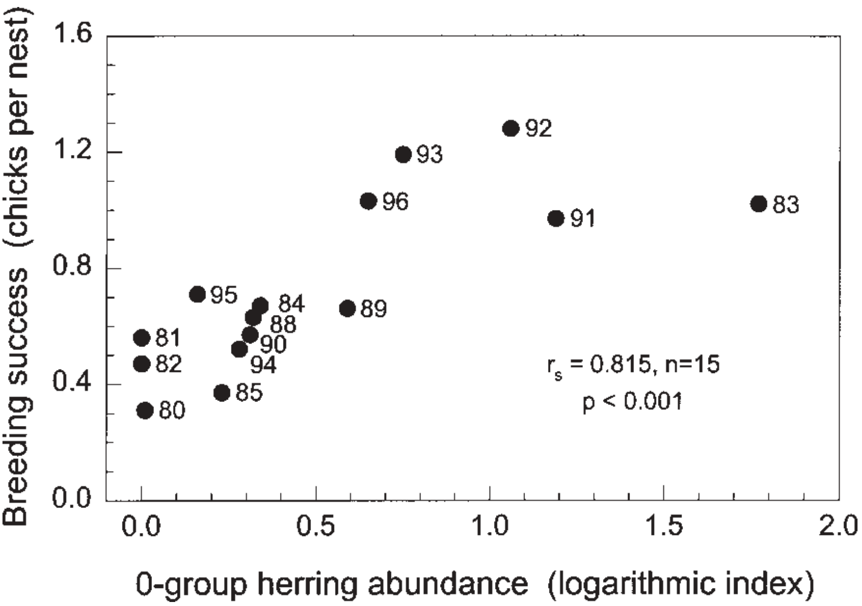

*Figure 6. The relationship between the abundance indices of 0-group herring in the Barents Sea and adjacent waters in early autumn (cf. Figure 1) and the breeding success of kittiwakes (Rissa tridactyla) (no. of chicks per nest) at Røst, North Norway in 1980-1996.*

failure (e.g., at Røst; Bakken 1989) and, perhaps more serious, elevated adult mortality through drowning in fishing gear (Strann et al. 1991) were proposed as important factors. Subsequent ringing data and evidence of inter-colony movements (Nikolaeva et al. 1996) also suggest that a net movement of birds eastward into the expanding colonies cannot be excluded.

However, in 1986 and 1987, counts at five colonies (Bear Island, Hjelmsøy, Syltefjord, Hornøy, and Kharlov) revealed an 80% collapse in numbers of breeding birds between one season and the next. There were also indications that the numbers of common murres wintering in the central Barents Sea in February 1987 were much lower than normal, at the same time as large numbers of dead, emaciated murres were being washed ashore along the mainland coast (Vader et al. 1990a,b). Furthermore, there was no evidence of an equally extensive and sudden recovery on any of the mainland sites in the subsequent years which would have suggested that birds had simply skipped a breeding season as found, for example, for shags (*Phalacrocorax aristotelis*) at a large (about 2,400 pairs) colony near Hjelmsøy (Anker-Nilssen et al. 1996). Although numbers of common murres on Hjelmsøy did quadruple between 1987 and 1988, the numbers in 1988 were still only 40% of the 1985 total (Anker-Nilssen and Barrett 1991). On Bear Island it is also likely that some of the population deferred breeding in 1987 as numbers of birds on the colony nearly doubled between 1987 and 1989, after which they have remained fairly stable (Bakken in Anker-Nilssen and Barrett 1991, Isaksen and Bakken 1995).

In 1987, conditions in the region were exceptional as the capelin stock was at a minimum, and the youngest age classes of herring produced in 1983-1985 (Figure 1) had left the Barents Sea after suffering heavy predation (especially those of 1984-1985) from an increasing Norwegian-Arctic stock of Atlantic cod (*Gadus morhua*) (Hamre 1994). Not only were the seabirds in the region badly affected, with near universal breeding failures (Vader et al. 1987), but thousands of starving harp seals (*Pagophilus groenlandicus*) invaded Norwegian coastal waters. Furthermore, the Atlantic cod population, the largest stock of predatory fish in the region, also suffered from a lack of food (Hamre 1994). As a result, the traditional coastal fisheries underwent a severe crisis. It was concluded that the common murres had suffered an extraordinarily high mortality during the winter in the near absence of their preferred prey (capelin) and any alternative prey (Vader et al. 1990a).

By 1990, the physical conditions in the Barents and Norwegian seas had improved, triggering increases in capelin growth rates and in herring and cod recruitment (Skjoldal et al. 1992), although the latter ultimately contributed to a second collapse in the capelin stock (Hamre 1994). After its initial collapse, the capelin stock had recovered rapidly to 5.6 million metric tons by 1991, but collapsed again two years later to near zero (Figure 1, Aglen 1996). This time, however, there was no evidence of an accompanying decline in the murre populations. On the contrary, on Hornøy and Kharlov, numbers continued to increase steadily at rates of 5 and 14% per year, respectively (Krasnov and Barrett 1995). This may have been due to an increase in the availability of alternative prey (age-I herring) which was absent in 1987. It is possible that, in the absence of capelin, the relative abundance of young herring was then a sufficient alternative food source for the diving seabirds in the region.

## Discussion

The situation at Røst is one of the clearest cases to date which demonstrate how repeated breeding and recruitment failures as a result of food shortages have led to a substantial decline in the breeding population of seabirds. There are several other records of food shortages seriously affecting seabird breeding success (reviewed by Montevecchi 1993, Furness 1996), but they were generally short-term effects which did not subsequently have measurable effects on breeding numbers (e.g., Springer et al. 1984, Byrd et al. 1993) or, if declines were detected, the cause was not limited to recruitment failure but also to factors such as increased adult mortality or emigration (e.g., at Shetland; Furness and Barrett 1991). There is, however, evidence that the recent declines in the Alaskan populations of both the black-legged kittiwake (*Rissa tridactyla*) and the red-legged kittiwake (*R. brevirostris*) is due to widespread recruitment failures through food shortages (possibly fisheries-induced) since the mid-1970s (Hatch 1993, Hatch et al. 1993).

In many situations, declines in one prey species are often compensated for by increases in the harvest of an alternative prey species (e.g., Hamer et al. 1991, Montevecchi and Myers 1996). Although puffins are known to feed on a wide variety of prey species (Harris 1984, Anker-Nilssen 1987), their diet is generally dominated by a few species of suitable caloric value, size, and availability during the breeding season. Even so, the disappearance of one species is often buffered by the availability of one of the others. Although evident in the Barents Sea colonies (Hornøy and Kharlov), this form of buffer is apparently absent at Røst where the situation has been unique in that puffins seem to be nearly totally dependant on one species only, herring. In the absence of herring, alternative prey of suitable quality (saithe, *Pollachius virens*, or the sand lance, *Ammodytes marinus*) was only occasionally available in quantities large enough to support normal chick growth and productivity (Anker-Nilssen 1992, Anker-Nilssen and Øyan 1995).

At Hornøy and Kharlov, on the other hand, the wide variation in prey choice during the summer showed how the birds there could compensate for decreases in the availability of one prey species by harvesting one or more other species. However, during the winter, the survival of common murres seemed to have become dependent on capelin during the years herring was absent from the Barents Sea. Although their populations thrived and increased when capelin was abundant, this dependence ultimately had severe, negative consequences when the capelin stock collapsed.

While longer-term changes in populations associated with food availability have been documented elsewhere (Randall and Randall 1986), such dramatic population declines through a sudden food shortage-induced mass adult mortality are rare. One exception is the situation in Peru where there have been recurrent, catastrophic mortalities of guano birds (cormorants and boobies) after the disappearance of their main food, the anchovy (*Engraulis ringens*) (Furness 1982). The guano birds, however, unlike the common murre, have an *r*-selected life strategy (large clutch sizes, early maturity, and the ability to breed more than once within a year) favoring the rapid recovery of the numbers of breeding adults. Murres are typical *K*-strategists, and their population recovery may take many decades after such a perturbation (e.g., Ford et al. 1982, Hudson 1985). Another example is the events associated with the aperiodic El Niño-Southern Oscillations (ENSOs) in the Pacific Ocean which cause total breeding failures, mass movements of populations to prospect new breeding sites, and increased adult mortality through collapses in food supply (Schreiber and Schreiber 1989, Ainley and Boekelheide 1990).

At a more local scale, mass mortalities of, for example, auks ("wrecks"), have been associated with food shortages exacerbated by gales, but not necessarily resulting in subsequent declines in breeding populations (Blake 1984, Hudson 1985). Harris and Bailey (1992), on the other hand, also associated an end to puffin and murre population increases at a Scottish colony with changes in the number and distribution of prey fish (sprat, *Sprattus sprattus*) and increases in juvenile and adult mortality rates, but neither case was as dramatic as the 80% decline in the southern Barents Sea common murre population.

The seabird population and breeding statistics discussed in this paper add to the increasing amount of evidence on the importance of seabird-fish interactions and how such data can be used as an additional tool in the monitoring of prey fish stocks. However, they also substantiate the increasing need for more detailed and contemporary information on the local distribution of seabird prey, including the noncommercial stocks such as those of the northern populations of sand lance, and for improving our knowledge of the most important factors determining their availability for seabirds.

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# Decline of Pigeon Guillemot Populations in Prince William Sound, Alaska, and Apparent Changes in Distribution and Abundance of Their Prey

**D.L. Hayes and K.J. Kuletz**
*U.S. Fish and Wildlife Service, Anchorage, Alaska*

## Extended Abstract

Pigeon guillemots (*Cepphus columba*) are cavity-nesting, pursuit-diving seabirds that forage in the nearshore environment on both demersal and schooling fishes. The population of pigeon guillemots in Prince William Sound (PWS) decreased from approximately 15,000 in the early 1970s to less than 5,000 in the 1990s (Agler et al. 1994). The populations at Naked Island6 nd four neighboring islands in PWS have shown a similar trend since the late 1970s (Figure 1). During this same period, the diet of pigeon guillemot chicks on Naked Island also changed. We believe there is a link between the change in diet and the population decline.

We studied the chick-feeding patterns and reproductive success of pigeon guillemots at Naked Island over 8 years. In the years 1979-1981 Pacific sand lance (*Ammodytes hexapterus*) made up the single largest component (mean = 42.1%, SD = 17.3%) of chick diet, while in the 5 years 1989-1990 and 1994-1996, sand lance accounted for a much smaller fraction (mean = 12.9%, SD = 3.2%; Figure 2). Demersal fishes such as gunnels (Pholidae), pricklebacks (Stichaeidae), and sculpins (Cottidae) have always been an important component of chick diet, and their relative contribution has increased since 1989. The proportions of Gadidae and schooling fishes such as Pacific herring (*Clupea pallasi*) and capelin (*Mallotus villosus*) have varied widely from year to year, but gadids were not a major component of chick diet until 1989.

At Naked Island, the percentage of sand lance in chick diet was positively related to both the number of guillemots ($R^2 = 0.74$, $P = 0.013$) and to the number of active nests ($R^2 = 0.69$, $P = 0.010$). To test the impor-

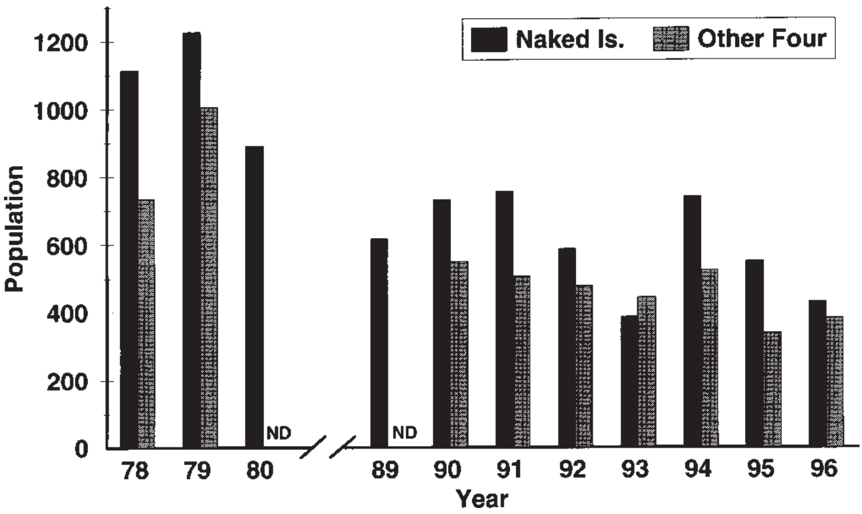

*Figure 1. Pigeon guillemot population at Naked Island and combined population at four other islands (Peak, Storey, Smith, and Little Smith islands) in Prince William Sound, Alaska. ND = no survey data.*

tance of sand lance to reproductive parameters, we grouped clutch size, hatching success, fledging success, growth rate, and fledging weight according to “sand lance” (1979-1981) and “non-sand lance” (1989-1990, 1994-1996) years. We found no significant difference between year groups for any of these parameters, although growth rate was highest in 1979, when sand lance was 60% of chick diet.

The productivity of guillemots at Naked Island was lower, but not significantly so, in the 1990s than it was in the late 1970s. After 1989, predation was more prevalent at our study colonies than it was previously, and was the cause of numerous failed nesting attempts. Guillemots at Naked Island, however, are doing better than their conspecifics in other regions. The weighted average productivity of guillemots on Naked Island (0.81 fledgling/nest) is higher than the combined weighted average for numerous studies of guillemots in British Columbia, Washington, and Oregon (0.65 fledgling/nest; Ewins 1993). Thus low productivity is not likely to be the cause of the population decline.

In PWS 135 carcasses of guillemot adults were recovered following the 1989 *Exxon Valdez* oil spill. Compared to the 1970s, oiled shorelines showed a greater decline in numbers of guillemots than unoiled shorelines (Oakley and Kuletz 1996). Although the spill may have been a contributing factor to the decline of guillemot populations in PWS, the decline began before the spill. Emigration, nest site competition, human

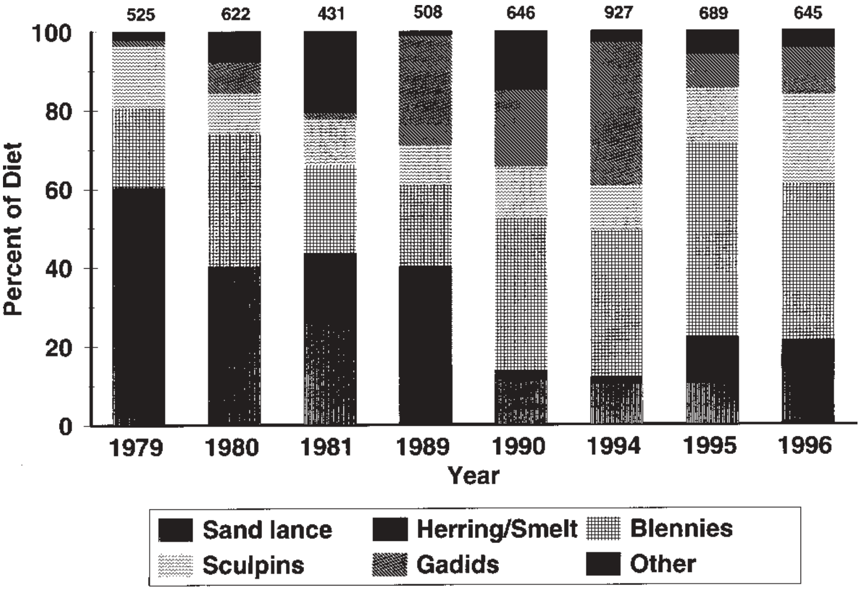

*Figure 2. Relative proportions of prey types in the diet of guillemot chicks on Naked Island, Prince William Sound, Alaska. Blennies include mostly gunnels and pricklebacks. "Other" includes greenlings, sandfish, flatfishes, rockfishes, and a few other types. Sample sizes are above bars.*

disturbance, and bycatch mortality were also considered as possible factors contributing to the decline. We lack the information to evaluate the possible role of emigration in the decline; the other factors have probably had little effect on the guillemot populations.

Data from numerous sources indicate that there has been a change in the Gulf of Alaska marine ecosystem that began around the late 1970s, which in turn has probably affected marine bird populations (Piatt and Anderson 1996 and references therein). The populations of many species of piscivorous marine birds and mammals have declined in PWS since the early 1970s (Kuletz et al. this volume). This ecosystem shift and the accompanying changes in the food web may account for many of the observed population declines. Winter mortality of adults and chicks as well as fewer nesting attempts also may have contributed to the decline, but these too are most likely food-related and thus linked to changes in the ecosystem.

Guillemots forage near their colonies and can dive to a maximum depth of about 50 m. Adults breeding at Naked Island are effectively limited to the broad, shallow-water shelf surrounding the island when foraging on demersal fishes. Demersal fish species in this limited area may not be abundant enough to support higher numbers of breeding guillemots. In addition, most of the demersal fish species have lower energy densities when compared to sand lance, herring, or capelin, all of which are high in lipid content.

Switching to alternate prey species when provisioning chicks has allowed breeding guillemots at Naked Island to maintain their productivity. The decline of these guillemot populations, however, appears to be related to lower availability or abundance of sand lance. The close positive relationship that we observed between sand lance in chick diet and the number of active nests, as well as the total pigeon guillemot population, suggest that the presence of high-quality forage fishes is important for maintaining large, productive colonies of pigeon guillemots in Alaska.

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# Long-term Changes in Diets and Populations of Piscivorous Birds and Mammals in Prince William Sound, Alaska

**K.J. Kuletz, D.B. Irons, B.A. Agler, and J.F. Piatt**
*U.S. Fish and Wildlife Service, Anchorage, Alaska*

**D.C. Duffy**
*University of Alaska Anchorage, Anchorage, Alaska*

## Extended Abstract

During the past two decades, significant population changes of marine birds, mammals, and fish have been observed in the Gulf of Alaska. In the late 1970s, there was a shift from a regime typified by high abundance of shrimp, capelin, and Pacific sandfish to one dominated by pollock, cod, and flatfish in the 1980s. Seabird diets indicated that capelin (*Mallotus villosus*), the dominant prey in the 1970s, was replaced by sand lance (*Ammodytes hexapterus*) and gadids (Gadidae) in the 1980s. Concurrent with changes in diet there were declines in seabird populations and productivity at many colonies (Piatt and Anderson 1996). However, seabird colonies in Kachemak Bay, in lower Cook Inlet, did not exhibit these declines (Slater et al. 1995). We sought to determine whether Prince William Sound showed evidence of changes similar to those of the Gulf of Alaska.

