First-Year Energy Storage Patterns of Pacific Herring and Walleye Pollock: Insight into Competitor Strategies

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Abstract
Changes in length and whole body energy content for Pacific herring and walleye pollock from Prince William Sound, Alaska, were monitored in 1996 to describe growth patterns of these two pelagic competitors during their first year. Metamorphosed walleye pollock were first captured in June, when they averaged 34 mm in standard length (SL) and their whole body energy content (WBEC) was 2.7 kJ/g wet wt. In August they had grown to 69 mm and 3.4 kJ/g wet wt. In October they averaged 81 mm and 3.6 kJ/g wet wt. Metamorphosed Pacific herring were first captured in July, and averaged 28 mm and 2.5 kJ/g wet wt. In August they had grown to 38 mm and 3.1 kJ/g wet wt. In October they averaged 75 mm and 5.0 kJ/g wet wt.

Walleye pollock metamorphosed earlier than Pacific herring and in August and October they were on average 31 mm and 6 mm longer than their herring competitors. In August the WBEC of the two species was similar. In October the herring had stored on average ≈1.4 kJ/g more energy than pollock to enter the overwinter period. The survival strategy for first year pollock includes an early metamorphosis followed by rapid growth in length. For herring, metamorphosing later when conditions are warmer and storing more somatic energy for overwintering appear to be primary tactics.

Introduction
In the northern Gulf of Alaska two of the most common pelagic forage fishes are the Pacific herring (Clupea pallasi Valenciennes 1847) and the
walleye pollock \((\text{Theragra chalcogramma} \ [\text{Pallas 1814}])\). Both species are mobile and vertically migrate in the water column, and during the first year of life they are competitors for the same prey resources (Willette et al. 1997). Both species are spring spawners; their larvae eat copepod nauplii (McGurk et al. 1993, Hillgruber et al. 1995) and then switch to consuming small copepods like \textit{Pseudocalanus} (Willette et al. 1997). During their first summer both are pelagic by habit and exist in the same geographic regions although they do not always coexist in the same depth strata. As they grow beyond the first year of life, the herring relies on its gill rakers to continue to capture copepods while pollock tend to supplement their copepod diet with macrozooplankton and fish to a greater degree. Pollock may also exploit benthic prey as well as pelagic species as they mature.

The objective of this report is to compare standard length (SL), body weight, and whole body energy content (WBEC) of recruiting herring and pollock. This was done to see if these measurements provided insight into the similarities and differences in their respective survival strategies during their first feeding season.

**Materials and Methods**

**Sampling**

During the spring and summer of 1996 age-0 herring were captured from four sites in Prince William Sound, Alaska: Simpson Bay, Eaglek Bay, Whale Bay, and Zaikof Bay (Fig. 1). Collection dates were 10-13 May, 10-15 June, 3-11 July, 1-5 August, and 3-8 October of 1996. Juvenile herring were captured with 50 m diameter \(\times\) 4 m deep purse seines with 3 mm stretch mesh. At each collection site the nets were set at least three times to capture specimens.

Sampling for juvenile pollock was done at the same sites, and dates with an otter trawl (head rope 21 m, foot rope 29 m, mouth 3 \(\times\) 20 m) with a 32 mm mesh cod end. At each collection site one trawl was made to capture recruiting 1996 year-class pollock. The number of pollock in the collections appears in the data plots.

After capture all fish were immediately frozen in seawater aboard ship and kept frozen until processing. Because the number of individuals captured at some sites, on some dates, was small the WBEC measurements for all herring and pollock captured at the different sites were combined for this presentation.

The sampling sites are remote from any facilities so to portray the thermal conditions during the study, water temperatures from the Seward Marine Center Laboratory seawater system are shown (Fig. 2). The laboratory is about 100 km downstream from Prince William Sound and seawater temperatures at a depth of 75 m and at the surface are recorded daily.
Whole Body Energy Content

In the laboratory the fish were partially thawed, just enough to handle but not enough so fluids were lost. All fish were measured for standard length to the nearest millimeter, then weighed to the nearest 0.1 g. Each fish was freeze-dried whole until there was no apparent moisture. After freeze drying, fish 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 of every fish. Whole dried fish were ground in a mill and measurements of caloric content made by bomb calorimetry. All calorimetric samples were weighed to the 0.0001 g level with a single 0.5-1.0 g sample burned per fish. Whole body energy content is expressed as kJ/g wet wt.

Aging

Comparison of the test parameters were made for young-of-the-year (YOY) pollock and herring. Scales were removed from every herring just above
Figure 2. Seawater temperatures at the surface (upper) and 75 m depth (lower) near Seward, Alaska (date = monthly mean and SD) during 1986-1996 (left). Monthly mean temperature values for 1996 (right panels).
or below the lateral line, three rows behind the operculum for determining age. They were cleaned manually and mounted on glass slides. Mounted scales were placed in a microfiche reader and winter annuli were counted in the conventional manner. Age-0 herring are easy to identify both by SL and scale age since they are much smaller than other age groups and have no winter growth rings in fall collections and only one winter ring the following spring. Herring with more than one annuli on the scales were not assigned an age, but their WBEC was plotted against SL. Pollock were not aged, only fish less than 105 mm SL were processed with the assumption that most Gulf of Alaska pollock this size would be YOY (Brodeur and Wilson 1996).