We reviewed studies of marine bird and mammal populations in Prince William Sound. The U.S. Fish and Wildlife Service conducted surveys of the sound in July 1972 to derive population estimates. Following the 1989 *Exxon Valdez* oil spill, similar surveys were conducted in 1989-1991 and 1993. Population estimates of species and species groups were examined for declines from the 1972 surveys. Detailed information on marine mammals came from separate studies.

We also reviewed diet information for marine birds and mammals during this period. Adult seabirds were collected in 1977-1979 and in 1989-1991. Chick diets were studied for black-legged kittiwakes (*Rissa*

*tridactyla*) in Port Valdez and for pigeon guillemots (*Cepphus columba*) at Naked Island.

Overall, the total summer marine bird population declined significantly in Prince William Sound by approximately 25% between 1972 and 1989-1993 (USFWS, unpubl. data). Most of the bird species that declined more than 50% were piscivorous, including surface feeders and diving birds. Species or groups that declined significantly included loons (*Gavia stellata, G. pacifica*), cormorants (Phalacrocoracidae), mergansers (*Mergus* spp.), Bonaparte's gull (*Larus philadelphia*), glaucous-winged gull (*L. glaucescens*), black-legged kittiwake, arctic tern (*Sterna paradisaea*), pigeon guillemot, *Brachyramphus* murrelets (marbled murrelets, *B. marmoratus,* plus a small percentage of Kittlitz's murrelets, *B. brevirostris*), parakeet auklet (*Cyclorrhynchus psittacula*), and puffins (*Lunda corniculata* and *L. cirrhata*).

Species that prey on benthic invertebrates, such as goldeneyes (*Bucephala clangula, B. islandica*), harlequin ducks (*Histrionicus histrionicus*), and black oystercatchers (*Haematopus bachmani*), did not decline. Surf scoters (*Melanitta perspicillata*) also feed on benthic invertebrates and declined in areas recolonized by sea otters (*Enhydra lutris*), which may compete for resources.

Marine mammal populations showed similar trends. Fish-eating species such as harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and Dall's porpoise (*Phocenoides dalli*) declined by as much as 70%, whereas sea otters were increasing until the oil spill (Loughlin 1994, USFWS, unpubl. data). Based on two long-term data sets, minke whales (*Balaenoptera acutorostrata*) also appear to have declined (Unpubl. data, Kuletz; Pers. comm., C. Matkin, North Gulf Oceanographic Society, Homer, AK). Killer whale (*Orcinus orca*) groups that fed on salmon, which have increased in Prince William Sound since the 1980s, increased or remained stable. The major group of marine-mammal-eating killer whales declined, roughly tracking the decline in harbor seals (Pers. comm., C. Matkin).

During 1977-1979, pigeon guillemots, marbled murrelets, and kittiwakes took mostly sand lance, capelin, and herring (*Clupea pallasi*), although gadids were present in their diets (Table 1). For 1989-1991, adult diet information was only available for the murrelet. In 1989 and 1991, the murrelet diet in Prince William Sound was almost entirely gadids, and no capelin were present. In contrast, in 1990, murrelets in Kachemak Bay fed almost entirely on sand lance (Table 1).

From 1979-1981 to 1989-1995, the proportion of sand lance in pigeon guillemot chick diets declined from an average of 42% to 13%, and gadids increased (Hayes and Kuletz 1997). Kittiwake chicks in Port Valdez, however, continued to be fed high proportions of sand lance during 1988-1995 (Unpubl. data, D.B. Irons).

The observed long-term changes in populations of marine birds and mammals, and the data on seabird diets, were consistent with the hy-

**Table 1. Percent frequency of occurrence (%) of three primary prey groups in adult seabird diets in Prince William Sound (PWS) in 1977-1979, and marbled murrelet diet in PWS in 1989 and 1991 and in Kachemak Bay in 1990.**

| | 1977-1979 | | | | 1989 & 1991 | | 1990 |
|---|---|---|---|---|---|---|---|
| Species[a] | PG | MM | BLK | TP | CM | MM | MM |
| Area[b] | PWS | PWS | PWS | PWS | PWS | PWS | K. Bay |
| | (N = 40) | (N = 27) | (N = 10) | (N = 8) | (N = 4) | (N = 27) | (N = 13) |
| Prey type[c] | | | | | | | |
| *Ammodytes* | 20 | 41 | 40 | 0 | 50 | 7 | 92 |
| Osmeridae and Clupeidae | 0 | 11 | 40 | 100 | 0 | 0 | 0 |
| Gadidae | 18 | 15 | 10 | 13 | 75 | 89 | 15 |

[a] PG = pigeon guillemot, MM = marbled murrelet, BLK - black-legged kittiwake, TP = tufted puffin, CM = common murre.

[b] PWS = Prince William Sound, K. Bay = Kachemak Bay.

[c] Other prey types or unidentified items not included.

pothesis that an ecosystem change occurred in Prince William Sound that negatively affected piscivorous birds. The timing of these changes was similar to that in the Gulf of Alaska, but the prey species composition was different. In most seabird diets in Prince William Sound, sand lance were prominent in the late 1970s and were replaced by gadids by 1989. Sand lance were, however, present in at least one northern fjord after 1989, perhaps representing regional differences within the sound. Capelin did not appear to have been a major component of seabird diet in Prince William Sound, except perhaps in southern areas in the 1970s. The use of juvenile herring by seabirds was sporadic and patchy. In the Gulf of Alaska as a whole, capelin had predominated in seabird diets, and was replaced by sand lance and gadids in the late 1980s.

By focusing at mesoscales (i.e., Prince William Sound and Kachemak Bay), we hope to identify what prey species are critical to seabirds. For fisheries research, seabird diet information may describe regional differences in prey species distribution and abundance, and perhaps lead to answers about why good forage species disappear in one region but remain in another.

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# Geographical Variation in Somatic Energy Content of Migrating Pink Salmon Fry from Prince William Sound: A Tool to Measure Nutritional Status

**A.J. Paul**
*University of Alaska Fairbanks, Institute of Marine Science, Seward, Alaska*

**Mark Willette**
*Alaska Department of Fish and Game, Cordova, Alaska*

## Abstract

The nutritional condition of nearshore migrating pink salmon fry (*Oncorhynchus gorbuscha*) from three different locations in Prince William Sound was measured during the spring of 1995. Two sample sites were on the west side of the sound where hatcheries release large numbers of fry, and one on the east where hatchery fry are rare. Whole body energy (kJ/g) wet weight was a good indicator of nutritional status while both wet and dry weight condition factors were less reliable measures of it.

The whole body energy content of the fry averaged 3.2, 3.6, and 4.4 kJ/g wet weight at the three study sites where fry were most abundant, moderately abundant, and least abundant, respectively. The energy content of the fish from the three regions was statistically different. Fry in the best nutritional state had a somatic energy content ≥4 kJ/g wet weight. Only 2% of the 89 fry sampled from the two west side sites on 31 May and 2 June 1995 had somatic energy contents ≥4 kJ/g wet weight, versus 76% of 42 fry collected from the single east side site on 27 May. These results in conjunction with zooplankton and stomach contents data from the three sites suggest that competition for food may have limited the growth of fry at the west side sampling sites where hatcheries were releasing large numbers of fish.

# Introduction

Pink salmon are an important fishery resource in the Prince William Sound (PWS) region of Alaska. Mortality of pink salmon embryos was elevated in oiled intertidal spawning habitats and growth rates of juveniles were reduced following the 1989 *Exxon Valdez* oil spill (Bue et al. 1996, Wertheimer and Celewycz 1996, Willette 1996). Adult pink salmon returns to PWS declined sharply after 1991 (Morstad et al. 1996). The possible causes of these declines in production have been the focus of a multidisciplinary program called Sound Ecosystem Assessment (SEA). Since the late 1980s four private nonprofit hatcheries have annually released approximately 600 million juvenile pink and chum salmon into PWS (Morstad et al. 1996). Wild pink salmon also produce a large but unknown number of fry (Eggers et al. 1991). As fry enter the marine environment they feed on a variety of epibenthic and pelagic plankton (Kaczynski et al. 1973, Heard 1991). Rapid growth and good condition likely lead to increased fry survival, because larger fish are less susceptible to predation (Parker 1971). The growth of juvenile pink and chum salmon may at times be limited by availability of food (Perry et al. 1996). Food availability is a function of zooplankton standing stock, production, and intraspecific and interspecific competition. Several other common pelagic species such as walleye pollock, Pacific herring, and Pacific sand lance co-occur with the juvenile salmon and may compete for many of the same prey resources (Willette et al. 1996). At present, it is difficult to quantify the impact of interspecific and intraspecific competition for food because of lack of information on absolute abundance of key species. However, food availability should be reflected in length-weight relationships and whole body energy content. This pilot study explored some methods that could be used to quantify the nutritional status of fry as a tool to evaluate density-dependent growth.

# Methods

Juvenile pink salmon were sampled at three study sites in PWS (Figure 1). These sites were selected to represent a hatchery release site, an area where wild and hatchery fry may be mixed together, and a site where only wild fry were likely to be captured. Zooplankton and juvenile salmon samples were collected at each site. Zooplankton were sampled with a 0.5-m ring net (243-µm mesh) towed vertically from a depth of 20 m. Juvenile salmon were sampled with a small-mesh purse seine (50 m × 10 m, 3-mm stretch mesh) deployed from a 6-m skiff. Zooplankton samples and fry samples for stomach analysis were generally collected every 3 hours from 6 a.m. to 9 p.m. at each site. The relative abundance of juvenile salmon at each study site was estimated from visual surveys of the shoreline conducted every 3 hours throughout a 24-hour period. Juvenile salmon with coded-wire tags (CWTs) released from PWS hatcher-

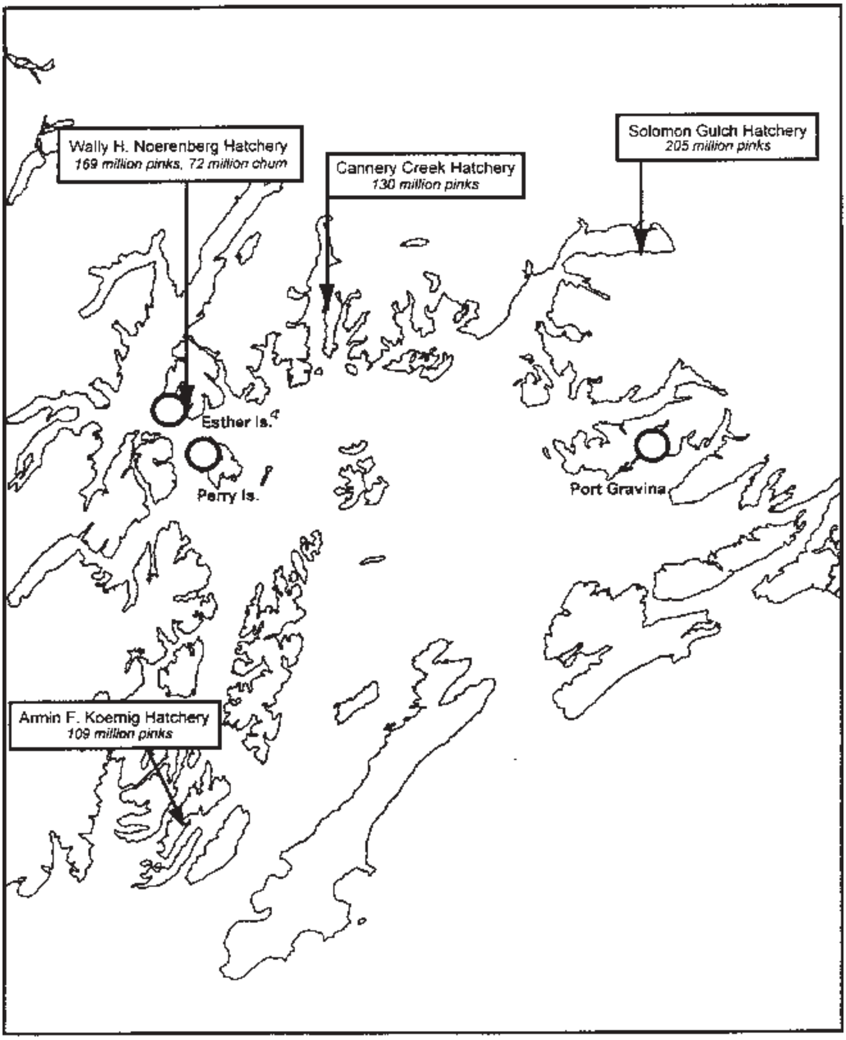


*Figure 1.* *Location and numbers of juvenile pink and chum salmon released into Prince William Sound in 1995. Circles indicate sites sampled for analysis of nutritional status of juvenile salmon.*

ies were recovered from selected net sets using a Northwest Marine Technologies tube CWT detector. The number of juvenile salmon in the catch was determined volumetrically. The proportion of the catch composed of hatchery-released fish was estimated by dividing the number of CWTs recovered by the tagged-to-untagged ratio for each tag-code group. Juvenile salmon samples collected for stomach analysis and zooplankton samples were preserved in 10% buffered formaldehyde solution. Juvenile salmon samples collected for energy analysis were frozen in seawater as soon as possible after capture.

Somatic energy content (SEC) was determined for 92 and 61 fry captured near the Esther Island salmon hatchery on 4 May and 31 May. Fry from Port Gravina (n = 42) and Perry Island (n = 28) were captured on 27 May and 2 June for energy analysis, respectively. The total number of fry captured at all sites was 223. In the laboratory the fish were partially thawed, just enough for handling but not enough to lose fluids. Data recorded for each individual were standard length (SL, to the nearest 0.1 mm), wet weight (0.001 g), dry weight (0.0001 g), whole body energy content (kJ/g wet weight), and both wet and dry weight condition factor [$CF = g\ wt \times 100/(cm\ standard\ length)^3$]. After freeze-drying for 24 hours, bodies were placed in a convection oven at 60°C until they reached a constant weight. Individual wet and dry weight values were used to calculate the moisture content. Dried tissues were pelletized and measurements of caloric content for the whole body made. Sample energy content was determined by bomb calorimetry, with one burn per fish that utilized 100% of the body. The data were plotted as individual somatic energy content versus length for each of the four collections. To explore the relationships of somatic energy content to wet and dry condition factor measurements the data from all 223 fry were combined as well as analyzed separately for each collection site. An analysis of covariance was conducted to test for differences in whole body energy content among sites with low, moderate, and high relative fry abundance. Relative fry abundance was used as a class variable in the analysis and fry length was the covariate.

In the laboratory, total zooplankton wet weight in each sample was measured to the nearest 0.1 mg after removing excess water with a vacuum pump. A stemple pipette was employed to obtain a quantitative subsample of approximately 1,000 animals from each sample. Large copepods (>2.5 mm), small copepods (<2.5 mm), and “other” zooplankters in each subsample were enumerated. Parsons and LeBrasseur (1973) determined that the feeding rate of juvenile pink salmon is approximately 3 times greater when feeding on large versus small calanoid copepods. LeBrasseur (1969) found that juvenile chum salmon select large copepods in proportion to their abundance and reject small copepods. Processing of juvenile salmon samples for stomach analysis involved measurement of fork length to the nearest 0.5 mm and whole body wet weight to the nearest 0.01 g. The stomach was then excised and total stomach contents weight was measured to the nearest 0.01 mg. The proportion of total stomach content volume composed of large copepods (>2.5 mm), small copepods (<2.5 mm), and "other" zooplankters in each sample was visually estimated. Analysis of variance was used to test for differences in total zooplankton biomass and abundance in three taxonomic groups among the three study sites. A factorial design with interaction was used in the analysis with date period and site as fixed effects (Kuehl 1994). Analysis of variance was also used to test for differences in length-adjusted total stomach content weight and the proportion of total stomach volume in three taxonomic groups among the three study sites. A factorial design with interaction was also used in this analysis with date period and site as fixed effects. The length-adjusted total stomach content weight was estimated as the residuals of the regression of natural logarithm of total stomach content weight on natural logarithm of fork length (Perry et al. 1996).

## Results

Visual shoreline surveys indicated that the relative abundance of juvenile pink salmon at the Esther Island site was high during all three sampling periods (Table 1). Relative fry abundance was initially low at the Perry Island site and then increased in late May. Fifty-five thousand juvenile pink salmon were scanned for CWTs in late May at the Esther Island and Perry Island sites. Expansion of these tag recoveries indicated that 100% and 85% of the fish at the Esther Island and Perry Island sites, respectively, were likely of hatchery origin. At Port Gravina only 169 juvenile pink salmon were captured. The magnitude of the catches at this site were too low to estimate the proportion of hatchery-origin fish, because only 1 in 600 juvenile pink salmon released from PWS hatcheries carries a CWT.

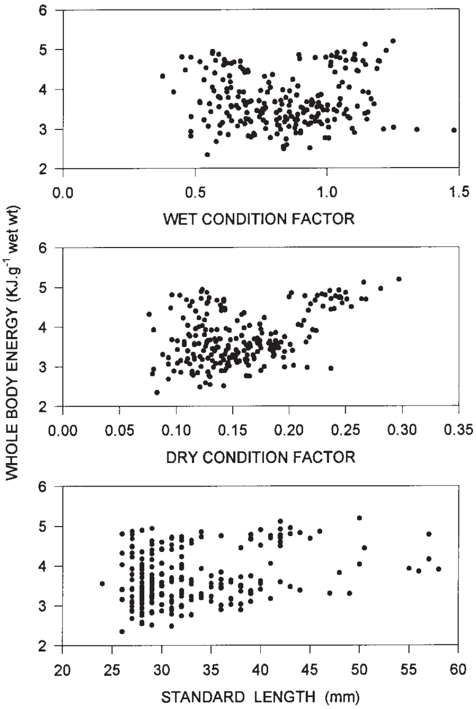
The fry from all the samples (n = 223) were combined to provide a data plot of SEC versus wet or dry condition factor and standard length (Figure 2). There was a wide range of values for SEC relative to all these parameters (Figure 2). Neither the wet nor dry condition factors for the fry from the three sites exhibited the same diagnostic trends in nutritional status as the calorimetric measurements (Figure 3). The SL condition factor measurements (Figure 3 upper, middle) suggested that the Esther Island fry had a higher nutritional status than the calorimeter analysis determined and the Perry Island fry a lower one. The condition factors did identify the Port Gravina fry as having the best nutritional status (Figure 3 upper, middle), which was in agreement with the calorimetric measurements (Figure 3 lower).

At the Esther Island hatchery site the SEC of fry averaged 3.7 kJ/g wet weight on 4 May and 3.2 kJ/g on 31 May (Figure 4). The highest energy content was nearly 5 kJ/g for fish from the first date, but those fry were likely recently released from net pens where they had been fed.

**Table 1. Summary of number of samples collected for estimation of zooplankton biomass-abundance and stomach fullness\diet composition of juvenile pink salmon at three study sites in Prince William Sound, 1995. The number of juvenile pink salmon scanned for recovery of coded-wire-tagged (CWT) fish at each site is also indicated.**

| | | Number of samples | | | |
|---|---|---|---|---|---|
| Period | Site | Relative fry abundance | Scanned for CWT | Zooplankton | Juvenile salmon |
| Early May | Esther Island | High | — | 20 | 130 |
| Mid-May | | High | — | 15 | 148 |
| Late May | | High | 31,295 | 11 | 198 |
| Early May | Perry Island | Low | — | 8 | 30 |
| Mid-May | | Low | — | 6 | 76 |
| Late May | | Moderate | 24,182 | 1 | 241 |
| Early May | Port Gravina | — | — | — | — |
| Mid-May | | — | — | — | — |
| Late May | | Low | — | 9 | 20 |

*Figure 2. Whole body energy content for 223 pink salmon fry collected from Prince William Sound, Alaska, versus wet weight (upper) and dry weight (middle) condition factor and standard length (lower).*



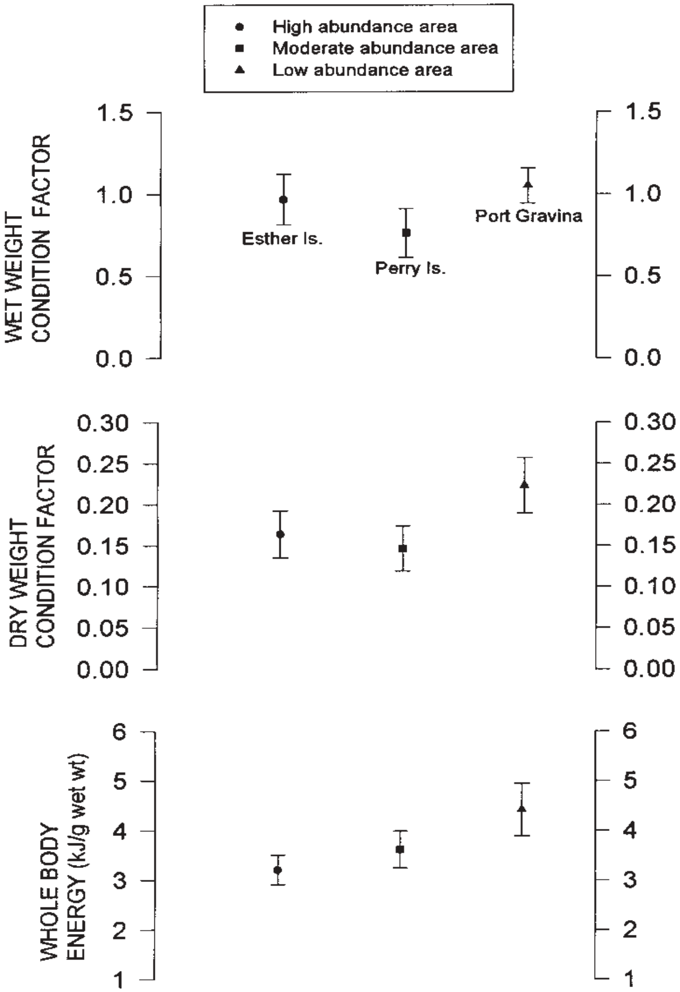


*Figure 3. Wet weight (upper) and dry weight (middle) condition factor and whole body energy content (lower) for pink salmon fry collected from three sites in Prince William Sound, Alaska, in the spring of 1995 (mean and standard deviation).*

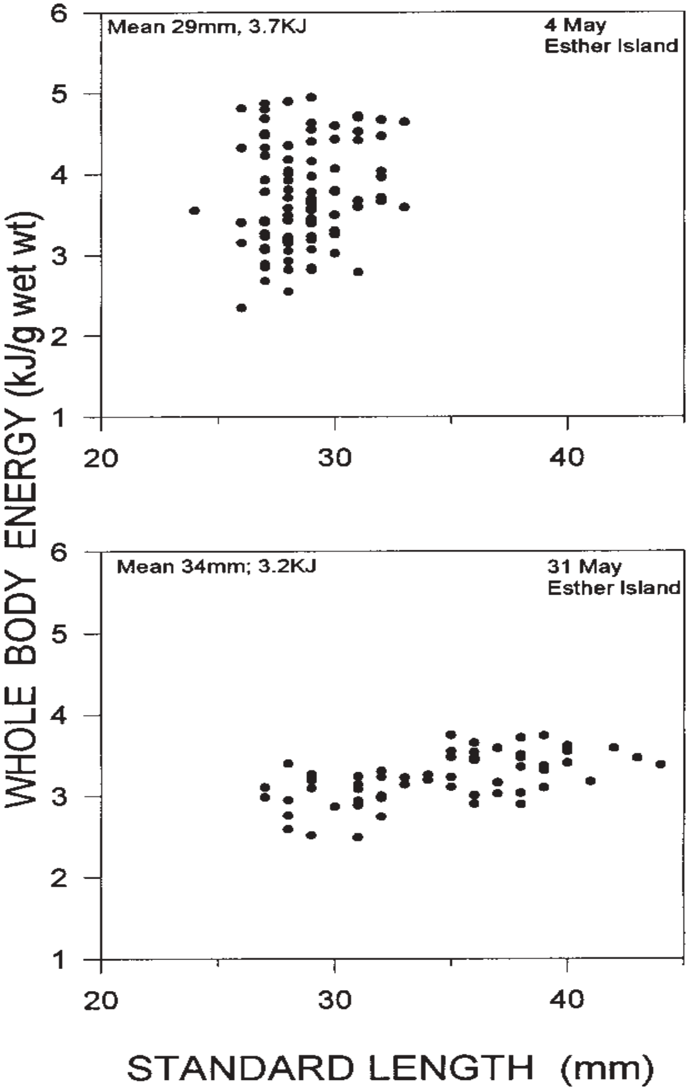


*Figure 4. Whole body energy content versus standard length for pink salmon fry collected near a hatchery on Esther Island in Prince William Sound, Alaska, on 4 May (upper) and 31 May (lower).*

The SEC of fry collected from the three study sites between 27 May and 2 June exhibited marked differences in the levels of energy stores (Figures 3 and 5). As noted above, the Esther Island hatchery site, where fry were most abundant, showed the lowest level of energy storage with a mean of 3.2 kJ/g wet weight. At Perry Island, with intermediate levels of fry abundance, the average SEC was 3.6 kJ/g wet weight, and a mean SL of 31 mm, while at Port Gravina where fry were the least abundant the average was 4.4 kJ/g, and 42 mm SL (Figures 3 and 5). A Mann-Whitney Rank Sum Test indicated that the SEC of fry from Esther Island (31 May) and Perry Island were significantly different ($P = 0.0001$). A similar comparison of Perry Island and Port Gravina energy values yielded the same conclusion. Among the Port Gravina fry, the highest level of somatic energy storage observed was 5.2 kJ/g wet weight. Even 30-mm-SL fry, which would be recent entries to Port Gravina, had ≥4.2 kJ/g wet weight (Figure 5). The sample from Port Gravina contained many fry over 40 mm SL, while in the samples from the other two areas the fry were shorter (Figure 5). Analysis of covariance indicated that standard length was not significantly related to SEC ($P = 0.7892$); however, the interaction term in the model was significant ($P = 0.0008$), indicating that the slope of the SL-SEC relationship differed among sites. Results from subsequent regression analyses indicated that the slope of the SL-SEC relationship was significantly different ($P = 0.0001$) from zero at Esther Island, but not different from zero at Perry Island and Port Gravina (Table 2). The least-squares mean SECs for fry at Esther and Perry islands were significantly different ($P = 0.0001$) from the mean SEC at Port Gravina; however, the least-squares mean SEC for fry at Esther Island was not significantly different ($P = 0.1638$) from Perry Island (Table 2). In the results from these paired comparisons using least-squares, the means (in Table 2) differed slightly from those obtained using the arithmetic mean shown in Figure 5.

Eight hundred and forty-three juvenile pink salmon were collected for stomach contents analysis, and 70 zooplankton samples were collected to estimate food abundance at the three study sites (Table 1). Mean total zooplankton biomass was significantly higher ($P = 0.0001$) at Perry Island and lower at Port Gravina compared to Esther Island (Table 3). The abundance of large calanoid copepods was also significantly lower ($P = 0.0001$) at Port Gravina compared to the other two sites. There was no difference ($P = 0.7658$) in the abundance of large calanoid copepods between Perry Island and Esther Island. Mean length-adjusted total stomach contents weight was significantly lower ($P = 0.0001$) at Perry Island and higher at Port Gravina compared to Esther Island (Table 4). The proportion of large calanoid copepods in the diet was significantly lower ($P = 0.0001$) at Port Gravina compared to the other two sites.

**Table 2. Results from regression analysis of standard length (SL) on somatic energy content (SEC) for juvenile pink salmon collected at three study sites in Prince William Sound, 1995.**

| Site | Relative fry abundance | Intercept | Slope | Least-squares mean SEC |
|---|---|---|---|---|
| Esther Island | High | 1.84 | 0.040 | 3.29 |
| Perry Island | Moderate | 4.21 | –0.019 | 3.52 |
| Port Gravina | Low | 4.95 | –0.013 | 4.50 |

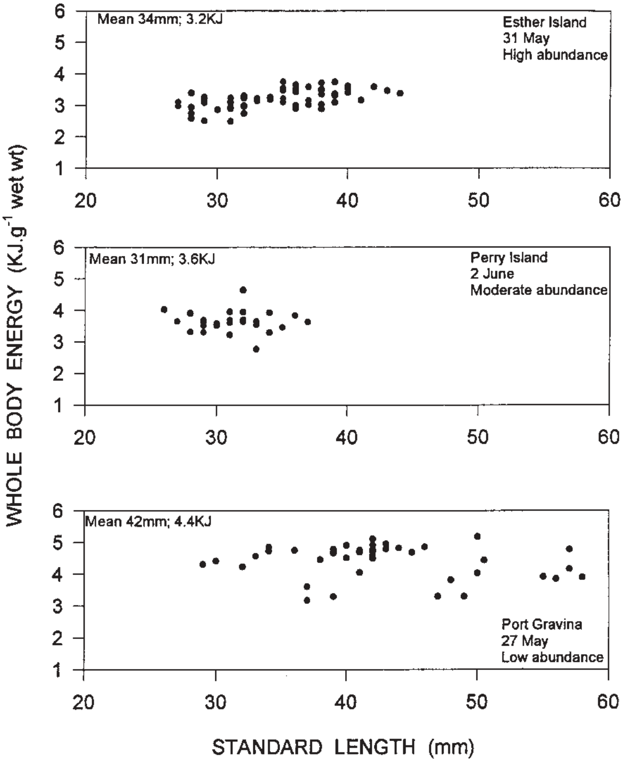


*Figure 5. Whole body energy content versus standard length for pink salmon fry collected in spring 1995 from three sites in Prince William Sound, Alaska, with different relative abundances of fry.*

## Discussion

This study showed that measuring SEC is useful for comparing the nutritional status of fry from different collections. The SL condition factor measurements were not sensitive enough to determine the subtle differences of SEC values associated with fry from the three collection sites. The highest SEC measures were 4-5 kJ/g wet weight, suggesting that fish with values <4 kJ/g were underfed. Few of the Esther Island (31 May) and none of the Perry Island fry were able to build their SEC to >4 kJ/g wet weight. Obviously our sampling was limited so this cannot be considered a representative finding for all of PWS. Additional samples from different regions, dates, and years need to be analyzed before it will be possible to determine the SEC values for well-fed fry. Perhaps SEC values of 5 kJ/g wet weight are exceeded when fry have the best feeding conditions.

These preliminary results suggest that high fry abundance may have limited the growth of PWS fry at two of three sampling sites. At the low fry abundance site (Port Gravina), total zooplankton biomass and the abundance of large calanoid copepods were lowest (Table 3). The proportion of the diet composed of large calanoid copepods was also lowest at this site (Table 4). The feeding rate of juvenile pink salmon is 3 times lower when the fish consume small rather than large calanoid copepods (Parsons and LeBrasseur 1973). Despite the apparently lower food abundance at Port Gravina, SEC values and length-adjusted total stomach contents weight was higher compared to the other two sites. The relationships between prey abundance, stomach content weight, diet composition, and SEC values at the Esther Island and Perry Island sites were less clear. Many of the fish collected for analysis of SEC at Perry Island (2 June) likely migrated from Esther Island in late May when an increase in relative fry abundance at Perry Island was observed (Table 1). Recovery of CWTs indicated that 85% of the juvenile pink salmon at Perry Island (2 June) originated from the Wally H. Noerenberg Hatchery on Esther Island (Figure 1).

This pilot study lacked the proper supportive food web data, such as competitor abundance, to adequately determine the causes for these results. Considerably more effort is needed to examine the nutritional status of juvenile pink salmon in PWS and evaluate competitive interactions. Focusing on the first few weeks after saltwater entry (or release from net pens) will likely prove to be most practical and perhaps most interesting. Evaluating the environmental conditions experienced by the fry during the first few weeks in the ocean is more practical, because at this time the fish have not dispersed greatly from their entry point. This is particularly important in examining the causes of observed nutritional status for wild fry, because we cannot at this time determine the origin of wild fry captured in the ocean. It is interesting to note that the slope of the relationship between SL and SEC was significantly greater

**Table 3. Mean zooplankton biomass and abundance of three taxonomic groups at three study sites in Prince William Sound, 1995.**

| | | Total zooplankton | Abundance (number/m$^3$) | | |
|---|---|---|---|---|---|
| Site | Relative fry abundance | biomass (g/m$^3$) | Large copepods | Small copepods | Other zooplankters |
| Esther Island | High | 0.52 | 111.6 | 2,735.4 | 294.4 |
| Perry Island | Moderate | 0.95 | 103.0 | 6,081.7 | 543.8 |
| Port Gravina | Low | 0.36 | 2.1 | 3,153.6 | 1,246.4 |
| *P* = | | 0.0001 | 0.0028 | 0.0001 | 0.0007 |

**Table 4. Mean length-adjusted total stomach contents weight and diet composition of juvenile pink salmon collected at three study sites in Prince William Sound, 1995.**

| | | Length-adjusted stomach | Proportion of total stomach contents weight | | |
|---|---|---|---|---|---|
| Site | Relative fry abundance | contents weight (g) | Large copepods | Small copepods | Other zooplankters |
| Esther Island | High | 1.16 | 0.45 | 0.32 | 0.23 |
| Perry Island | Moderate | 0.60 | 0.62 | 0.24 | 0.14 |
| Port Gravina | Low | 1.47 | 0.05 | 0.29 | 0.66 |
| *P* = | | 0.0001 | 0.0001 | 0.0037 | 0.0001 |

than zero at Esther Island and not different from zero at the other two sites (Table 2). This type of relationship would be expected if competition for food is greatest during the first few weeks after ocean entry. Competition at this time may be greatest, because the fry inhabit very nearshore areas (Cooney et al. 1978, Godin 1981) where predation risk is likely lower (Walters and Juanes 1993). As the fish grow, predation risk declines (Parker 1971) and the fish tend to be distributed farther from shore (Simenstad et al. 1980), exploiting a greater area for feeding. This behavior may reduce competition for food among larger individuals.

## Acknowledgments

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# Proximate Composition of Some Northeastern Pacific Forage Species

**Susan A. Payne, B. Alan Johnson, and Robert S. Otto**
*National Marine Fisheries Service, Alaska Fisheries Science Center, Kodiak, Alaska*

## Extended Abstract

Baseline proximate composition values are valuable for understanding the relative importance of forage species as prey in the northeastern Pacific. Samples of 14 Bering Sea and Gulf of Alaska forage species were collected opportunistically from August 1991 through June 1995 and were analyzed for protein, oil (total lipid), ash, and moisture content. Total lipids were extracted by the method of Reppond et al. (1995). Proximate values were obtained from whole organisms as would be consumed by predators. The only species with enough samples for hypothesis testing were eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), and Pacific sandfish (*Trichodon trichodon*). Juveniles of walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*), and Pacific herring (*Clupea pallasi*) are also included to provide proximate information for smaller prey than those taken in commercial fisheries. Other species included are pricklebacks (*Lumpenus* spp.), lanternfish (Myctophidae), squid (Gonatidae), surf smelt (*Hypomesus pretiosus*), rainbow smelt (*Osmerus mordax*), deepsea smelt (Bathylagidae), and juvenile prowfish (*Zaprora silenus*).