The relationship between the percentage of whole body that is dry weight to WBEC in pollock has been described (Harris et al. 1986). The relationship for juvenile herring was established in this study.

Results and Discussion

Thermal Conditions

Based on temperatures at Seward (Fig. 2), the 1996 thermal conditions were close to the mean monthly values recorded in the upper 75 m of the water column during 1985-1996. Thus, from a thermal-metabolic perspective the YOY fish encountered temperatures that were typical of those seen during the last decade.

Walleye Pollock

The changes in WBEC of juveniles during the 1996 growing season are shown in Fig. 3. In May only individuals greater than 90 mm SL were captured (Fig. 3A); those fish had recruited in 1995 and overwintered. May specimens had an average WBEC of 4.0 (±0.4) kJ/g. On 13 June recently metamorphosed 1996 year-class pollock (Fig. 3B) were captured and they had a mean SL of 34 mm (±6 mm) and a mean WBEC of 2.7 (±0.2) kJ/g. By 3 August the 1996 recruits had increased their mean SL to 69 mm (±6 mm), which was a 109% increase in the mean SL (Fig. 3C). Those fish had an average WBEC of 3.4 (±0.3) kJ/g, which was a 26% increase in the mean for YOY fish since the June sampling. By 6 October YOY pollock had an average SL of 81 mm (±10 mm) and WBEC of 3.6 (±0.2) kJ/g (Fig. 3D). In October there were no fish with WBEC less than 3.0 kJ/g while in August they were relatively common (Fig. 3).

Herring

In May and June only herring that had overwintered were present in the catches (Fig. 4A,B). There was a tendency for WBEC to exhibit considerable variability relative to SL in all seasons. In May the average WBEC for all fish was 4.5 (±1.0) kJ/g wet wt, which increased to 5.6 (±1.6) kJ/g wet wt in
Figure 3. Whole body energy content (kJ/g wet weight) relative to standard length for juvenile walleye pollock captured in Prince William Sound, Alaska, during 1996.
June. In July the 1996 year class first appeared at about 25-30 mm SL (Fig. 4C). The 1996 recruits less than 30 mm SL had a WBEC of 2.5 (±0.3) kJ/g wet wt in July while fish greater than 70 mm SL that had overwintered had 4-8 kJ/g wet wt. By August the YOY fish measured 20-60 mm SL, and fish less than 60 mm had an average WBEC of only 3.1 (±0.6) kJ/g (Fig. 4D). In October (Fig. 4E) few fish greater than 100 mm SL were captured and they had a mean SL of 75 mm (±13 mm) and WBEC of 5.6 (±2.8) kJ/g wet wt.

The relationship between the percent dry weight of whole bodies and WBEC for YOY herring was linear in nature. The following equations describe these relationships:

\[
\text{WBEC kJ/g dry wt} = 0.55 \times \text{(% dry wt)} + 9.47; \quad r^2 = 0.86 \quad (1)
\]

\[
\text{WBEC kJ/g wet wt} = 0.38 \times \text{(% dry wt)} - 3.44; \quad r^2 = 0.96 \quad (2)
\]

Species Comparisons
Graphic representations of the mean (± SD) size and WBEC of both species occurs in Fig. 5. The months of August and October are the only periods when both YOY pollock and herring were captured. In August the pollock were markedly bigger (mean SL = 69 mm, mean wet wt = 2.8 g) than herring (mean SL = 38 mm, mean wet wt = 0.7 g). By October the mean SL was 81 mm for pollock vs. 75 mm for herring. In August the pollock WBEC averaged 3.4 kJ/g wet wt vs. 3.1 kJ/g for herring. A Mann-Whitney rank sum test indicated that these values were significantly different \((P < 0.0001)\). Thus, during June through August YOY pollock are a more energy-rich prey than YOY herring. By October the herring had markedly higher WBEC (mean = 5.0 kJ/g wet wt) than the pollock (mean = 3.6 kJ/g).

The most obvious difference in the growth strategies of the two species was the much earlier metamorphosis of the pollock. They had nearly a month more to grow than the herring. The pattern for growth between Julian days 164 and 279 in SL for both species, based on mean values in Fig. 5 was linear, during June to October (Table 1). The growth rate for pollock was 0.4 mm per day vs. 0.5 mm per day for YOY herring. The change in WBEC between Julian days 164 and 279 was 8 J/g per day for pollock and 30 J/g per day for herring. The herring allocated over 3 times more of their energy intake to somatic storage than the pollock.