Species from the Gulf of Alaska and Bering Sea are ranked together according to proximate composition to illustrate potential similarities (Figure 1). Eulachon was the highest in oil (16.8-21.4%) and lowest in moisture (64.6-70.8%) content. A single spawned-out eulachon was 8.7% oil and 77.3% moisture. Capelin oil ranged from 2.1% to 14.0%; capelin rank similarly in oil and moisture to Pacific sandfish, Pacific sand lance, and pricklebacks. Squid and juveniles of walleye pollock, Atka mackerel, Pacific herring, and prowfish were low in oil (<1.8%) and high in moisture (>80.3%) content. Surf smelt, rainbow smelt, pricklebacks, Atka mackerel, Pacific sand lance, and Pacific sandfish ranked high in median

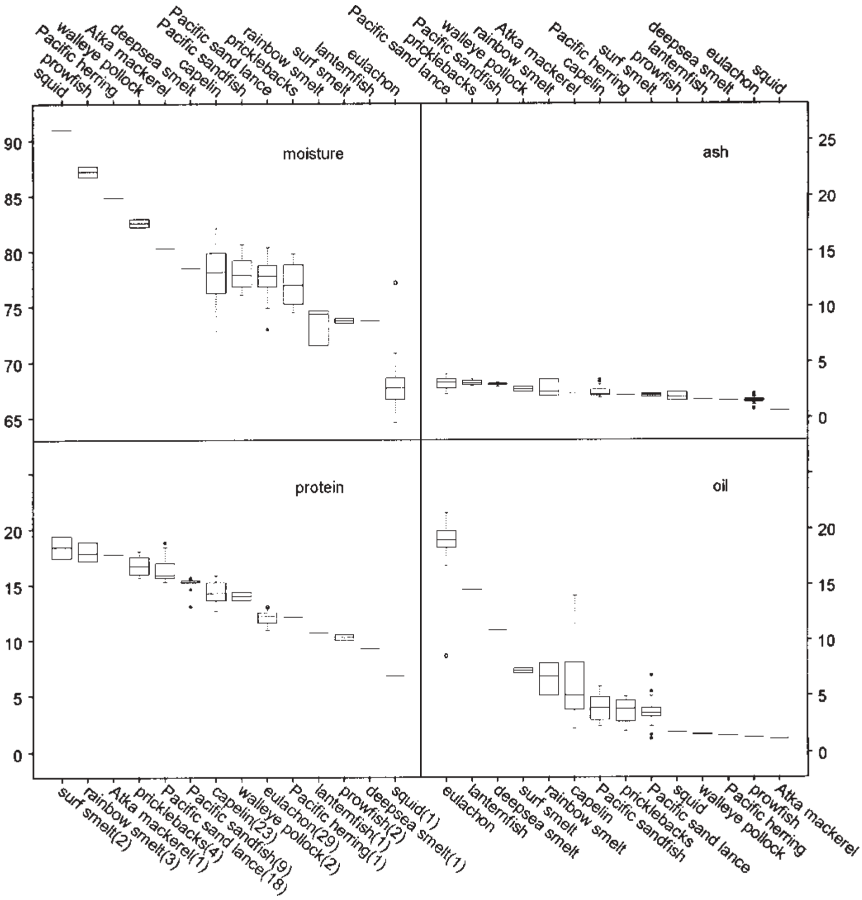

*Figure 1. Percent composition of protein, oil, moisture, and ash for forage species (n), Gulf of Alaska and Bering Sea combined. The box represents the 0.25 and 0.75 quartiles; the median is the line in the box; the whiskers at the 1.5 × inter-quartile range; and extreme observations are single points. The overlaid point (o) is for the spawned-out eulachon.*

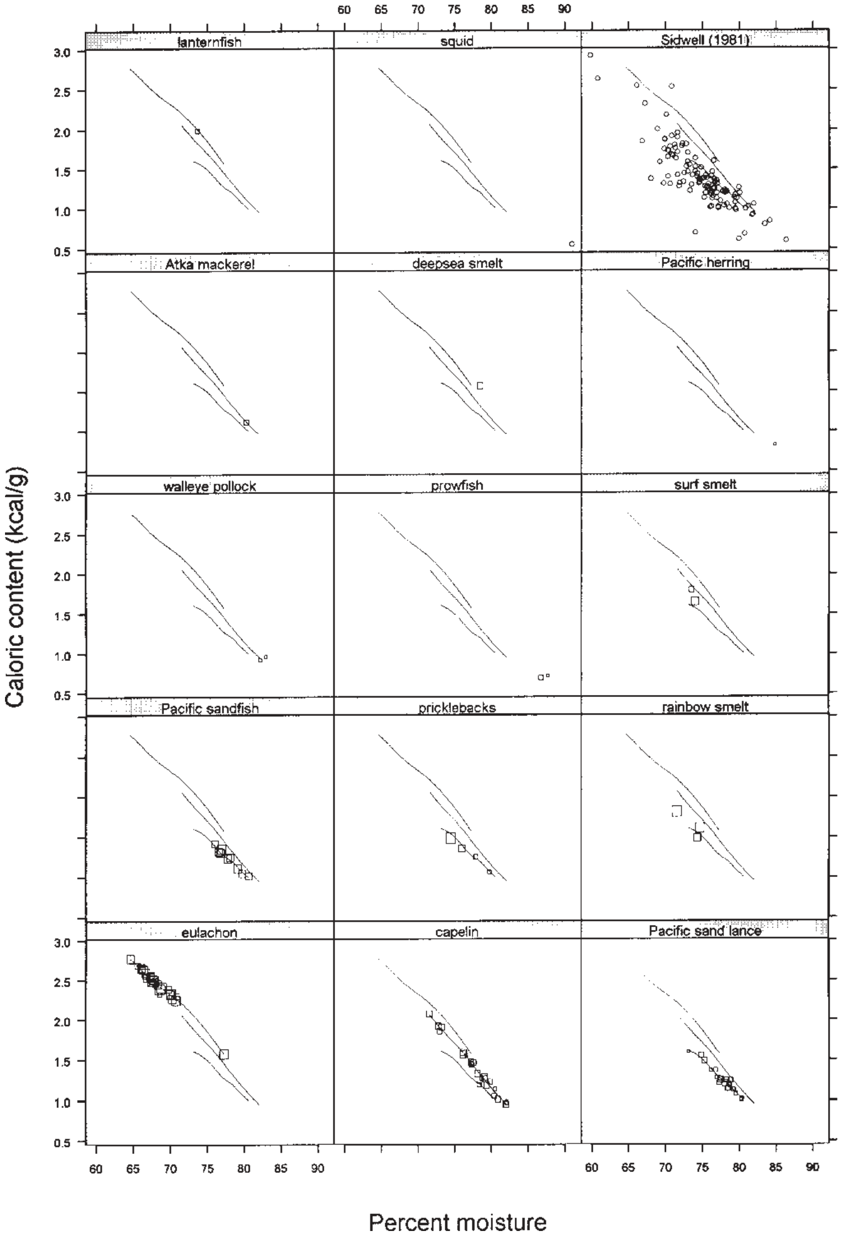

*Figure 2.* *Relation of caloric content (kcal/g = protein × 5.65 + oil × 9.50) to percent moisture. Squares represent relative length across species. Unknown length is represented by a circle. The three reference lines are robust loess fits for eulachon (n = 30), capelin (n = 23), and combined Pacific sand lance and Pacific sandfish (n = 26).*

protein content (>15.4%). Median ash content for all species ranged from 0.6% to 3.3%.

Total wet mass caloric content (kcal/g = protein × 5.65 + oil × 9.50) was calculated for additional comparisons and is presented as it relates to moisture (Figure 2). Eulachon and capelin were higher in caloric content than most forage species from the northeastern Pacific and those whole fish included in Sidwell (1981). Pacific sand lance, Pacific sandfish, and pricklebacks appear virtually identical. Single observations of lanternfish and deepsea smelt contained higher caloric content than capelin. Squid and juveniles of walleye pollock, prowfish, and Pacific herring had high moisture content and low caloric values.

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# Variation in Lipid Content of Forage Fishes and Its Effect on Energy Provisioning Rates to Seabird Nestlings

**Jill A. Anthony and Daniel D. Roby**
*Oregon State University, Department of Fisheries and Wildlife, Oregon Cooperative Wildlife Research Unit, Corvallis, Oregon*

## Extended Abstract

Differences in nutritional quality of forage fishes are a primary determinant of energy provisioning rates to nestlings of piscivorous seabirds (Ricklefs 1983, Roby 1991). Energy provisioned by parents influences not only the growth and survival of young, but potentially other factors that regulate seabird populations (e.g., post-fledging survival and recruitment rates). The primary factor determining energy density (kJ/g wet mass) of forage fishes is lipid content (% dry mass). Forage fishes vary considerably in lipid content, lipid:protein ratio, energy density, and nutritional quality (Payne et al. In press). This *Exxon Valdez* oil spill (EVOS) restoration research project is designed to develop a better understanding of how shifts in the diet of seabirds breeding in the EVOS area affect productivity and recovery of injured populations.

Fresh forage fishes and chick meals from pigeon guillemots (*Cepphus columba*), black-legged kittiwakes (*Rissa tridactyla*), and tufted puffins (*Fratercula cirrhata*) were collected in Prince William Sound (PWS), Alaska, during the 1995 breeding season. Samples were weighed and immediately frozen for later sorting, identification, measurement, sexing, and aging to the extent possible. Samples were dried to constant mass to determine water content. Lipid content of dried samples was determined by solvent extraction using a soxhlet apparatus and a solvent system of 7:2 hexane/isopropyl alcohol (Radin 1981). Lean dry samples were ashed in a muffle furnace to determine ash-free lean dry mass (>95% protein). Energy density and energy content were calculated from proximate composition (water, lipid, ash-free lean dry matter, and ash), using published energy equivalents for these fractions (lipid = 39.3 kJ/g, protein = 17.8 kJ/g; Schmidt-Nielsen 1990).

Lipid content of forage fishes consumed by seabirds in PWS varied from a low of 3% in some juvenile walleye pollock (*Theragra chalcogramma*), to as much as 48% in some juvenile herring (*Clupea pallasi*). Energy density ranged from 2.0 kJ/g in some prowfish (*Zaprora silenus*) consumed by puffins to 10.0 kJ/g in some juvenile herring consumed by kittiwakes. Thus, seabirds can experience as much as a five-fold difference in energy intake rates based solely on the quality of forage fishes consumed.

Among the forage fishes collected in PWS as part of the Alaska Predator Ecosystem Experiment (APEX) Project, juvenile herring, sand lance (*Ammodytes hexapterus*), and capelin (*Mallotus villosus*) had the highest energy densities, and were important prey of kittiwakes (Figure 1, Table 1). Juvenile gadids (e.g., pollock), prowfish, and juvenile salmonids (*Oncorhynchus* spp.) had the lowest energy densities, and were important prey of puffins. Nearshore demersal fishes (e.g., gunnels [Pholidae], pricklebacks [Stichaeidae], sculpins [Cottidae]), important prey of coastal-foraging guillemots, were intermediate between herring and gadids in lipid content and energy density.

The lipid content of herring, sand lance, and capelin, though generally high, was variable depending on age, sex, and collection site. The lipid content of juvenile herring increased dramatically from age class 0+ to older fish. Lipid content, however, was highly variable (5-48% of dry mass) even within an age class, suggesting large variation in condition of juvenile herring from PWS. Some of this variation could be attributed to differences between sites in the average lipid content of herring. The pattern of increasing lipid content with age was also evident in sand lance, but was less pronounced than in herring. Moreover, variability in lipid content within an age class was less in sand lance compared to herring. Surprisingly, the lipid content of 1+ juvenile sand lance was somewhat greater than in adult sand lance. Adult female sand lance had higher lipid content and higher energy density than adult male sand lance. Juvenile pollock exhibited a different pattern of lipid content as a function of age: 0+ pollock had slightly higher lipid content than 1+ or 2+ pollock (but lower than 0+ herring or sand lance; Table 1).

The observed inter- and intraspecific differences in lipid content of forage fishes reflect differences in life history as they influence reliance on stored energy reserves for survival or reproduction. For example, sand lance spawn in the fall (Dick and Warner 1982), and adults, especially females, presumably deposit lipid reserves during late summer for subsequent investment in gametes. In contrast, juvenile pollock feed year-round and selection has favored allocation of assimilated energy to rapid somatic growth over storage of lipid.

Energy provisioning rates to seabird young (kJ/day) can be estimated from measurements of feeding frequency (meals/day), chick meal size (g wet mass), and energy density of chick meals (kJ/g wet mass). Measurements of these three parameters were available for guillemots

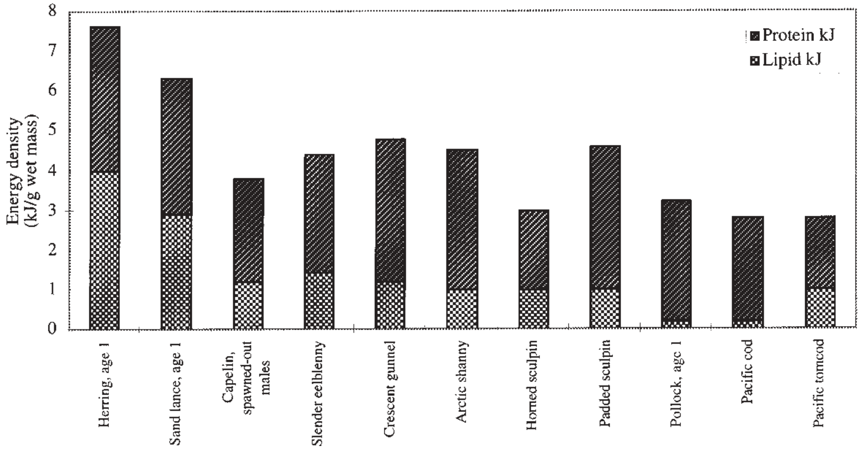

*Figure 1. Energy density (protein kJ, lipid kJ) of forage fishes in Prince William Sound, Alaska.*

breeding at Naked and Jackpot islands, kittiwakes breeding at Shoup Bay and Eleanor Island, and tufted puffins breeding at Seal Island, all in PWS. Several striking patterns emerge: (1) energy provisioning rates were apparently much higher (4-7 times) for guillemots than for puffins, suggesting that postnatal development in tufted puffins is energetically efficient and diet composition is dictated primarily by availability; (2) guillemots breeding at Jackpot Island provisioned their young at a much higher rate than those breeding at Naked Island, apparently due to the preponderance of schooling forage fishes in the diet of the former; (3) kittiwake energy provisioning rates to young were intermediate between those for guillemots and puffins; and (4) diet quality was higher for kittiwakes than for either puffins or guillemots, compensating for kittiwakes' low frequency of feeding young. The high energy density of kittiwake chick diets suggests that breeding adults are selecting prey based on quality.

In summary, our results from the first field season support the hypothesis that the recovery of seabirds breeding in the EVOS area is limited by availability of high-quality forage fishes (specifically sand lance, herring, or capelin). The productivity of pigeon guillemots and black-legged kittiwakes in the EVOS area is determined in part by differences in nutritional quality of forage fishes. By implication, the productivity of two other seabird species that were injured by the spill, common murre (*Uria aalge*) and marbled murrelet (*Brachyramphus marmoratum*), may also be constrained by availability of high-quality forage fishes.

**Table 1. Proximate composition of some forage fishes from the EVOS area, 1995.**

| Species, age | N | Sex | Location | Fresh Mass (g) | % Water | % Lipid (dry mass) | % AFLDM[a] (dry mass) | Energy content[b] | Energy density[c] |
|---|---|---|---|---|---|---|---|---|---|
| Herring, 0+ | 49 | ? | S. Graveyard | 3.19 (0.56) | 77.6 (0.10) | 9.7 (0.9) | 81.0 (0.8) | 12.5 (2.85) | 4.0 (2.85) |
| Herring, 1+ | 25 | ? | Naked I. | 13.2 (3.97) | 77.9 (2.60) | 22.3 (9.0) | 64.1 (8.0) | 62.2 (24.9) | 4.4 (0.97) |
| Herring, 1+ | 30 | M | Pt. Gravina | 18.5 (5.10) | 67.7 (3.35) | 29.1 (6.9) | 62.8 (5.9) | 129.8 (53.3) | 7.1 (1.40) |
| Herring, 2+ | 4 | ? | Jackpot | 36.9 (13.3) | 74.2 (3.00) | 31.5 (8.2) | 58.7 (7.0) | 225.0 (110.0) | 5.8 (1.11) |
| Sand lance, 0+ | 27 | ? | Naked I. | 1.86 (0.53) | 78.4 (0.68) | 12.1 (1.5) | 78.8 (0.7) | 6.6 (2.30) | 4.2 (0.30) |
| Sand lance, 0+ | 36 | ? | Block I. | 2.04 (0.40) | 76.0 (1.43) | 17.9 (3.0) | 78.4 (8.6) | 10.2 (2.64) | 4.9 (0.28) |
| Sand lance, 1+ | 10 | ? | Block I. | 9.36 (0.78) | 71.4 (1.10) | 27.7 (2.8) | 65.1 (2.5) | 59.3 (6.90) | 6.3 (0.40) |
| Sand lance, 2+ | 6 | F | Block I. | 16.1 (3.94) | 73.8 (1.50) | 21.7 (3.5) | 71.0 (3.2) | 83.4 (21.1) | 5.3 (0.30) |
| Sand lance, 2+ | 5 | M | Block I. | 13.6 (2.08) | 75.6 (1.00) | 17.5 (1.7) | 73.9 (1.9) | 64.3 (7.47) | 4.8 (0.21) |
| Capelin, adult | 10 | M | Naked I. | 21.9 (1.53) | 79.2 (1.50) | 13.0 (6.8) | 77.4 (5.2) | 82.6 (14.4) | 3.8 (0.66) |
| Pollock, 0+ | 87 | ? | Naked/Seal I. | 1.16 (0.40) | 79.3 (1.5) | 7.7 (0.8) | 80.5 (0.8) | 4.1 (1.48) | 3.5 (0.26) |
| Pollock, 2+ | 14 | ? | E. Graveyard | 33.1 (7.2) | 78.2 (1.1) | 5.9 (2.4) | 80.7 (1.8) | 120.0 (31.3) | 3.6 (0.29) |
| Tomcod, 0+ | 13 | ? | Naked I. | 2.11 (0.66) | 81.7 (6.6) | 5.8 (0.6) | 78.9 (2.1) | 6.2 (2.0) | 2.8 (0.1) |
| Pacific cod, 0+ | 38 | ? | Naked I. | 3.1 (1.7) | 83.2 (1.2) | 6.0 (1.1) | 80.2 (0.9) | 8.9 (5.1) | 2.8 (0.1) |
| Pacific cod, 1+ | 5 | ? | Kachemak B. | 13.2 (2.8) | 77.0 (1.7) | 4.4 (0.5) | 79.2 (0.8) | 44.9 (13.2) | 3.4 (0.4) |
| Crescent gunnel | 10 | ? | PWS | 11.6 (2.2) | 74.2 (1.5) | 13.2 (4.5) | 74.8 (2.4) | 52.4 (9.4) | 4.8 (0.6) |
| Slender eelblenny | 14 | ? | PWS | 8.2 (2.9) | 76.8 (1.0) | 15.6 (2.6) | 73.3 (2.5) | 36.0 (14.6) | 4.4 (0.3) |
| Arctic shanny | 19 | ? | PWS | 6.4 (3.0) | 75.7 (1.2) | 14.4 (3.4) | 73.5 (1.3) | 28.5 (13.8) | 4.5 (0.5) |
| Padded sculpin | 21 | ? | PWS | 8.3 (4.2) | 78.7 (1.6) | 9.8 (3.8) | 73.2 (2.6) | 30.1 (19.7) | 3.6 (0.5) |
| Four-horned sculpin[d] | 7 | ? | PWS | 1.5 (0.6) | 81.5 (2.3) | 8.6 | 74.8 | 4.5 | 3 |

Standard deviation in parentheses.

[a] Ash-free lean dry mass, [b] kJ/fish, [c] kJ/g wet mass, [d] individual fish pooled for proximate analysis

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# Ecosystem Impacts of Harvesting Small Pelagic Fish in Upwelling Systems: Using a Dynamic Mass-Balance Model

**S. Mackinson, M. Vasconcellos, T. Pitcher, and C. Walters**
*University of British Columbia, Fisheries Centre, Vancouver,*
*British Columbia, Canada.*

**K. Sloman**
*University of Swansea, School of Biological Sciences, Wales,*
*United Kingdom*

## Abstract

A dynamic mass-balance model, ECOSIM, is used to compare the trophic impacts of harvesting small pelagic fish in three upwelling ecosystems, previously described using the ECOPATH mass-balance approach: Peru, Venezuela, and Monterey Bay. Four different simulated fishing regimes were considered for up to 100 years. Heavy exploitation of small pelagics resulted in increased biomass of their food and competitors, while their predators usually declined. Higher trophic levels were found to take the longest time to recover. Predicted ecosystem responses under assumptions of top-down and bottom-up control suggest that, in the Peruvian system, food limitation through bottom-up control cannot explain the switch of species from anchovy to sardine. Predictions of the fishing mortality for maximum sustainable yield in small pelagics were higher than those obtained by single species approaches. By asking "what if?" questions, this work highlights some of the insights that ECOSIM may offer in the development of ecosystem management principles for pelagic fisheries. Limitations and notes of caution in running the model are discussed.

## Introduction

Overfishing is a worldwide problem concerning fishers, fisheries managers, scientists, and environmentalists. Over the last 50 years a dramatic catalogue of stock collapses have involved small pelagic forage fish. The consequence of these collapses has been most visible in terms of the economic impacts. For example, collapse of the Peruvian anchovy stock in the early 1970s had significant effects on the whole Western economy.

Structure and stability of ecosystems has been widely discussed in the ecological literature (see, for example, MacArthur 1955; Elton 1958; DeAngelis 1975; Pimm 1979; May 1981, 1983), but despite some pioneering analyses (Beddington and May 1977) there have been few rigorous attempts to model and predict the potentially devastating long-term ecosystem consequences of overfishing. In the case of the Peruvian ecosystem there is clear belief, but little evidence, that the loss of 4-5 million guano-producing birds associated with the anchovy stock will have had some profound ecosystem impact. Beverton (1990) concluded that the likelihood of harvesting small pelagic species to extinction was remote, but warned against more subtle consequences to the ecosystem that may result from collapse of a major population. He suggested that there was “some inferential (and disturbing) evidence that the disappearance of some 10 million tons of biomass and loss of recruitment in the form of adult Norwegian spring spawning herring and 2 million tons from the North Sea may have resulted in reorientation of the flow of production into alternative stable states.” Some believe this reorientation of flow was responsible for the “gadoid outburst” (Cushing 1980) in which there was a significant increase in the production of gadoid species corresponding with the decline of herring stocks. In a review of cases of replacement, Daan (1980) concluded that for the North Sea some sort of replacement was “likely.” However, under his rather strict criteria for replacement, only one out of nine candidate cases (northeast Pacific sardine and anchovy) could be considered as true replacement rather than coincidence.

Despite the reality that fisheries are generally not restricted to catching one species alone, the development of single species models for fishery management has centered around that very assumption. Due to our lack of ability to model complex systems, such methodology is still prevalent. The multispecies assessment approach (e.g., Mercer 1982) takes for granted the idea that what is taken from one stock may be lost from another. However, mainly due to the large number of parameters required to be estimated, multispecies models have generally been difficult to implement and the growing concern that it is necessary to consider interactions within an ecosystem has remained largely unmet. Management based on an “ecosystem principle” demands that we have a crystal ball to ask “what if?” questions (Larkin 1996).

This investigation uses a dynamic mass-balance model (ECOSIM; Walters et al. 1997) to compare the ecosystem impacts of four contrasting fishing regimes on small pelagic fish in three upwelling ecosystems. ECOSIM is a dynamic extension of ECOPATH (Christensen and Pauly 1992a). In each of the simulated ecosystems, small pelagic fish sustain important fisheries. Predicted impacts are discussed for individual models and compared between systems. The effects of using assumptions of “top-down” and “bottom-up” control mechanisms on the model predictions are discussed. Finally, the validity of results is evaluated by comparison to other model predictions and published observations, and some of ECOSIM’s limitations.

### *Terms and definitions*

To clarify further discussion, terms and definitions used herein are as follows: *Small pelagics* are the target species or group of small pelagic fish from each system which is subject to the four fishing regimes. The *last impacted group* is the species or group that was the last to show any change in biomass over the simulation period. The *top-down control* view holds that predation is the most important factor in controlling and limiting organisms in the ecosystem, whereas the *bottom-up control* view asserts that organisms on each trophic level are limited by food resources. *System recovery time* is the time taken for the last impacted group to return to starting baseline biomass (simulations A and C) or to stabilize at a new equilibrium (simulations B and D). *Fished group recovery time* is time taken for the fished group to recover to original biomass (simulations A and C) or to stabilize at a new equilibrium biomass (simulations B and D). *Resilience* describes the speed at which a system (or group) returns to its former state after it has been disturbed and displaced from that state (Begon et al. 1990). *Resistance* describes the ability of a system (or group) to avoid displacement in the first place (Begon et al. 1990). *Stability* encompasses both resilience and resistance. Here it is defined as the ability of a system to return to an equilibrium state after a temporary disturbance (Holling 1973). Our assumption is that recovery time is a measure of the internal stability of the system.

## Methods

For three upwelling ecosystems, the Peruvian upwelling (after the anchovy collapse in the early 1970s), Venezuelan shelf, and Monterey Bay (previously described using the ECOPATH mass-balance approach; Christensen and Pauly [1992a], see Appendix I), the primary food groups, predators and competitors of small pelagic fish along with other commercially important groups or species were identified (Table 1). To examine predicted impacts on these groups and stability and resilience, four fishing regimes up to 100 years were simulated using ECOSIM (Appendix II) (Figure 1).

There are two main operational modes of ECOSIM: (1) dynamic simulation, where fishing mortality is changed with time, and (2) equilibrium simulation, where equilibrium biomass is estimated over a range of fishing mortality. To examine the ecosystem impacts under the four fishing regimes, the dynamic simulation was used with a top-down con-

**Table 1. Model and group characteristics with main features of ecosystem that affect the fished group.**

| Model | Peru 1970 | Montery Bay, CA | Venezuela |
|---|---|---|---|
| Fished group | Anchovy | Omnivorous fish[a] | Small pelagics[b] |
| Baseline fishing mortality, F[c] | 0.54 | 0.16 | 0.08 |
| Trophic level of fished group | 2.5 | 2.6 | 2.6 |
| Food[d] | Zooplankton | Macrozooplankton<br>Mesozooplankton<br>Phytoplankton | Zooplankton<br>Phytoplankton |
| Competitiors[e] | Sardine<br>Other pelagics | Micronekton[f] | Carangids<br>Mackerel |
| Main fish predators[g] | Horse mackerel<br>Hake<br>Mackerel | Demersal fish[h]<br>Carnivorous nektonic fish[j]<br>+ top predators | Scombrids/ barracuda[m]<br>Mackerel |
| Top predators[k] | Pelican<br>Sea lion | Sea mammals[l]<br>Seabirds | Sharks<br>Scombrids/ barracuda |
| Commercially important fish[m] | Sardine<br>Horse mackerel<br>Hake<br>Mackerel | Micronekton<br>Demersal fish<br>Carnivorous nektonic fish | Other demersal fish[n]<br>Carangids<br>Scombrids/ barracuda |
| Reference | Jarre et al. 1991 | Oliviera et al. 1993 | Mendoza 1993 |

[a] Omnivorous fish - anchovies and sardines.

[b] Small pelagics - engraulids and clupeids (80% sardines).

[c] Fishing mortality specified in ECOPATH model, calculated as F=catch/biomass.

[d] Most important food groups determined by % composition in diet of fished group. In each case the groups listed showed approximately equal importance.

[e] Identified as those species/groups that had a large overlap in diet composition with the fished group (niche prey in ECOPATH).

[f] Micronekton - lanternfish, squid, large gelatinous nekton and large crustaceans.

[g] Main fish predators, listed in order of the importance in predation mortality to the fished group.

[h] Demersal fish - flatfish, hake, rockfish, bottom sharks.

[i] Other fish species that sustain important fisheries in the ecosystem. Identified by looking at the fishing mortality on each species.

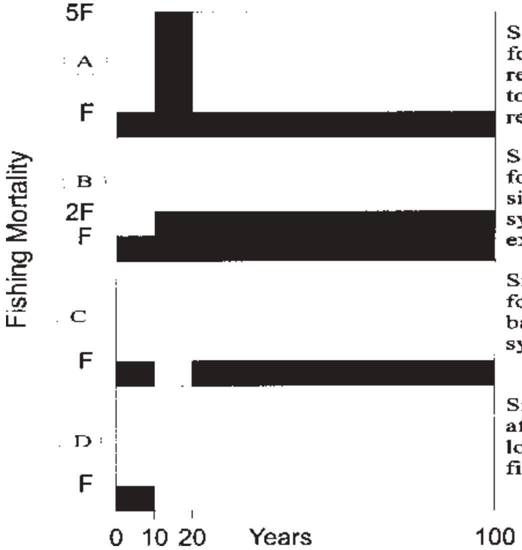
[j] Carnivorous nektonic fish - sharks, salmon, jack mackerel, tuna.

[k] Top predators in the system - those having the greatest calculated trophic level.

[l] Sea mammals - dolphins, seals, sea lions, sea otters.

[m] Scombrids/barracuda - king mackerel, little tunny, Atlantic bonito, barracuda, sennet.

[n] Other demersal fish - families Mullidae, Priacanthidae, Sauridae, Sparidae, Gerreidae.



Simulation A: Increase F, 5-fold for 10 years and then release to base level. Designed to examine group responses and recovery of systems.

Simulation B: Increase F, 2-fold for the duration of the simulation. Designed to look at system response to heavy exploitation.

Simulation C: Reduce F to zero for 10 years then resume to baseline F. Designed to consider system rebuilding/ resilience.

Simulation D: Reduce F to zero after 10 years. Designed to look at effects of stopping fishing.

*Figure 1. Simulated fishing regimes (A-D) on small pelagics. In each simulation a 10-year period was allowed to run to establish clearly the baseline biomass of each group, with which to compare change. Fishing regimes are implemented by changing the baseline fishing mortality.*

trol assumption. Later, equilibrium simulations were used to consider the effects of assuming bottom-up control mechanisms, and compare predictions of sustainable yield of small pelagic fish.

# Results

## *Ecosystem responses to imposed fishing regimes*

For all systems, imposing a 5-fold increase in fishing pressure (simulation A) results in an immediate and dramatic reduction in biomass of small pelagics. In Peru and Monterey, biomass rapidly stabilizes but at a much reduced level, whereas in Venezuela, biomass declines for the duration of the fishing period. Corresponding with depletion of small pelagics, biomass of food groups tend to increase (one exception is the decline of mesozooplankton in Venezuela). Food groups also respond to changes in biomass of competitors of small pelagics. For example, in the Venezuelan system, increasing biomass of micronekton appears responsible for declines of mesozooplankton. A close look at the Peru system (Figure 2) reveals that increasing biomass of zooplankton (food of anchovy) exhibits a temporary decline when sardines and other pelagic fish (competitors) reach their peak biomass.

Responding to changes in the biomass of prey, fish predators of small pelagics all display an initial decrease in biomass. The degree to which they are impacted further depends upon the relative importance of small pelagic fish in the predator's diet. As would be expected, those predators that rely solely upon small pelagics as their prey are impacted most heavily in terms of relative biomass change and time to recover. Predators that do not rely primarily on small pelagics, such as horse mackerel and mackerel in the Peruvian system, tend not to be heavily impacted, the increase in biomass of other species compensating their diet loss. Increasing biomass of horse mackerel (predators) is likely to be responsible for the decline in sardine after its initial increase (Figure 2). In all three systems, competitors of small pelagics represent important food items in the diet of the fish predators and hence there are close links between changes in biomass. Top predators in Peru and Venezuela are negatively impacted by the reductions in small pelagics during the fishing period, whereas sea mammals (top predators) in Monterey Bay appear to benefit, perhaps as a result of the increased biomass of other groups. When fishing mortality is returned to the baseline in Peru, sea lions (top predator) start to recover slowly, whereas the biomass of pelicans (joint top predator) continues to decline (Figure 2). Comparing the relative trophic levels of the fished group and the last impacted group in each system we see that the recovery time of predators is consistently longer than that of the fished group (Figure 3).

When fishing pressure is returned to the original baseline, most groups exhibit a time lag, and fluctuations in biomass continue for several years. Over the 80 remaining years of the simulation period, the Peruvian system was the only one that failed to recover to its former state (i.e., not all groups returned to original biomass). Table 2 ranks system recovery times.

After imposing a 2-fold sustained increase in fishing pressure (simulation B), Monterey and Venezuela recovered at a new equilibrium biomass (Figure 4). The Peruvian system did not. Continuous heavy fishing produced the same general trends as those observed in simulation A. Food of the fished groups tended to increase, competitors increased (as a result of competitive release), fish predators biomass responded to changes in biomass of different prey, and top predators displayed long-term changes with significant time lags. Commercially important sharks and scombrids in the Venezuela system suffered significant long-lasting reductions (Figure 4). In Peru, important commercial predatory fish such as horse mackerel and mackerel increased biomass at the expense of their prey, sardine and other pelagics, that declined after a temporary increase. Biomass of hake declined steadily, corresponding with the reduction in biomass of anchovy. Table 3 provides a summary of the predicted impacts on commercially important fish in the three ecosystems.

Temporary cessation of fishing for 10 years (simulation C) resulted in immediate rapid increases in biomass of small pelagics in all ecosystems. On return to the base-level fishing pressure, small pelagics responded with an immediate decrease, although the rate of response was slower (Figure 5). As expected, the direction of change in biomass of food groups, competitors and predators was opposite to simulation A. In Monterey Bay (Figure 5) the resulting increase in omnivorous fish (small pelagics) reduced the biomass of macrozooplankton (food), producing a decline in micronekton, its principal competitor. During the fishing period there is a clear increase in carnivorous nektonic fish (predator) but no apparent change in demersal fish (also a predator). However, subsequent to fishing pressure being returned to the baseline there is a small decrease in biomass of demersal fish, possibly due to an increase in biomass of sea mammals (top predators). Recovery times are ranked in Table 2.

When fishing is curtailed completely (simulation D), the Venezuelan and Monterey systems recovered to a new equilibrium (Figure 6). The Peru system displays the most dramatic responses, biomass of different components showing high rates of change. In the Venezuela system (Figure 6) the sustained high biomass of small pelagics supports the increased biomass of predators such as sharks and scombrids. A rise in the biomass of phytoplankton (food) along with a decline in mackerel (predators) may be responsible for the increased biomass of carangids (competitors).

## *Effects of top-down and bottom-up control assumptions*

Altering the ecosystem control mechanism from an assumption of top-down to bottom-up, results in a marked difference of the predicted biomass changes in terms of both rate and magnitude. Figure 7 provides an example for the Venezuela system. In all systems, changes in biomass are greater and more variable under the assumption of top-down control.

In both top-down and bottom-up scenarios, analysis of the equilibrium simulation (equilibrium biomass at various levels of fishing mortality), confirms the structural changes within the systems that were revealed using the four fishing scenarios, but there are further inferences that may be made. For example, under top-down control there is evidence in the Peruvian system of alternating fluctuations between anchovy and sardine; when one is decreased by fishing the other increases. This is less apparent under bottom-up control (food resources *limiting* interactions) and not evident when we examine pure donor control (food resources *governing* interactions), suggesting that the possibility of species switching between anchovy and sardine cannot only be due to competition for food but must in part be determined by predation mechanisms.

Predicted equilibrium yields also vary significantly between the two control scenarios. Similar results to those in the Venezuelan system (Figure 7) are found in the Peruvian and Monterey systems. For top-down

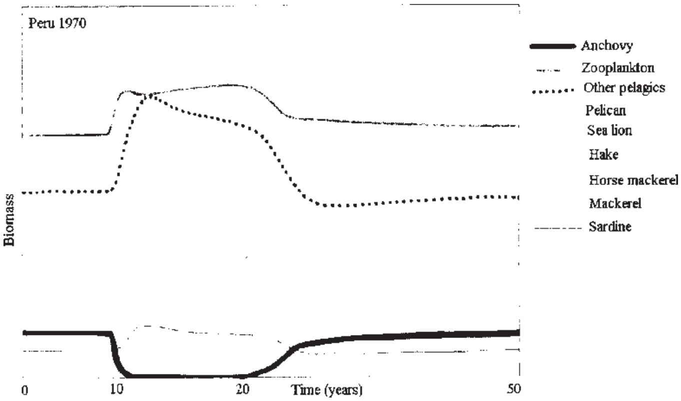


*Figure 2.* *Simulation of the Peruvian system subject to 10 years' hard fishing on anchovy (simulation A). ECOSIM outputs colored biomass curves. For each group, the plotted scale for biomass differs. This makes quantitative interpretation difficult. For ease of interpretation and reproduction, figures of simulations display only changes of the relevant groups identified in Table 1 over a period of 50 years.*

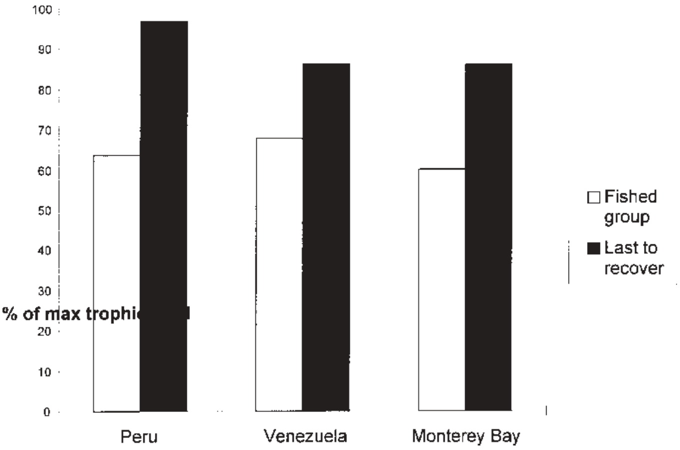


*Figure 3.* *Comparison of relative trophic level (measured as a percentage of the maximum trophic level calculated by ECOPATH) of fished group and last group to recover.*

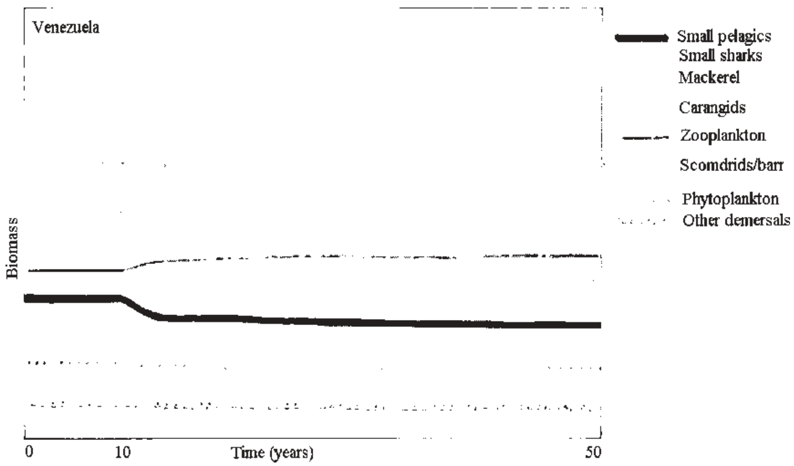


*Figure 4. Simulation of Venezuela system subject to sustained exploitation of small pelagics (simulation B).*