The survival strategy for YOY pollock includes an early metamorphosis followed by rapid growth in length. Presumably with rapid growth in length comes increased swimming speed useful in capturing prey and avoiding predators. Herring metamorphosed later than the pollock, but they exhibited a slightly faster growth in SL in the warmer conditions. They also stored more energy for overwintering. Pollock appear to feed and grow in length through the winter (Paul et al. 1998) while herring rely
Figure 4. Whole body energy content (kJ/g wet weight) relative to standard length for juvenile Pacific herring captured in Prince William Sound, Alaska, during 1996.
Figure 5. Changes in standard length (mm; A, B), whole body wet weight (g; C, D) and whole body energy content (kJ/g wet wt; E, F) for age-0 walleye pollock and Pacific herring.
more on stored energy (Paul and Paul 1998). Thus, these two competitors have evolved very different energy allocation strategies for surviving their first year.

**Acknowledgments**

This study was sponsored by the Exxon Valdez Oil Spill Trustee Council through the Sound Ecosystem Assessment project. Several Sound Ecosystem Assessment staff carried out fish collections. C. Adams, P. Shoemaker, M. McEwen, and R. Schmidt helped with laboratory procedures. Facilities were provided by the University of Alaska, Institute of Marine Science, Seward Marine Center.

**References**


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**Table 1. Equations describing changes in standard length (SL) and whole body energy content (WBEC) for age-0 Prince William Sound walleye pollock and age-0 Pacific herring.**

<table>
<thead>
<tr>
<th></th>
<th>Equation</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pollock</td>
<td>SL(mm) = 0.40X − 26.2; $r^2 = 0.88$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WBEC (kJ/g wet wt) = 0.008X + 1.6; $r^2 = 0.86$</td>
<td></td>
</tr>
<tr>
<td>Herring</td>
<td>SL(mm) = 0.52X − 73.0; $r^2 = 0.99$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WBEC (kJ/g wet wt) = 0.02X − 1.3; $r^2 = 0.94$</td>
<td></td>
</tr>
</tbody>
</table>

The X value is the Julian day between days 164 and 279 for pollock and days 188 and 279 for herring.


Feeding Behavior of Herring *(Clupea pallasi)* Associated with Zooplankton Availability in Prince William Sound, Alaska

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**Extended Abstract**

The goal of our project was to examine the feeding ecology of age-0 Pacific herring (*Clupea pallasi* Valenciennes 1847) within their nursery areas in Prince William Sound, Alaska. One of the many questions that led us to this goal was what defines the juvenile habitat and what influences within that habitat affect juvenile herring behavior and distribution. We were interested in the trophic interactions that juvenile herring encounter, in particular, their seasonal feeding behavior. Early hypotheses suggested that feeding dynamics in the spring and summer when zooplankton biomass is at its peak were critical to the success of the juveniles. Current work emphasizes fall and winter feeding behaviors as being important for the juveniles to survive to the next spring phytoplankton bloom (Paul and Paul 1998, Foy and Paul 2000).

Age-0 herring were collected from Simpson Bay in March, May, June, August, October, and November 1996, and February and March 1997 (Fig. 1). We focused on Simpson Bay, located in the eastern part of Prince William Sound, because of the high biomass of juvenile herring encountered during this study. Herring were collected from commercial seining vessels with 150-mm stretch mesh anchovy nets during dusk and daylight conditions. Fifteen fish were taken from each catch for the following diet analyses. Sample sizes for each month ranged from 35 to 135 fish. Fish were preserved in a 10% buffered formaldehyde solution. After 24 hours, samples were transferred to 50% isopropanol for diet analysis. Each fish was blotted dry, weighed to the nearest 0.01 g, and standard length (SL) measured to the nearest 1.0 mm. Energy density of assimilated food (kJ g⁻¹ food wet wt) was determined from literature values of zooplankton
Figure 1. Map of the Simpson Bay study area in Prince William Sound, Alaska, where age-0 herring were captured for diet analysis.

energy density and the species composition in the herring diets (Foy and Norcross 1999, Foy and Paul 2000).

CTD measurements were taken in the water column in each month sampled. For March and July 1996, the average of multiple CTD sites at a depth of 5 m was used. In October 1996, loggers were placed in the bay at 5 m of depth and recorded temperature every 0.5 hour. Zooplankton were sampled with 0.5-m, 300-µm-mesh vertical ring nets to a depth of 30 m from multiple sites in the bay. Taxa were identified as close to species as possible. Weights were taken from multiple subsets and used for the biomass estimates.