**Table 2. Rank of system recovery times (time to reach original or new equilibrium after disturbance; rank 1 = quickest to recover).**

| Model | Simulation A | Simulation B | Simulation C | Simulation D |
|---|---|---|---|---|
| Peru 1970 | 3[a] | 3[b] | 3[a] | 3[b] |
| Venezuela | 2 | 2 | 1 | 1 |
| Monterey | 2 | 1 | 2 | 2 |

[a] no recovery, [b] no equilibrium

**Table 3. Predicted impacts to commercially important fish from heavy exploitation of small pelagics.**

| Model | Predicted impact - direction of change in biomass on commercial fish | | | |
|---|---|---|---|---|
| Peru 1970 | Sardine<br>Temporary increase followed by decrease | H. mackerel<br>Temporary decrease followed by increase | Hake<br>Decrease balanced later | Mackerel<br>Initial decrease |
| Monterey Bay | Micronekton<br>Increase | Demersal fish<br>No observable change | Carnivorous nektonic fish<br>Decrease | |
| Venezuela | Other demersal fish<br>Decrease followed by increase | Carangids<br>Temporary decrease | Scombrids<br>Large decrease | |

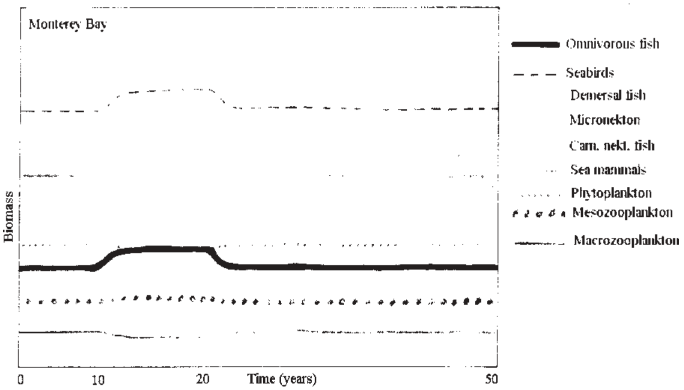


*Figure 5.* *Simulation of Monterey Bay system subject to 10 years no fishing on omnivorous fish (simulation C).*

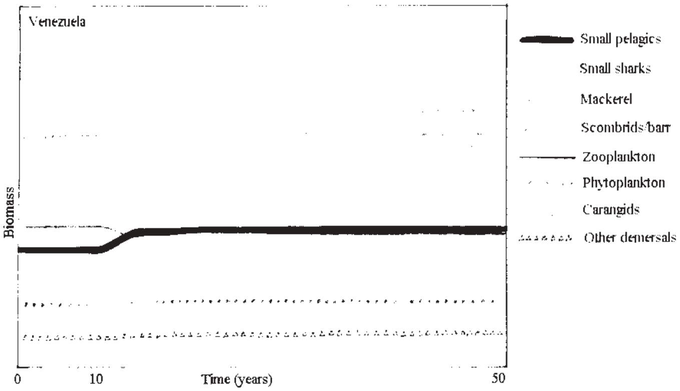


*Figure 6.* *Simulation of Venezuela system subject to complete closure of fishery on small pelagics after initial 10 years (simulation D).*

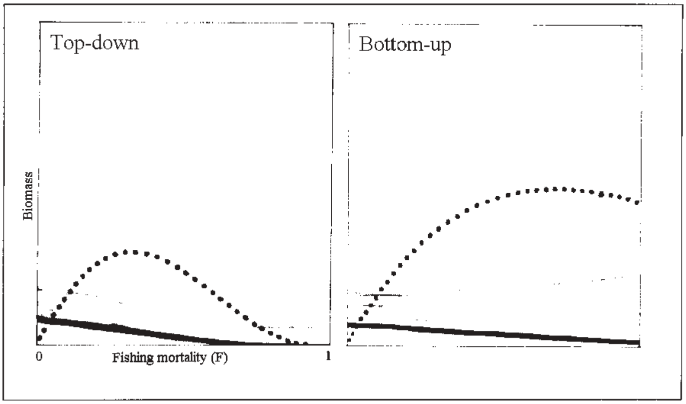


*Figure 7. Equilibrium simulations for Venezuela under top-down and bottom-up control (dotted lines, equilibrium catch; thick black lines, biomass of fished group; thin gray lines, biomass of other groups).*

control, catch increases to a maximum and then decreases to zero as *F* continues to rise and the small pelagic stock collapses. Bottom-up control generally produces a catch curve that achieves an asymptote at maximum *F*, predicting that the stock can sustain much higher fishing pressure before it begins to decline. In the case of Venezuela (Figure 7), this occurs because the decline of omnivorous fish results in a corresponding decline in biomass of their predators. Thus, predation pressure is reduced, allowing the omnivorous fish to increase in biomass again, and so sustain a higher catch.

Values of fishing mortality at maximum sustainable yield ($F_{MSY}$) predicted under the two control scenarios are compared in Figure 8. Using top-down control, $F_{MSY}$ values fall in the range 0.3-0.8. Under bottom-up control, predicted $F_{MSY}$ are more than twice as high.

## Discussion

Through the dynamic simulations we see how the effects of reducing or increasing the biomass of small pelagics propagate in time. Cascading effects were observed and in each ecosystem, predatory species took the longest time to recover. Complex interaction of groups within a system makes it impossible to determine specific causes of impacts, so we can only generalize about the likely directions of change (Table 4).

The observed dynamics demonstrate that small pelagics play a central role in the three upwelling ecosystems studied. Their direct link to phytoplankton and zooplankton food resources has significant implications for system productivity, a point well emphasized by the declines of competing species (often commercially important) when the biomass of small pelagics increased. Measurable attributes that further show the importance of small pelagics are: (1) their high throughput of energy, (2) their intermediate trophic level, and (3) high connectivity to other components in the ecosystem.

Within the upwelling systems studied here, small pelagics display poor resistance to disturbance, biomass changes occurring rapidly at the onset or release of fishing pressure. However, the short recovery time relative to higher trophic levels indicates a greater degree of resilience, a feature that is likely a consequence of their high throughput. Within the systems they can be considered dynamically fragile (responding rapidly to perturbations) but globally robust (recovering to previous or new equilibrium; Begon et al. 1990). Their high connectivity to other groups dictates that changes in biomass of small pelagics ought to have important consequences to the stability of the ecosystem. Due to its longer recovery time, we consider that the Peru system has a lower internal stability than Monterey Bay and Venezuela. Whether system recovery time is linked to attributes of ecosystem stability and maturity in marine ecosystems is addressed in a current investigation (Vasconcellos et al. In press).

When the systems were imposed with periods of continuous change (simulations B and C) new stable equilibria were reached, indicating the potential for alternative stable states. For future analysis it would be interesting to include examination of the hypothesis of "species-deletion stability" (Pimm 1979) in which the system is said to be species deletion stable if all remaining species are retained at local equilibria.

Depleting stocks of small pelagics through fishing will have important consequences for fisheries on other commercially important species. Where these other species are dominant predators of the small pelagics the likely outcome is a reduction in their biomass and catch. The converse may be true when the target species is a competitor, the increased biomass of food sustaining greater biomass of the competitor.

Most now agree with the premise that both forces act upon populations and communities simultaneously (Matson 1992). Changing the top-down or bottom-up assumptions of system control resulted in significant changes in the predicted biomass of component groups. Greater biomass fluctuations and reduced stability were apparent under top-down control. Changes in the anchovy and sardine in the Peru ecosystem imply that interactions between these species cannot solely be explained by resource competition. Daan (1980) concluded that the species satisfied his criteria for replacement, the direct food competition providing the food resource as the common base. Contrary to this, Soutar and Isaacs (1974) showed that, if anything, the two species have historically been positively correlated, changes in carrying capacity leading to similar response of the two stocks rather than to competitive effects

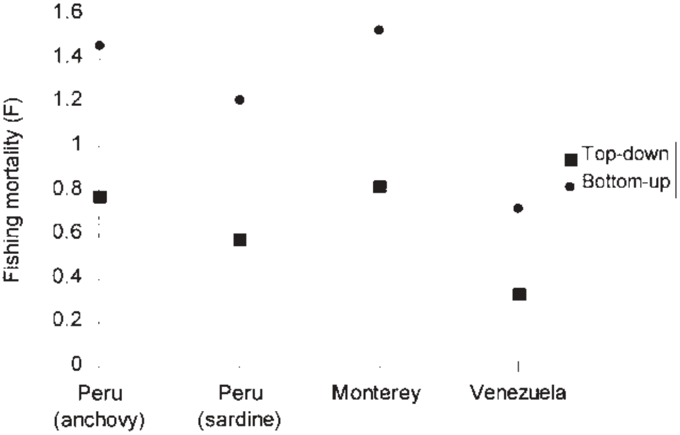


*Figure 8. Predicted $F_{MSY}$ values under top-down and bottom-up control assumptions (values for sardine in the Peru system are also provided).*

**Table 4. Direction of generalized ecosystem responses to fishing small pelagics in upwelling ecosystems.**

| Fishing pressure | Response, direction of change | | | | |
|---|---|---|---|---|---|
| | Small pelagics | Food | Competitors | Predators | Top predators |
| Increased fishing | – | + | + | + or – | – |
| Decreased fishing | + | – | – | + or – | + |

leading to replacement under normal conditions. Whether competition on a large geographic scale is the causal mechanism is yet to be decided (Lasker 1985).

A very dramatic message is conveyed from the predictions of sustainable catches under the two control mechanism assumptions; one that should sound a note of extreme caution for potential users examining harvest strategies. Predicted $F_{MSY}$ values for bottom-up control are more than twice as high as those predicted under top-down control. At best, it would be foolish to base a harvest strategy on such predictions. If we consider average fishing mortality (*F*) values for clupeoids estimated from recent fishing experience to be 0.2-0.3 (Patterson 1992), clearly stocks would not be capable of sustaining the predicted values under such an assumption. $F_{MSY}$ values calculated for sardines vary from 0.25 (MacCall 1979) to 0.23-0.49 (Kim 1984). Current results under top-down control agree with the previous observations that ECOSIM predicts high $F_{MSY}$ values, in the range of 0.3-0.8. This is because at low to medium *F* values the decrease in biomass of small pelagics causes a subsequent decrease in biomass of their predators, allowing the catch to be greater. This would not happen in single species models (Walters et al. 1997).

Some notes of caution relating to the interpretation of simulations have already been addressed. In addition, there are several points regarding sources of error. These relate to (1) ecosystem model construction and (2) implicit limitations of ECOSIM in representing trophic interactions. These are more thoroughly addressed by Walters et al. (1997), but will be summarized here. First, each ECOPATH model may differ in terms of the time span which the data represent, the number of groups used, and the parameters which are estimated. It is difficult to determine what effect differences in data quality have on the simulations but it has been implied that poor data may reduce the reliable period over which the simulation should be run (Walters et al. 1997). Second, there are inherent simplifying assumptions; ECOSIM is based purely on diet relationships and can account for only small-scale spatial relationships with the absence of complex life histories. Also it does not take into account environmental variability, a factor frequently ignored in complex food web models (Hunter and Price 1992). A further limitation is that predictions are only in terms of biomass, thus not allowing for numerical responses.

Walters et al. (1997) warn about the risk of using ECOSIM to extrapolate to circumstances far from the equilibrium for which ECOPATH data are available. However, if we only project a short time horizon and consider only short-term dynamics, long-term effects are easily missed. Despite the reserve expressed about long simulation periods, we have shown that they can be useful in predicting the directions of biomass change. This simple finding serves as a warning to keep in mind potential delayed responses, a point that should be emphasized especially when considering complex and unstable ecosystems.

As a group, small pelagics are the most economically important fish group (Whitehead 1985). They play a central role in their ecosystem, changes in their abundance affecting community structure. For these two reasons alone, it is imperative that we understand how these changes are brought about and assess the likely consequences to other commercially important fish and other species within the ecosystem. ECOSIM may be a useful tool in providing guidance and understanding on questions that are now a necessity to implementing "ecosystem management" principles.

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# Appendix I

## *ECOPATH—steady state mass-balance ecosystem model*

ECOPATH is a steady state model based on a set of simultaneous linear equations (one for each group *i* in the system) (Christensen and Pauly 1992b). The master equation simply states that at equilibrium, for all *i*: Production by (*i*) utilized within the system -catches of (*i*) -consumption of (*i*) by its predators = 0. This can also be put as:

$$0 = B_i \times (P/B)_i \times EE_i - F_i \times B_i - M_0 B_i - \sum_{j=1}^{k} Q_{ij} \qquad (1)$$

where $B_i$ is the biomass of *i* during the period in question; $P/B_i$ is the production to biomass rate of *i*, equal to the total mortality rate (*Z*) under the assumption of equilibrium (Allen 1971); *EE* is the ecotrophic efficiency, i.e., the fraction of the production ($P = B_i \times P/B_i$) that is consumed within the system; *F* is the fishing mortality on *i*; $M_0$ is the mortality rate not accounted for by consumption within the system; $Q_{ij}$ is the amount of *i* consumed by *j*.

ECOPATH solves the set of simultaneous equations to produce a balanced box model ecosystem in which the energy flows are quantified.

# Appendix II

## *ECOSIM—dynamic mass-balance approach for ecosystem simulation*

By converting the linear equations of ECOPATH models to differential equations, ECOSIM provides a dynamic mass-balance approach, suitable for simulation (Walters et al. 1997). Constructing a mass balance model from equation (1) there are three changes: (a) replace the left side with a rate of change of biomass; (b) for primary producers, provide a functional relationship to predict changes in $(P/B_i)$ with biomass $B_i$ (representing competition for light, nutrients, and space); and (c) replace the static pool-pool consumption rates with functional relationships predicting how the consumptions will change with changes in biomass of $\mathrm{B_i}$ and $B_j$. Generalizing for both equilibrium and nonequilibrium situations, this gives (Walters et al. 1997):

$$dB_i/dt = h(B) - M_0B_i - FB_i - \sum_{j=1}^{n} c_{ij}(B_i \times B_j) \tag{2}$$

where $h(B)$ is a function of $B_i$ if $i$ is a primary producer or

$h(B) = g_i \sum_{j=1}^{n} c_{ij}(B_i \times B_j)$ if $i$ is a consumer, and $c_{ij}(B_i \times B_j)$ is the function used to predict $Q_{ij}$ from $B_i$ and $B_j$. For primary producers a simple saturating production relationship is used.

Using previously constructed ECOPATH models, ECOSIM calculates corresponding changes in biomass of each component when the fishing mortality of any particular group is altered. These dynamic simulations are plotted as colored biomass curves. The scale differs for each curve. By altering the rate of flow between vulnerable and nonvulnerable prey, different functional relationships for predators and prey can be considered. These can range from pure donor control, where the prey availability governs interactions, to top-down control where predation pressure dominates. Using equilibrium simulations, where equilibrium biomass is plotted over a range of $F$ values, ECOSIM provides the facility to predict the potential equilibrium yield for the fished group.

# Workshop Discussion

## Moderator, D.E. Hay

A. J. PAUL: I have one issue to bring up, and that's the future of this group. I'm wondering whether we have any cohesion, whether we have a future, what we're going to do, and how we're going to do it. I'd really like some input on that, but virtually every topic is open for discussion.

P. ANDERSON: I'm from National Marine Fisheries Service. The only comment I'd like to make is that it seems a lot of our forage species populations are virtually unmanageable. Their dramatic fluctuation is caused by environmental changes or predation, and the best thing we can do for management of these species is to protect their spawning environment. In the case of sand lance or capelin, we need to make sure that their nearshore spawning environment gets protected. I know that in Shelikof Strait, Kodiak, and lower Cook Inlet we have oil development occurring and more development is planned. We all know that drilling muds and such contaminations might pose a serious threat to the nearshore sediment.

D. PENTTILA: I'm with Washington State Department of Fish & Wildlife. I concur with this comment and that's what we've been doing in Washington state with good results for 25 years. It was the attitude of the forage fish unit, right after it was formed, that caused us to make habitat protection and the documentation of the spawning habitat important aspects of the unit's work. That was, and it still is, one of our principal duties.

T. PITCHER: I'd like to make a very obvious point here. Spawning habitat's great for salmon and species that spawn inshore, and it may be okay for Alaskan forage fishes too, but I wonder what you do about horse mackerel, the offshore mackerel species, the anchovy, and sardine. How do you protect their spawning habitat?

K. STAHL-JOHNSON: I'm with the Alaska Marine Conservation Council. Maybe limiting the size of the vessels used will reduce impact on spawning. Identification of essential fish habitat is one of the things that the new authorization of the MFCMA act has required the federal agencies to work on. But there is a conflict between human uses and human impacts on these habitats. As biologists, we obviously understand the need to protect. It's really important for us to bring to the public an understanding of policy decision. I hope everybody will try to identify our essential fish habitat for management purposes, given all the other uses that human populations want with the marine environment. This might be a topic for another symposium somewhere down the road.

A. SILVA: I'm from Lisbon, Portugal. I'll try to answer the question that was asked about fish like horse mackerel, sardines, and anchovy. I think spawning may be protected by limiting fisheries during the spawning season. For example, fishermen on the Portugal coast voluntarily stop fishing for sardine during the spawning season. They are trying to protect the spawning, and it's also the season when there are rough seas.

D. HAY: I have three points to suggest for discussion: (1) what is a forage fish and what is an ecosystem? (2) do forage fishes affect ecosystems or other species? (3) whether the answer to (2) is yes or no, what do you do about it, how do you manage the resources?

When I saw this agenda, I wanted to know what a forage fish was, so I called up my word processing thesaurus, and I couldn't find anything. Then I tried the Oxford English Dictionary, which said forage is food animals take for themselves by browsing or grazing. I could not find a satisfactory definition of a forage fish. So I still am not sure what a forage fish is.

In the tropics, a forage fish must be a phytoplankton eater. In the Northern Hemisphere our fish are mainly in the second trophic level and pollock are mainly in the third trophic level. So I'm really puzzled about what a forage fish is; it just seems to be a very common nearshore fish.

P. ANDERSON: I suggest that we talk about forage species. Why do we have to restrict it to fish? If forage really means something that is eaten in high volume, then we must also look at shrimps, octopus, squids, all of the species. We need to broaden our view and use the term forage species.