Temperature was 11ºC in July and declined through the winter until February at 4ºC (Fig. 2a). Temperatures were consistently low in March 1996 and 1997. The response of the zooplankton community to the 1996 spring phytoplankton bloom occurred in June with the biomass peaking at over 1.5 g m⁻³ (Fig. 2b). Biomass was lowest in February and began to increase slightly in March 1997. Fish eggs, copepod nauplii, large Calanoida adults (Metridia sp.), and Euphausiaceae dominated species composition in March. Small Calanoida were most abundant during the summer months
Figure 2. (a) Monthly 5 m mean (±SD) temperatures recorded in March, July, and October 1996 to March 1997. (b) Mean (SE) zooplankton biomass (g m\(^{-3}\)) from May 1996 to March 1997.
Age-0 herring were first encountered in Simpson Bay in August. The monthly mean of the energy density of the prey items found in the diets ranged from 2.6 to 4.4 kJ g⁻¹ food wet weight (Fig. 3). The energy density of food items taken by the age-0 herring was highest in March of 1996 and 1997. The rest of the year the energy density of the prey was statistically similar regardless of species composition. Diets in March 1996 were dominated by fish eggs, Cirripedia nauplii, and Harpacticoida. In March 1997, diets contained mostly Euphausiacea, Neomysis sp., and Metridia sp. Small Calanoida were present in the diets throughout the summer and fall and Larvacea dominated the October diets. November and December diets were composed of Gastropoda larvae and Polychaeta juveniles. The species composition of the prey in November and December suggests that the fish are feeding near the bottom and may in fact be relatively inactive. Therefore, when the availability of zooplankton is low in March, the quality of prey may make feeding at this time worth while.

Figure 3. Mean (±SE) diet energy density (kJ g⁻¹ food wet wt) for age-0 Pacific herring from March 1996 to March 1997.
Figure 4. (a) Mean (±SE) diet wet weight (% fish wet wt) for age-0 herring from March 1996 to March 1997. Empty stomachs not included. (b) Proportion of herring empty stomachs encountered from March 1996 to March 1997.
Figure 5. Standard length (solid line) and weight (dashed line) of age-0 herring used for diet analysis.

The mean of the biomass of the stomach contents for only the fish that had food ranged from 0.3 to 2.7% of the wet weight of the fish (Fig. 4a). Larger food intake by the 1996 year class is expected as the fish enter the bay and the zooplankton biomass is still high. Food intake is at its lowest in the winter when food availability and temperatures are lowest. The increased food intake in March of 1997 shows that the age-0 herring were actively feeding on the high energy dense prey. The lower food intake in March of 1996 is due to the lack of energy dense prey available at the time we sampled. The proportion of empty stomachs increased slightly prior to the spring bloom but then decreased throughout the summer (Fig. 4b). A sharp increase in November corresponds to low food intake. Zero empty stomachs out of 75 fish in March 1997 supports food intake estimates that suggest fish were feeding on high energy zooplankton taxa.

The SL size of the age-0 fish from the 1995 year increased from 54 mm and 2.6 g in August to 64 mm and 3.8 g in October (Fig. 5). Fish below 60 mm and 2.5 g were caught in August and November but were not found in the bay in subsequent sampling months. Increases in length and weight from October to March are hypothesized to be a result of mortalities of the smallest fish causing the increase in mean size of fish in the bay. This
suggests that the size of the fish going into winter and therefore the feeding behavior in the summer and fall is critical to survival (Foy and Paul In prep.). No growth is expected during the winter and fish are assumed to remain in the bay between the sampling periods, both of which are realistic at this time of year due to low temperatures and prey availability. Age-0 herring from the 1995 year class began to grow between May and June because of warmer temperature and prey availability.

In conclusion, two important trends where found in relation to the feeding behavior of age-0 herring in Simpson Bay. First, increased age-0 herring feeding in response to the peak in prey availability in June and July is expected. The response of the herring to the availability of high-energy prey in March was not expected due to the low temperatures and total zooplankton biomass. This feeding in March suggests that the duration of winter and starvation for age-0 herring may be more dependent on photoperiod than the temperature of the water column. Second, achieving larger size and therefore higher energy stores prior to winter is critical in order to survive through the winter.

References


Some Processes Affecting Mortality of Juvenile Fishes During the Spring Bloom in Prince William Sound, Alaska

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Extended Abstract

Piscivory among herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) during the spring bloom in Prince William Sound, Alaska, was examined using field data. A midwater wing trawl equipped with a net sounder was used to sample adult pollock (>30 cm). Herring, immature pollock (<30 cm), and various juvenile fishes were sampled with small-mesh purse seines and variable-mesh gillnets. The diet composition of herring and pollock was estimated from specimens collected in 1994 (*n* = 4,106), 1995 (*n* = 7,342), and 1996 (*n* = 3,958). Herring, immature pollock, and adult pollock diets were generally dominated by large calanoid copepods (mostly *Neocalanus*) during the bloom of these copepods in May, but both fish species switched to alternative prey in June (Willette et al. 1999). An analysis of the functional responses of herring and adult pollock feeding on large calanoid copepods was conducted to determine the copepod biomass at which these fishes switched to alternative prey as well as their probable feeding modes (Willette et al. 1999). Initially, nonlinear regression analyses were conducted to estimate handling times (*H*) using several possible values for the cross-sectional area of the reactive field (*γ*) and swimming speed (*U*) as constants. Then handling times estimated during the first stage were used as constants to estimate *U* using two values of *γ*.
consistent with ram filter and particulate feeding. For filter feeders, $\gamma$ was assumed to be the cross-sectional area of the mouth gape. Functional responses of herring and adult pollock were best described by type III models (Table 1) with parameters consistent with particulate and filter feeding modes, respectively (Willette et al. 1999). Herring began to switch to alternative prey as the biomass of large calanoid copepods in the upper 20 m of the water column declined below 0.2 g per m$^3$ Adult pollock switched to alternative prey as copepod biomass in high-density layers declined below about 1.0 g per m$^3$ (Willette et al. 1999). Analysis of covariance indicated that herring and pollock tended to switch from large copepods to nekton prey after the copepod bloom declined (Willette et al. 1999). During this period, herring and immature pollock largely consumed juvenile gadids and salmonids less than 6 cm in length, whereas adult pollock consumed squid and fish less than 15 cm (Table 2). Herring generally consumed fish 5-25% of their length, immature pollock 5-35%, and adult pollock 3-40% (Willette et al. 1999).