D. HAY: The notion of forage, though, is something that grazes.

P. ANDERSON: Or something that is grazed upon.

R. STEPHENSON: Doug, you didn't read the brochure that was sent to you to invite your paper. It had a definition, which I found a bit restrictive, but it seemed to me it read something like, ". . . small schooling fishes which are important food items for mammals, birds, and other fishes." I think that's a quite restrictive definition. One has to go beyond fishes, but I think the idea that there are species which are important food items in ecosystems is appropriate. The other element that's important here is the act of things feeding on other things; or forage, the verb.

D. HAY: I think that captures it. It's greater than fish, it's grazed upon, and it's important.

F. PARRISH: In coral reef systems, a “forage fish” is basically a multispecies conglomerate that inhabits the reef, and involves every type of reef fish and crustacean. When I came here I looked at all these papers for some general modeling idea in relation to something that’s a forage base of a particular predator. That doesn’t hold just for monk seals, but it holds also for predators such as jacks, it holds for large things such as sharks, and a number of other species. So, as you go into the tropical systems, this gets an even broader definition.

T. PITCHER: How does this differ from all of the fish in the ecosystem?

K. STAHL-JOHNSON: The majority of the fishes that we’re speaking of go from some larval to juvenile stage, and become forage. So, stage of development compounds the definition.

D. HAY: The default position is that there is no such thing as a forage species. The last piece of the structure we have is a population.

T. PITCHER: This is a factual hypothesis, there is no such thing as society, only people. But we all know what society is.

D. HAY: It’s a term that has a use. The terminology is useful, but the definition isn’t?

T. PITCHER: That’s what I’m saying.

D. HAY: But it’s biologically intractable.

G. HUNT: What if you think of an ecosystem as a community gone wild? Everybody knows what a community is but nobody can define it because it’s a construct of who’s working where when. In fact, it’s not much different from an ecosystem except on a smaller scale.

D. HAY: Do you want to put community in here too? I think that would be a red herring in this meeting.

V. WESPESTAD: Okay, it’s time to throw that notion out because we’ve discussed a whole range of topics, and the operating unit is a geologically or geographically distinct unit with a cohesive biological structure, interrelated. There are large patches of ocean that have distinct units whether or not you call them communities, they’re linked assemblages.

D. HAY: Then in a sense the term is useful, it has this geographical context. One speaks of the Barents Sea or the Bering Sea so it’s a geographical term, which implies a biological component.

G. HUNT: It’s also a group of species that interact, directly or indirectly.

T. PITCHER: What do migratory salmon do, live in several ecosystems and pop through?

G. HUNT: They pop in and out of the community. Or ecosystems.

K. STAHL-JOHNSON: That's how the systems all work together.

T. PITCHER: Can we look back at forage and these systems together? I suggest that together they probably mean more than just a few terms. The kind of fish we've been looking at when we intuitively use the word forage fish is fish that are subjected to both top down and bottom up influences. They're kind of in the middle of the food web, so that things happening to top predators can affect them and harvesting humans can affect them, but they're also pretty closely linked to generation of biomass through the phytoplankton/zooplankton chain. So they're in the middle of the system and get influenced from both directions.

D. HAY: Population dynamics is one aspect of the bigger picture, because there are physical limiting factors. Is this closure on this question?

The next question is do forage fish affect ecosystems? Please use the sense of the question, not the exact terminology.

The third question is if yes or no, so what?

T. PITCHER: Can you say what you mean by affect? The answer's either yes or no. They're an integral part of the system.

D. HAY: Well, the term which first came up was "important." I sense that we could break into two groups. People like Vidar Wespestad, and on the other hand like Bob Furness.

D. HAY: If we could discuss this issue for 30 minutes or so, at least we'd capture some discussion under the context of whether there's any long-term impact of prey on their predators. Are they important, are they not?

T. PITCHER: I think we'd probably have to take those two questions together.

D. HAY: The status quo position is that we should just keep doing what we're doing.

R. FURNESS: I think it's absolutely clear that changes in forage fish stocks can have an enormous impact on birds, and the classic example is Peru with the enormous mortalities of seabirds. The Norwegian example is also very clear, that the collapse of herring or capelin stocks, in the short term, has had an enormous impact on breeding success of some bird species. That does lead to another question: Is there a need to set aside a certain amount of forage fish for the birds and for the mammals? It really depends on whether you believe that there has to be a certain number of seabirds or certain numbers of Steller sea lions. If there was a likelihood of a species going extinct because of a drop in forage fish stocks as a result of a fishery, then that's another matter. But if the rough population of puffins goes from 1.4 million down to

400,000, the average birdwatcher probably couldn't tell the difference between 1.4 million and 400,000. It's a hell of a lot of puffins, though. So I don't really see that the 400,000 is a problem, but I wouldn't see any arguments saying close the herring fishery because a million puffins have disappeared. You then have to determine what is the size that your willing to let populations to go down to. I suppose then you're talking about populations where there's a risk of extinction.

UNIDENTIFIED: Another aspect is whether or not you expect the herring to come back up. If the herring were depressed and stayed low, perhaps you would have a different feeling about measures that should be taken.

D. HAY: Of course forage fishes affect other things. Does fishing on forage fishes negatively impact other things in the ecosystem?

R. FURNESS: It's quite clear that environment factors can affect forage fishes dramatically and we're going to see natural fluctuations in forage fish stocks. The fluctuations which may be caused by fishing, may or may not be large in relation to natural fluctuations. If fisheries are only causing small changes relative to what would happen due to natural fluctuations, then presumably you consider that a trivial effect. From the angle that John Piatt was presenting, where you have a functional response, a lot of these predators need food density above a certain threshold. If a fishery is going to deplete stocks, then that threshold density may disappear, and even if there isn't a stock recruitment effect, the very act of fishing reduces the density of fish. I think if there's a fishery on forage fishes, then that must have a negative effect on natural predators, but that effect might be trivial. It might be a lot less than the effect of natural fluctuations from year to year. Anyway most of the predators must be adapted to fluctuations in food supply because forage fishes naturally fluctuate, so the long-lived predator has to be designed to cope with that.

D. HAY: I would have said that most fisheries models already incorporate that in terms of parameters of natural mortality.

K. STAHL-JOHNSON: But natural mortality changes. The thing that we don't grapple with very effectively is that you can't predict what those changes are going to be. We're so slow in our data analysis oftentimes we're past the point before we know what happened, and we haven't measured the right parameters. We don't know what real natural mortality is in our models and how it changes.

R. STEPHENSON: Doug, I think you came dangerously close to solving this when you said you "agreed that things are eating other things, but is this important?" We're talking about those situations where a species, because it's relied on heavily by another species, or by many species, would cause impacts if it was removed or reduced in numbers. It's a question of degree. I don't think it's as useful to characterize forage species as such, but forage situations where a species is providing a high proportion of the diet of something else, or is contributing to the diets of a lot of things, and therefore is particularly important to natural feeding.

In that case we'd be identifying herring not as a forage species but we'd be looking at herring in certain systems because of its contribution to normal feeding. I think the situation then becomes a lot clearer.

B. ANTONELIS: It seems like this is getting to the ethics question. Do we feel comfortable taking X amount out of all these other species' mouths and affecting these populations?

D. HAY: If we've jumped ahead to the ethics question, then you have already anticipated the answer, that things are important and they can have negative impacts. It's not clear that they do. They may well negatively affect abundance. If you demonstrate that, then I think you're into the philosophical question are forage fishes more important to birds or more important to humans?

B. ANTONELIS: I think we already answered that question, we know that it affects these other populations I think we've seen some good examples here.

D. HAY: Well, it affects them, but the question is abundance, right? Does it affect the abundance, and is the effect negative, and perhaps is it reversible?

G. HUNT: I don't see a very great difference between the forage fishes that go to a bird or a mammal and a fisherman. They're both consumers and the one happens to be, "natural," and the other is us folks. But when you ask which is more important, they're both reversible. If abundance is low, the fisherman does something else for awhile and then maybe goes back to it when they're available. The bird does the same thing, changes the species it uses.

It's really a political question because the fisherman makes noise when he doesn't have fish, and puts pressure on the managers, who pressure the biologists for solutions. The bird and mammal people do the same. When you start asking is it important, it becomes a political question rather that a moral or biological question, short of extinction.

D. HAY: That view is Euro-centric, or rather it's a North American/European view. I don't think people would go that far in other countries where they depend on fish for food. In other words, do we really put birds ahead of us in the scheme of things?

G. HUNT: There are some people who do, but that's beside the point. Some of those people have a fairly loud voice. In the Antarctic, where there is no major human population, there are a lot of questions about conflicts for fisheries and forage fishes.

K. STAHL-JOHNSON: It's clear from everything presented here and from our intuitive understanding that when you push the system one way there's a cause and effect relationship. We have to understand what we're trying to do in fisheries management, managing human populations. We're not managing the ecosystem, we're managing our activity in it. On this planet we are just another species; are we going to say our activities are more important than those of other species. This is a really basic discussion, but when you get into deciding how much of a resource you want out of an ecosystem, you have to understand the variables that are going to change. You have to decide whether "the human need is more important than the sealions' need" or the other way around. Balance is what we strive for.

D. HAY: I agree. Dr. Fischer showed that the world catch of fisheries was up to about 80 million metric tons a year, but that has declined a little bit. In other words, the industrial fisheries of the world have really expanded over the last two or three decades. Another way of phrasing this is "Can these ecosystems coexist with these big industrial fisheries?" Or is that a simplistic question that doesn't take into account their geographical placement?

T. PITCHER: Before we get deep into the ethics argument, who's better, seabirds or people? I want to look at the word "important." It's a more ecological view in terms when we're asking is the impact important. I would rephrase that to look at the relative contribution of top down and bottom up influences in the ecosystem, and include humans as harvesters of the top down influence. By harvesting, can we shift the nature of that ecosystem? By "nature" I mean its complexity, its biodiversity, and its trophic links. Can we shift that ecosystem to something very different from where we started? At that point we can start voicing ethical concerns about whether it is a legitimate impact of human harvesting, before we even get into relative values of different species.

I think the answer to that is almost certainly yes. And I can give you some specific examples where humans have shifted ecosystems to less complex and less stable systems with huge ecological and economic impacts. But I'm not going to give you the whole seminar on Lake Victoria now.

G. HUNT: Well, you don't need to go to Lake Victoria, because Georges Bank would be one place where you could argue that the removal of one set of predators allowed another one to come up.

R. FURNESS: One of the justifications for sand lance fishing in the North Sea is that the predatory fish stocks have been overfished so there are fewer cod, fewer haddock, fewer everything except sand lance, and sand lance are currently on the increase because there's less predation. What you're saying is let's fish sand lances because there are lots of them and the predators that should be eating them aren't there. Once you start doing that, one assumes there is less chance that these predator stocks will recover.

Recently there has been some simulation modeling done to look at the North Sea sand lance fishery. The conclusion of that modeling has never been published, but the conclusion was that if a million tons of sand lance was not taken out of the North Sea, the increase in the stocks of cod, haddock, whiting, etc., would be worth more money than the sand lance harvest. The best economic way to manage the North Sea would be not to fish sand lance, but to leave them to be eaten by the predatory fish and then harvest the excess predatory fish. There are political reasons why that's not acceptable.

I'd like to ask the Norwegians if they've looked at the Barents Sea ecosystem in the same way. Is there an argument for not harvesting capelin in order that you might end up with more cod? It seems to me that's one of the major questions with forage fishes. Should they be fished at all, or should they be left there for the other stocks?

D. HAY: With due respect, have we not moved into the third question. We've heard from Tony, who said we really could move back to a pristine system if we did things differently. The other point of view, which I can't articulate fully, is that we're doing fine. We fish things, things are stable, we expect some fluctuation, and things are okay. Will someone address this issue, the commercial fisherman's point of view?

V. WESPESTAD: I think you can phrase it differently. It seems to be the consensus that stability is good, diversity is good, and you know that when you lose diversity you get instability, and that's bad. Implied with that is lower production. Our monoculture agriculture probably produces 10 times as much as wild production. When we're changing things we're doing bad things. Those are value statements, without looking at the full range of possible outcomes. I submit that extinction is normal, persistence is abnormal. Ninety-nine percent of all species that existed are gone. And, we'll be gone in another three or four millennia. When man's gone, who cares?

T. PITCHER: We can probably harvest from the sea something like 500 million tons of krill, and eat it as krillburgers, and support a planet with twice as many humans. It might buy us 100 years of time. Do we want that?

G. HUNT: The market value says something about the value of ecosystems. I think the New England fishermen would say we haven't done a brilliant job in managing Georges Bank. They're unhappy that the diversity of species there has changed in the direction it has. Whether that's a forage fish issue or some other issue I'm can't address, but I would argue that ecosystems with a diversity of fish of high commercial value is more desirable to fishermen than one stripped of that diversity and now has a few species that nobody wants. That's getting it down to dollars; it's got nothing to do with morality.

D. HAY: Well, that's some notion. For lack of a better word, diversity has some sort of value-added appeal.

T. OKEY: That's the direction I'd like to see these conversations start, because initially this discussion was a selfish argument versus a selfless argument: Can we have the fish for ourselves or is there really inherent value in other species and do they deserve some too? I really think both sides are selfish arguments. We are much more likely to say that there is not an effect when there is. We do not really know how our harvesting changes the function, or functions, of the entire ocean ecosystem, which we depend on in ways we're not aware. I submit that we're simply dependent on the ecosystem that we evolved in, and that's why we have to take a precautionary approach.

D. HAY: What I suspect about the Atlantic cod is that history books will show that it declined for a decade or two. I think that history will judge us hard on the basis of our marine extinction. That is completely irreversible. That worries me a lot more than temporary mismanagement of salmon or herring, or overexploitation, or the irreversible loss of key habitats associated with them. That to me is clearly evil in any sense of the word. Maybe we don't really have extinction problems.

R. STEPHENSON: We don't have to think this through from scratch, because our definition of that threshold (you described as evil) is being set down for us by agreements that our countries are signing. It used to be that irreversible damage, extinction, was all that mattered; now our nations are backing up a little further and they're talking about mitigating perturbations. So I think the front is moving, and we should look to some of these international agreements for our guidance in this regard.

G. HUNT: As you think about these ecosystem regime changes that may have been a result of fishing, removing one set of predators so another unharvested set takes over, it's not clear how soon those reversed themselves. It's not just a matter of temporarily pushing down one stock and as soon as you remove the pressure on that stock, all the food is waiting to be harvested. Another species has come in, and it may not be easy for the cod to come back up again. It's not clear to me that we're not getting close to irreversible change within our life span, that we're going to see these things reversed that quickly. So I would be hesitant to say extinction is the only thing to get worried about. Causing a major shift in a community such that that the community's structures changes fundamentally, that's a pretty wild thing to turn loose.

D. HAY: I'm playing the devil's advocate up to a point. I remind you that an enormous industrial fishery has been imposed in the last 50 years, and that most fish species rebound after they've been overharvested.

G. HUNT: If we really knock them down and something else replaces them, do they come back? I've noticed in Puget Sound we have a lot of dogfish now where we used to have salmon. Is this a temporary change or have we replaced one predator with another? It's going to take the salmon a lot of work to get rid of the dogfish.

D. HAY: Are we talking decades, centuries or millennia?

G. HUNT: I don't know, but dogfish live quite a while, don't they?

D. HAY: Decades don't worry me, centuries trouble me, and millennia worry me.

G. HUNT: I don't worry about centuries and millennia because they're beyond my vision. But decades I can deal with.

D. HAY: Two more points and then it's closure for this part?

K. STAHL-JOHNSON: Look at this from the perspective that the majority of the people in this room are employed to understand fisheries so that fishermen can make a livelihood. We ask fishermen, "how do you identify a stable economic market with all the stock fluctuations in the ocean." How can they make an economically viable living on this resource? There is a big industrial fleet that says, "we're going to take it all 'cause it's going to make a lot of money for a few people and we're going to go home to the bank." Then there are all the small community fishermen around the world saying. "I want to make a living for my family and my grandchildren forever," and we can't lump them together. Our responsibility is to provide some basic principles that we can build policy on that allows for the long-term diversity and an economic base, so you're not harvesting sand lance because that's the only thing there.

D. HAY: I bet that that's not the case.

K. STAHL-JOHNSON: Well, it all depends. George Hunt talked about dogfish in Puget Sound. In Kodiak during the last two years the fishermen are very surprised that they're seeing a lot of dogfish on their halibut skates. Are high-end fisheries are turning into low-end fisheries? What's our responsibility?

D. HAY: The sentiments are one thing, but the characterization of what we're supposed to be doing is another. My point of view from the Canadian government perspective is that what we said we're supposed to be doing and what we are actually charged with doing are a little bit different, and they might be in transition.

J. SCHWEIGERT: We saw an interesting slide showing fluctuations in abundance between sardines and anchovy over the scale of a couple hundred years. These things are going to happen naturally. In many cases the impact from fisheries are negligible compared to nature's influence, so I'm not sure that we need to worry about this a whole lot.

D. HAY: We've heard from the other side; that surprises me. A few years ago the Minister of Fisheries was John Crosby from Newfoundland. He said that we are the Department of Fisheries, not fishes, and that we will manage for fisheries, not fishes. Now that the UN agreements are kicking in, we manage for other things, risk aversion. So things are changing, they're in transition.

O. PALSSON: I'm Olafur Palsson from Iceland. Regarding the question of whether or not we should leave these forage fishes as they are and not touch them. We have some good examples in Iceland. We have utilized these resources in some places whereas in the other areas they have practically not touched them, and who is better off? It probably depends on the ecosystems. We might be able to use these stocks much more in the Arctic regions than, for example, here in the temperate, or some more temperate zones in the southern areas. I think how we can handle this depends on the ecosystems themselves.

D. HAY: So the Icelandic view is that the management approach is ecosystem dependent?

O. PALSSON: I'm not talking for any Icelandic group, just for myself.

UNIDENTIFIED: As for the capelin in the Barents Sea, we are moving toward the point of view that this is something that we can harvest when there is an excess of this fish. But that, given the nature of the ecosystem, we will have a very variable fishery. For at least 10 years or so, we really believed that we could have a stable fishery on this stock, and then the herring came back and more or less turned things upside down. What we are discussing now is what's going to be the next issue. If the capelin stocks increase a little more, should we have a small human consumption fishery for capelin for the Japanese market? The bottom line on much of this is really economy, because in our country we try to analyze what multi-fish management strategy will give the most profit to Norwegian fishermen, and that may include reducing the whale stock or whatever. Although I haven't dealt with the economy on the marine mammal/fish models yet, it should be possible to do, but the price of certain items is hard to predict.

UNIDENTIFIED: That's the economic price of that diversity.