An analysis of covariance was conducted to test the null hypothesis that mortality of juvenile pink salmon ($Oncorhynchus gorbuscha$) was not related to the duration of the bloom of large calanoid copepods from ocean entry to the time the fish reached 6 cm in length (Willette et al. 1999). The analysis was structured to enable examination of the simultaneous effects of the zooplankton bloom on juvenile growth rate and predator switching behavior. Juvenile body weight at release, juvenile growth rate, number of juveniles released from each hatchery each day, and zooplankton bloom duration were included as independent variables in the model. Mortality of juvenile pink salmon from fry to adult was estimated for 147 coded-wire-tag (CWT) groups of pink salmon (Geiger 1990) released from four hatcheries in Prince William Sound (1989-1995). Only CWT groups with fish less than 0.35 g body weight at release were included in the analysis, due to small sample sizes for groups composed of larger fish. Growth of juvenile CWT salmon was estimated from an analysis of covariance function relating growth to juvenile release and environmental data (Willette 1996, Willette et al. 1999). Mortality of CWT pink salmon was significantly reduced when the zooplankton bloom was prolonged during the juvenile life-stage (Willette et al. 1999). This result was generally consistent with our analyses of predator stomach contents suggesting that predator switching behavior was the cause. However, mortality was also positively correlated with juvenile growth rate, juvenile body weight at release, and the number of juveniles released (Willette et al. 1999). Model predicted values exhibited some coherence with auto-correlated patterns of mortality by date of juvenile release (Fig. 1). Examination of temporal patterns in the independent variables indicated that these mortality patterns were probably caused by interactions among the independent variables rather than the effect of any single variable. Changes in predator abundance or size composition may be related to temporal trends in the residuals. Growth rate of CWT juvenile pink salmon was positively correlated (Table 3) with
Table 1. Nonlinear regression parameters for type II and III functional response models for herring and adult pollock feeding on large calanoid copepods.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Type</th>
<th>( \gamma ) (m(^2))</th>
<th>Estimated U (km/day)</th>
<th>( H ) (day/g)</th>
<th>MS Regression</th>
<th>MS Error</th>
</tr>
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<tbody>
<tr>
<td>Herring</td>
<td>II</td>
<td>0.0001</td>
<td>43.0 (7.3)</td>
<td>0.167</td>
<td>7.86</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.0791</td>
<td>0.6 (0.5)</td>
<td>1.930</td>
<td>7.91</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.0001</td>
<td>17.2 (2.0)</td>
<td>-1.913</td>
<td>2.99</td>
<td>0.33</td>
</tr>
<tr>
<td>Adult pollock</td>
<td>II</td>
<td>0.0022</td>
<td>8.1 (3.8)</td>
<td>0.248</td>
<td>208.02</td>
<td>5.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.2788</td>
<td>0.1 (0.2)</td>
<td>0.524</td>
<td>156.47</td>
<td>6.96</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.0022</td>
<td>16.7 (5.0)</td>
<td>0.142</td>
<td>243.46</td>
<td>4.54 *</td>
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<tr>
<td></td>
<td></td>
<td>0.2788</td>
<td>0.4 (0.5)</td>
<td>0.438</td>
<td>185.24</td>
<td>6.16</td>
</tr>
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</table>

Handling times (\( H \)) estimated during the first stage of the analysis were used to estimate swimming speed (\( U \)) using 2 values of \( \gamma \) associated with ram filter and particulate feeding. The best-fit model for each species is indicated with an asterisk, and the standard error of the estimated swimming speed is indicated in parentheses.

Table 2. Mean prey length (cm) and prey-predator length ratios (%) for various nekton in the diets of herring, immature pollock, and adult pollock. Data from 1994-1996 combined.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Herring</th>
<th>Immature pollock</th>
<th>Adult pollock</th>
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<tr>
<td></td>
<td>Length</td>
<td>Ratio</td>
<td>Length</td>
</tr>
<tr>
<td>Herring</td>
<td>-</td>
<td>-</td>
<td>11.5</td>
</tr>
<tr>
<td>Gadids</td>
<td>2.8</td>
<td>14.1</td>
<td>3.4</td>
</tr>
<tr>
<td>Salmonids</td>
<td>4.0</td>
<td>18.9</td>
<td>4.0</td>
</tr>
<tr>
<td>Capelin</td>
<td>-</td>
<td>-</td>
<td>9.2</td>
</tr>
<tr>
<td>Sand lance</td>
<td>-</td>
<td>-</td>
<td>9.9</td>
</tr>
<tr>
<td>Squid</td>
<td>-</td>
<td>-</td>
<td>6.9</td>
</tr>
<tr>
<td>Other fish</td>
<td>1.9</td>
<td>10.4</td>
<td>2.4</td>
</tr>
<tr>
<td>Unidentified fish</td>
<td>2.2</td>
<td>11.4</td>
<td>4.2</td>
</tr>
</tbody>
</table>
Figure 1. Actual (open circles) and predicted (closed circles) survival of coded-wire-tagged juvenile pink salmon released from the Armin F. Koernig, Wally H. Noerenberg, and Cannery Creek hatcheries in Prince William Sound, 1990-1995. Data are plotted by Julian date of release from each hatchery within each year of release.
Table 3. Parameters estimated from an analysis of covariance.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard error</th>
<th>p-value</th>
</tr>
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<tbody>
<tr>
<td>Intercept</td>
<td>-5.762</td>
<td>1.468</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mean zooplankton volume</td>
<td>3.201</td>
<td>0.445</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mean ocean temperature</td>
<td>2.421</td>
<td>0.780</td>
<td>0.002</td>
</tr>
<tr>
<td>Number juveniles released:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>low</td>
<td>4.850</td>
<td>0.676</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>high</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zooplankton × release number:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>low</td>
<td>-2.729</td>
<td>0.480</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>high</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Mean growth rate of coded-wire-tagged juvenile pink salmon was the dependent variable and mean zooplankton settled volume, mean ocean temperature, and number of juveniles released from each hatchery each day were the independent variables.

Figure 2. Relationships between zooplankton settled volume during juvenile life and growth rate of coded-wire-tagged juvenile pink salmon released in groups of less than and greater than 20 million.
ocean temperature and zooplankton settled volume during the period from juvenile release to recapture (Willette et al. 1999). The parameters of the relationship between growth and zooplankton settled volume were also significantly different between small and large release groups (Fig. 2), indicating that juvenile pink salmon probably compete for limited prey resources in nearshore nursery habitats (Walters and Juanes 1993). Our analyses indicate that bottom-up processes affect mortality of juvenile fishes during the spring bloom through effects of temperature and prey density on juvenile growth rate. However, bottom-up processes also modify top-down processes involving feeding-mode shifts toward piscivory among the later life-stages of herring and pollock, thus increasing mortality of juvenile fishes.

References


Are Changes in Bering Sea Crab and Groundfish Populations Related?

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Extended Abstract

Are decadal changes in abundance of crabs and groundfish in the Gulf of Alaska and eastern Bering Sea related? One popular opinion is that groundfish predation caused declines in crab populations. Research into crab-groundfish relationships off Alaskan coasts is scanty, and purported cause and effect relationships remain speculative. Routine examination of stomach contents of a few commercially important groundfish species in the eastern Bering Sea shows that Pacific cod (Gadus macrocephalus) are the primary crab consumer (Livingston 1991, Livingston et al. 1993, Livingston and deReynier 1996). Other species that eat much fewer crabs include yellowfin sole (Pleuronectes asper), rock sole (Pleuronectes bilineatus), Pacific halibut (Hippoglossus stenolepis), Alaska plaice (Pleuronectes quadrituberculatus), walleye pollock (Theragra chalcogramma), and skates.

We examined three hypotheses about crab-groundfish relationships in the eastern Bering Sea: H01 (Predation hypothesis): Increased predation by groundfish caused declines in crab recruitment; H02 (Common forcing hypothesis): Physical forcing caused inverse responses in recruitment of crabs and groundfish; and H03 (Species replacement hypothesis): Declines in crab abundance preceded species replacement by groundfish. To test the predation hypothesis, time series of groundfish biomass were compared with indices of crab year-class strength lagged to age 1. To test the common forcing hypothesis, we compared annual crab and groundfish year-class strengths lagged to the common year of hatching or spawning. Finally, for the replacement hypothesis, time series of crab abundance were compared with groundfish year-class strength lagged to age 0.
Time series of abundance and recruitment were obtained for five crab stocks and three groundfish stocks in the eastern Bering Sea (Table 1). Length-based analyses provided abundance and recruitment estimates for red king crab, *Paralithodes camtschaticus* (Zheng et al. 1997), and Tanner crab, *Chionoecetes bairdi* (Zheng et al. 1998). Estimates for blue king crab, *Paralithodes platypus*, were based on catch-survey analyses (Zheng et al. 1997), and area-swept estimates were obtained for snow crab, *Chionoecetes opilio* (Stevens et al. 1998). Stock synthesis models provided biomass and recruitment estimates for Pacific cod (Thompson and Dorn 1997), yellowfin sole (Wilderbuer 1997), and rock sole (Wilderbuer and Walters 1997).