D. HAY: Are there any other countries or jurisdictions that could speak to that?

T. ANKER-NILSSEN: We should probably be more careful because we understand only very few of the changes caused when we deplete stocks. We mainly focus on those commercially used. One example could be very local stocks of herring only produced when the population is at its peak. These local stocks, which we don't pay too much attention to, may be very important for local business, and for species we don't pay attention to in any other way. So from a biodiversity perspective we should be careful to heavily utilize only certain species.

D. HAY: My view as a western North American in this case is that we have done things right, maybe for the wrong reasons. For some reason, we still have scads of Pacific salmon. Because we have an interception fishery, we haven't wiped out Pacific salmon the way they have done in the Atlantic. That's one thing that's been done right. We intrinsically realized that there was that kind of diversity.

I'll try to summarize what we've heard here. Everyone agrees that forage fishes affect their predators, and I think there are extreme views. I would judge Tony Pitcher's view to be one extreme whereby perhaps we should back off on fishing as it affects forage fishes, to go back to some kind of original state. Maybe I'm not doing you justice there.

T. PITCHER: Not really, I didn't say that was what I advocate, I said that was something that we should consider.

D. HAY: Very good, I don't mean to attribute wrong views. I don't think Vidar Wespestad, seriously, suggests that a few extinctions are no problem. But it's very difficult to draw that line somewhere in between. I suspect that we have gone more toward being benevolent to birds and mammals than if we had a different group of people.

A. SILVA: More is known about the effects of forage fishes on seabirds and marine mammal populations than on predatory fish. It's more difficult to monitor fish populations and to relate their abundance fluctuations to fluctuations of forage fish populations, but we must get to it. There is an extra stressor, the fishery, on predators. One conclusion that should emerge from this symposium, is that further studies need to be done of forage fish populations on their fish predators.

D. HAY: Another item we should discuss is recommendations, and you just made one. I don't like to say further study, because every set of recommendations starts with that.

B. ANTONELIS: The Aleut people I've worked with in the last 10 years in the Pribilof Islands just switched from a fur industry to a fishery. They recently made a discovery; what was good for the seals was good for them. As long as the seal population remained viable, that'd mean that there would not be any regulations that might affect their long-term fishery. From a totally practical approach, it seems that if we can maintain mammals, birds, whatever organism you're talking about, and still maintain a sustainable fishery, as on that island, then they're going to be happy.

D. HAY: Alaska has the lowest population density in the world. It might be a luxurious point of view to be preservationists instead of conservationists.

K. STAHL-JOHNSON: Where'd you come up with Alaskans are preservationists. That's a good generalization, I like that.

D. HAY: I do sense that we have a different audience here. If this audience had heavily represented the commercial fishery the economic considerations would be first and foremost. I don't know about these UN regulations. Maybe we're in the vanguard of what's going to come.

The third question I had was what do we do about it, what are the recommendations? Earlier someone brought up the idea of fishing down predatory species, fish mitigation. We've heard recently that one could add iron to the ecosystem to make it more productive. These are things we haven't really even thought about. Is that familiar to anyone?

D. HAY: We still hear of it, but I think it's not going anywhere.

T. PITCHER: I read it in *Nature* about a month ago regarding the Indian Ocean, but they didn't say that if you added iron it would increase the productivity.

D. HAY: I'm trying to capture the different kinds of things that we could think about, and what kind of management activities do you do to get to where we want to go? Wherever you want to go is somewhere in between no fishing whatsoever, no interference with the forage fishes, to complete economic management of the resources so that it's the industrial fisher or the economic resources that take priority, even if that means that you fish only krill.

T. PITCHER: Rather than be forced into a camp which tries to restore the planet to what it was like before we evolved, the point I was trying to make is that we do have a choice between the extremes. We have a choice between a simple system which is very productive and could produce a lot of human food, and producing very high quality, large, desirable food, but perhaps in smaller quantities. There is a whole range of options for managing the harvest of natural systems in between those two extremes. Given that we're able to devise a more rigorous science of ecosystem management than we produced in this meeting, we need to go a bit further before we're confident we can do it and predict effects, but we're en route.

We have the tools for ecosystem management, we have the options of tuning our harvesting regime to what is desirable for a particular local area, whether that area is the whole of Norway or just the Pribilof Islands. The scale is our political choice. I wonder whether the development of that ecosystem management tool is something that we really want to focus our attention on, beyond the ethical questions. Can we get to management tools which are tractable and predict effects across whole ecosystems? We've heard a lot of reports which suggest that we're heading in that direction, but I don't think we're there yet.

J. SCHWEIGERT: I think we're a long way from being able to manage any of the forage fish species. I think the cost of trying to develop any sort of longterm indices of abundance for most of these forage species is probably going to be prohibitively expensive, and I don't really see that we're going to be there any time soon.

O. PALSSON: In Iceland we have a simple multi-species model. It's sort of an official guideline for the next 10 or 20 years and includes cod, capelin, and shrimp. Capelin and shrimp are prey, and the objective is to increase the size of the cod stock and correspondingly decrease catches of capelin and shrimp by some 50%. This is more or less an official plan, approved by the Minister of Fisheries, and it is based on a simple model.

R. STEPHENSON: At a recent ICES meeting we had a session on management under multiple objectives, which was an attempt to try to get people to articulate biological and socioeconomic objectives that we'd try to work toward, because this is the key. We know some of the things we don't want to see happen, but we haven't really articulated where we want to go.

What we want are viable fisheries within sustainable ecosystems. So there's a sense that we want things that yield dollars, and we want this to be able to persist into the long term. I am interested in some of the bioeconomic modeling which shows maximum returns in the long term with somewhat diverse ecosystems of the kind that most of us think are a bit idealistic right now, and which most of us think our fishing industry would argue aren't worth preserving. If amortized over a long period, if you remove subsidies, and if you get industries to look at things over the long haul, the objectives are actually more similar than they are different. If we were to do the kind of long-term scenario development that is being done, for example, in Iceland, and to some degree in Norway, we'd see that in the long term you can actually show bioeconomic advantage to some of the long-term approaches, and we'd reduce our current fishing effort and maintain more diverse systems for the long haul.

S. TJELMELAND: In actual management for the spring spawning herring, we do forecasts over 10 years in Norway.

D. HAY: So the question might be what is long term? Ten years, 100 years, or 1,000 years?

R. STEPHENSON: Most of the differences of opinion we see right now is because people are looking at the short term, two, three, four, or five year time horizons, rather than the longer term. I don't know whether you need an actual definition of what is long term.

D. HAY: I think you do.

O. PALSSON: Ten or 20 years.

D. HAY: Ten or 20 years? On the Pacific coast we have fish that live 120 years. Long term for them is 1,000 years. In fact, if you're looking at ecosystem management, you've got to look forward. We build buildings that last 100 years. Should we not look at ecosystems that last just that long?

G. IRVINE: I think we should. One of the things that's been troubling me is how you put some of these different philosophies together. We're looking at systems that may change in 20 to 50 years, whether they be shifts in regimes or cycles. We don't understand the mechanisms that are responsible for them, so how can we actually manage, and what are we managing for? What is long term? It has to encompass some sense of that change if in fact it's somewhat cyclical.

G. HUNT: Are any of the forestry models usable? You talk about sustained yield and trees that don't go away, but they do get burned and so forth. You've got some chance that can foul up your model, just like we have. But you look at them in terms of growth and what is the optimal age to let them go to. If you're interested in old growth, you have to be thinking about a cycle that's three to 600 years; if you're trying to get some pulp tree, you're thinking in cycles that are much shorter. So perhaps when you ask what is long term it depends on the species or the ecosystem or the portion of the ecosystem that you're focusing on.

With most of the commercial species, and many of the forage fishes, if we could move to a 10- to 20-year horizon, we would double or triple the horizon we're using right now, and we might be getting a quite different set of answers as to what would be good. If I understood the Norwegian model correctly, when they looked at the long term, they found it pays to take into account what cod were eating and what herring were eating in terms of how to handle the capelin. It seems to me they were looking longterm, multispecies, and saying given the fact that these things are in the environment, we'll have a better catch if we take these things into account honestly as opposed to ignoring them.

D. HAY: The first part of your question, if forestry is an example, might work, but maybe not within some jurisdictions. I know that in Sweden they cut down half as many trees as we do and get twice as much money for them.

G. HUNT: In Sweden that's an industry where the companies often own the land, and therefore they have a vested interested in keeping the it working on a sustainable basis, whereas nobody owns the ocean and everybody grabs what they can. If we could get people thinking about an ownership for the future, then in fact they may take it in a different way.

K. STAHL-JOHNSON: If you leave a stand of trees up, minus a forest fire, you still have a stand of trees in 10 years, and you can have that long-term vision. But if you have a warming event over a 10-year period, you have lost your crustaceans in the North Atlantic or the North Pacific. The cycle changes, we don't have stability, and you can't use the same principle.

S. CROCKFORD: In what marine ecosystem or area do we have the longest time depth of understanding, and is that enough? If we had information that goes back to 1900 for some area, do we feel for that area we have a clear understanding of what's going on in terms of natural cycles and how people are interacting in their harvesting activities there? How long is that period?

D. HAY: Probably the North Sea. If you ask the fish managers from the North Sea, I think most of them would say that things are just fine there. The major problems they have are international agreements and so on.

S. CROCKFORD: I'm thinking in terms of what our understanding is of the natural fluctuations. You wanted to say how long, and I'm suggesting that for some areas we have a greater length of understanding, and perhaps that's one of the factors you should take into account if you're trying to determine a length of time. Do you want to say 200 years, or do you want to say 100 years?

S. TJELMELAND: When we can see 100 years.

D. HAY: Rob Stephenson would reduce fishing pressure, but he doesn't tell us how.

R. STEPHENSON: By pointing out the benefits of such action so that it is the consensus of government and industry.

V. WESPESTAD: You're taking care of some business, but it seems the science is missing in these discussions.

J. TRAYNOR: We seem to be looking at understanding the effect of forage fish as though it costs nothing. We provide this option, we will take that option, we will provide another estimate, a second estimate, but in fact this is a significant investment, and the managers have to know that. It gets back to the fact that the science that goes into this is a significant effort either in terms of process oriented studies or in much more significant monitoring efforts.

D. HAY: That almost sounds like a recommendation for future work. Somehow you have to make the managers understand, but who are the managers

A.J. PAUL: One thing that I found dealing with modelers is they can model for decades with no real numbers. If all these decisions are going to be made on multispecies management models, it would be more efficient, with less potential for disaster, if there was some effort put into deciding what questions need to be answered. To try to identify the material to send to the modelers so that they could make some realistic predictions.

D. HAY: I think you're right, and there's one thing we didn't do. We didn't come to any conclusions.

A.J. PAUL: I noticed people from different parts of the world are in general studying the same kinds of questions. We know what seabirds are eating, whether or not it's good food. But when it comes to describing the health of different fish stocks, what makes those stocks tick we don't really know very much. Very few of the papers here were about zooplankton. We gave a poster showing the presence or absence of copepod nauplii at the time of pollock larvae first feeding. If nauplii aren't there, the pollock larvae don't do very well. That translates into whether or not it's a good year for recruitment. There has to be some food for the little fish and not much effort is spent on studying the base of the food chain. Mostly people examine the top predators and don't even attempt to study the lower trophic levels. That has to change if we are going to understand processes that regulate fish production.

D. HAY: It was mentioned that spatial factors are important. I think one of the recommendations that might surface is not changing fishing, but changing where fishing is done. That's something that might be emerging in one way or the other, it's a possibility.

Speaking as a member of the Canadian Department of Fisheries & Oceans, as far as I can see, we respond to clients. The clients, by and large, are the people in the fishing industry. But that doesn't mean that that is exclusively the clients. If birds and marine mammals had voices, they would also be clients.

UNIDENTIFIED: They do have a voice in the Audubon Society and Greenpeace and all those environmental or animal rights groups. Those people are definitely speaking up for the animals. You talk about fishermen and making fishing decisions on the premise of fishermen, but that's not the issue anymore.

D. HAY: Those voices have only been around for a decade or two, and they have been here longer than most other parts of the world. The context in which I make that statement is that this is an international meeting, and some things have developed further in some parts of the world than others.

D. PENTTILA: In fisheries management agencies those voices are held largely in contempt.

T. PITCHER: In terms of the voice for conservationists, for mammals, birds, and the general maintenance of the integrity of ecosystems, there is a fairly new initiative sponsored by the World Wildlife Fund in conjunction with Unilever in Europe and other large fishing industry companies in North America. It's an institute called the Marine Stewardship Council, which is in the process of developing a series of criteria and guidelines to be applied to commercial fisheries. The Marine Stewardship Council will certify commercial fisheries as being responsibly and sustainably managed if they meet certain criteria. When a fishery is certified, a logo will be issued by the World Wildlife Fund to be put on the industrial product coming from resource. The logo may even be used in restaurants. That's a very powerful example of part of the conservation movement and the fishing industry getting together in a way that's actually independent of governments. Lots of governments have signed off on the Rio convention and that's great, but then what happens? Not a lot, actually, but this is a very powerful consumer-led initiative.

As for meetings like this, the proceedings of this meeting will be read by the people who are developing those criteria and guidelines. If there are things that you want to say about how forage fisheries should be harvested and managed, now is the time to say it.

T. OKEY: I'm from the Center for Marine Conservation. It's important to realize that perhaps one of the most important clients is the general public. If scientists and resource managers can presume that from the beginning, then they can actually play a role in communicating to the public, because that's one place, in my opinion, that scientists have been lacking.

D. HAY: If you work for most agencies, you're not your own person when it comes to speaking up. That's one of the biggest problems we've got. As I see it, part of the problem is that the people in government agencies often know more about these things than many other people, and they often can't address the issue as directly as it should be.

G. HUNT: Maybe a recommendation should be that although the government may have policies, their scientists should not be gagged from speaking out on the issues. We might end up by actually getting the results that fishermen need a lot more quickly if people were able to take into account the best information available as opposed to the information that some minister thinks should be available.

D. HAY: Information dissemination is recommendation two. Recommendation one was future work.

T. PITCHER: I was excited to see the diversity of studies going on out in the wild with wonderful methodology and very fair presentations of the results. Many of those studies were driven by the need to better understand the impact of the actual fishing industry, that's great. On the other hand, I was slightly disappointed that only a minority of presentations actually addressed any theories or had any kind of theoretical construct behind what they were doing. Most people in that second category failed to state their hypotheses and clearly test them. For example, the impacts of fish on seabirds has been very elegantly addressed. That is a good model for the rest of us who perhaps are not as rigorous as the seabird people.

D. HAY: I thought that the meeting had a fairly good mix of process studies and overview studies. When you move away from the fish, the overview studies are the most interesting to me.

T. PITCHER: I agree with you about that mix. But the mix between things that are theory-led and things that are empirically-led was not as much toward the theory end as I would have liked.

D. HAY: It is clear that people are sometimes doing a lot of work in relative isolation, so better communication is a good idea. This meeting has brought a few ideas together that hadn't previously existed. Better Internet access is another very good way to communication in addition to these meetings.

S. CROCKFORD: I'd like to bring up the idea of adding time depth to some of these studies in trying to look at how the systems fluctuate naturally. I'm looking at it from the aspect of the work that I do in archeology where there is some information available to biologists that perhaps they're neglecting in a detrimental way. Human beings as harvesters, as samplers of the ecosystem, have been leaving records for thousands of years. That information is available to biologists, and it's an aspect that we should perhaps start looking at more closely.

D. HAY: I'll try to capture that by saying retrospect of ecosystem analysis, implying that you go back in time and try to find out what was going on.

S. CROCKFORD: I don't think that's clear enough, because a lot of biologists will go back in time as far as the recorded records go, and they won't thinking about going further back than that.

S. TJELMELAND: You mentioned communication and use of the Internet. I have a suggestion that might be a recommendation. In the near future I think there will be much more conflict of interest between those speaking for the fishermen and those speaking for the fish. In order to have an orderly discussion of this, we could recommend that the models that are actually used for assessment, the models on which the quota decisions are based, should be publicly accessible through the Internet.

D. HAY: I need a short sentence to reflect that.

G. HUNT: Public accessibility to the model parameters and the assumptions behind the model so that scientists other than those in the particular labs which develop the models could actually look at them and interact with the modelers.

UNIDENTIFIED: Go a step further and make them explain to the lay people.

G. HUNT: Yes, because the fishermen are going to want to know what's in the model, too. If the fishermen understand why the model's being run the way it is, they'll also understand why the manager is choosing the option that he or she is.

J. BLACKBURN: I don't think that it's possible. The current models that are being used are not understandable by the people who are using them. The one they're using for the pollock in the Gulf of Alaska and the Bering Sea is a synthesis model, and people continually argue about what it means.

J. TRAYNOR: If it's being used for management, that's an even better reason to make it available.

J. BLACKBURN: What does making it available mean?

D. HAY: To make it accessible. In our case we used to have stock assessment meetings which fishermen could attend. Even though they didn't understand the models, the fact that we would argue about them leant credibility to the process. It was comforting for them to know that we were not of a single mind

T. PITCHER: I think we have to get away from the high priesthood of assessment. If you can't do a model on a spreadsheet, it's too complex.

K. STAHL-JOHNSON: I agree, we need to take the issues of the practical application to fishermen. We need to make sure that as we work forward in a perspective of maintaining the fisheries, that we make the science accessible, that these models are applicable to what we're seeing out in the field. I live in a town that is 90% fishermen. Most fishermen I know are conservation oriented, and do understand these principles. It's a mistake for managers to think otherwise.

V. WESPESTAD: I want to point out that the Bering Sea pollock analysis is available on the Internet. It is in a spreadsheet with all the data, all the equations and everything, and it's fully available to anyone at any time.

G. HUNT: I wonder when we talk about birds and mammals that it's sometimes cast as birds and mammals versus fishermen. If birds and mammals can't make it, there's a very good chance that the fisherman who is trying to fish for the same resource won't make it either. Animals such as  birds and mammals have evolved to deal with normal levels of fluctuation and survive, and are good indicators in the system. If fluctuations have gone to such extremes that they drop out of the system, that should be a warning that the system is probably outside of its natural boundaries in terms of wiggling. There's great value in keeping the interdisciplinary discussions going among the bird folks, the mammal folks, and the fish folks, because we're talking about the same thing, and maybe the fishermen are talking about the same thing, too. Nobody wants to see the system collapse, and we're bringing a different view to how it works.

A. J. PAUL: Just to conclude I want to note the list of eight points that Dr. Hay devised as discussion chair:

1. Need for better ecosystem modelers.
2. Build bio-economic models with longterm perspectives.
3. Quantify forage species-fish predator interactions.
4. Improved communication of our science to public and government.
5. Retrospective ecosystem analysis.
6. Improve our understanding of natural morality processes.
7. Distinguish between fishery and environmental changes.
8. Better data on lower tropic levels.