For each hypothesis and crab-groundfish species pair, a one-tailed *t*-test was conducted to determine whether the correlation coefficient, *r*, was significantly (*α* = 0.05) less than zero. Following the advice of Pyper and Peterman (1998), significance tests were based on the effective number of degrees of freedom (*df* *) to account for autocorrelation in the time series of abundance and log-transformed recruitment.

Of the 45 correlations examined, only 4 were statistically significant. Most (26) correlation coefficients were of the wrong sign (+) contrary to the hypotheses. For the predation hypothesis, Bristol Bay red king crab year-class strength was significantly related to the biomass of Pacific cod (*r* = −0.68, *df* *) = 7). For the common forcing hypothesis, significant correlation existed between year-class strengths of Bristol Bay red king crab and rock sole (*r* = −0.75, *df* *) = 4) and between St. Matthew blue king crab and Pacific cod (*r* = −0.45, *df* *) = 13). And for the replacement hypothesis, Bristol Bay Tanner crab abundance was significantly related to rock sole year-class strength (*r* = −0.74, *df* *) = 6). Quite a few more correlations were statistically significant when autocorrelation was ignored with unadjusted degrees of freedom (*df* = *n*−2). However, such tests violate the assumption of serial independence of the observations (Pyper and Peterman 1998).

Statistical significance does not necessarily imply biologically meaningful relationships. We expect 2 out of 45 correlations to be significant at the 95% confidence level by chance alone. Multiple statistical tests increase the probability of Type I error. For instance, the negative relationship between red king crab year-class strength and abundance of Pacific cod may be spurious. In a detailed study of predation and population trends, Livingston (1989) concluded that cod predation was not responsible for declines of red king crab in Bristol Bay in the early 1980s. Estimates of red king crab consumed by cod during 1981 and 1983-1992 (Livingston 1991, Livingston et al. 1993, Livingston and deReynier 1996) constitute only 0-11% of the crab population. Most king crabs in cod stomachs are softshell females > 80 mm CL (Livingston 1989)—well beyond the size at which year class strength is determined. Interestingly, a good case for a predation mechanism exists for Tanner and snow crabs as juveniles of both species are heavily preyed upon by Pacific cod (Livingston 1989), yet strong year classes of both crab species co-occurred with high cod biomass resulting in positive correlations. Negative correlations between
Table 1. Abundance and year-class strength indices for crab and groundfish stocks in the eastern Bering Sea. Time lag is either the number of years from hatching to recruitment (crabs) or spawning to recruitment (fish). Recruitment is not necessarily recruitment to the fishery (see data source for definition).

<table>
<thead>
<tr>
<th>Stock</th>
<th>Time series</th>
<th>Abundance measure</th>
<th>Year-class strength index</th>
<th>Time lag (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bristol Bay red king crab</td>
<td>1972-1997</td>
<td>Males ≥ 95 mm CL</td>
<td>Male recruits ≥ 95 mm CL</td>
<td>6</td>
</tr>
<tr>
<td>Pribilof Islands blue king crab</td>
<td>1975-1997</td>
<td>Males ≥ 120 mm CL</td>
<td>Newshell males 120-134 mm CL</td>
<td>7</td>
</tr>
<tr>
<td>St. Matthew I. blue king crab</td>
<td>1978-1997</td>
<td>Males ≥ 105 mm CL</td>
<td>Newshell males 105-119 mm CL</td>
<td>7</td>
</tr>
<tr>
<td>Bristol Bay Tanner crab</td>
<td>1975-1997</td>
<td>Males ≥ 93 mm CW</td>
<td>Male recruits ≥ 93 mm CL</td>
<td>7</td>
</tr>
<tr>
<td>EBS snow crab</td>
<td>1975-1997</td>
<td>Males ≥ 50 mm CL</td>
<td>Newshell males 50-60 mm CL</td>
<td>4</td>
</tr>
<tr>
<td>EBS Pacific cod</td>
<td>1978-1997</td>
<td>Biomass ≥ age 3</td>
<td>Age 3 recruits</td>
<td>3</td>
</tr>
<tr>
<td>EBS yellowfin sole</td>
<td>1965-1997</td>
<td>Biomass ≥ age 2</td>
<td>Age 5 recruits</td>
<td>5</td>
</tr>
<tr>
<td>EBS rock sole</td>
<td>1975-1997</td>
<td>Biomass ≥ age 2</td>
<td>Age 4 recruits</td>
<td>4</td>
</tr>
</tbody>
</table>

EBS = eastern Bering Sea. CL = carapace length. CW = carapace width.
year-class strengths of Bristol Bay red king crab and rock sole and between St. Matthew Island blue king crab and Pacific cod are consistent with apparent opposite responses of year-class strengths of groundfish (Hollowed and Wooster 1995) and red king crab (Tyler and Kruse 1996, Zheng and Kruse In press) to dynamics of Aleutian low pressure systems in winter. An inverse relationship between Tanner crab abundance and rock sole year-class strength seems plausible. There is considerable overlap in geographic distributions and diets, including polychaetes, bivalves, amphipods, ophiuroids, and echinoids (Tarverdieva 1976, Lang 1992). Depletion of Tanner crab could improve the growth and survival of rock sole competitors through a feeding response.

The lack of general inverse relationships between crabs and groundfish in the Bering Sea is largely attributable to the variety of patterns of year-class strengths among crab stocks. Many groundfish populations experienced common patterns. Strong year classes in the mid-1970s through the 1980s caused large increases in biomass throughout the 1980s, and moderate year classes in the 1990s caused a leveling off or decline in biomass in the 1990s. Year-class strength of most crab stocks declined from the early to mid-1970s—opposite the groundfish trend—but thereafter crab trends were stock specific. Year-class strength of St. Matthew Island blue king crab increased from the mid-1970s through 1990, whereas year-class strength of the Pribilof Islands stock continued its decline until the early 1980s and since then recruitment was moderate through 1990. Year-class strength of Tanner crab increased sharply in the late 1970s to early 1980s and then declined. Snow crab year-class strength was very high in the mid-1970s and throughout the 1980s but fell off in the early 1990s. Finally, year-class strength of red king crab continued to decline through the 1980s with a relatively strong one in 1990. Several red king and Tanner crab stocks in the Gulf of Alaska had patterns similar to Bristol Bay red king crab with the exception that the 1990 year class does not appear to be strong in the gulf. We suspect that common beliefs about inverse crab-groundfish relationships stem largely from the notoriety of the red king crab declines, the lack of knowledge about divergent trends for other crab species, and lack of appreciation for the statistical consequences of autocorrelation in time series of fish data.

Based on our exploratory data analysis, we reject the notion that groundfish predation and competition provide sweeping explanations for crab population fluctuations in the eastern Bering Sea. Most crab-groundfish relationships were positive, and we found few instances in which inverse relationships were statistically significant. Although we reject tenets such as “the groundfish ate all the crabs,” we feel that more complex crab-groundfish relationships are certainly deserving of further study. It may be that inter-specific relationships are non-linear, that spatial distributions must be considered to uncover true underlying relationships, and that databases of groundfish stomach contents are not reflective of total
crab consumption due to limited temporal and spatial sampling. We plan to explore these crab-groundfish relationships in greater detail in a forthcoming paper.

References


Optimum Control in a Predator-Prey Model Based on a Two-Species Exploited Ecosystem

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Abstract

Various “biological reference points” are applied when choosing a rational regime of a fishery for a single species system. In the present paper an attempt has been made to illustrate the necessity of including multispecies considerations in precautionary fisheries management advice. As a starting point for such a precautionary approach it is possible to choose the simplest form of multispecies model which should have at least one steady equilibrium point.

The area of allowable management for a two-species system is constructed using as coordinates the fishing mortality rates of both species and some boundaries of the area that correspond to crash lines for this ecosystem. Trophic interactions of the “predator-prey” type reduce the allowable area of control as compared with areas that would be assumed if the interactions between fish populations were neglected. For example, the point corresponding to the MSY criterion for the prey species lies on the boundary of the allowable area and should be considered as a crash point with respect to the predator population.

The area of allowable control is also constructed for two competing population models. The problem of maximizing economic profit of a two-species fishery in an equilibrium state and during a set time period (for example, one year) inside the allowable area of control is touched upon.

Introduction

The theoretical basis of multispecies modeling in biology was set in the 1920s. The analytical models of community populations dynamics were worked out by Volterra (1931) and Lotka (1925) in the form of differential equation sets that took into consideration biological interactions between
species. Qualitative analysis of those models showed that fluctuations in population abundance can be caused by the interaction between species. At the same time or a little earlier Baranov (1918, 1925) worked out the basis of the “fishery theory” having built the mathematical model for an exploited fish population. The main advantage of this model consisted of the fact that it was possible to estimate its parameters on the basis of biological and fishery data for specific important targets of the fishery. Later these two scientific schools developed separately. Modern catch-at-age analysis grew from Baranov’s ideas. At the same time production models of the fishery are connected to Volterra’s models.

Recently a new approach to selecting a rational management scheme for a fishery was detailed within the framework of ICES (International Council for the Exploration of the Sea) stock assessment working groups. This approach is based on the estimation of various “biological reference points.” The algorithms of the definition of these points are described in various papers (Jakobsen 1992, 1993; ICES 1996, 1997a), but they concern only isolated populations, i.e., an ideal situation. One of the objectives of the multispecies assessment working group (ICES 1997b) was to evaluate how the existence of multispecies interactions affect the estimates of the biological reference points.

The objective of this paper is to apply this approach to simple multispecies community management and to show the need to take into account the trophic interactions between fish populations when defining a rational fishing strategy as these interactions influence “a vector of rational management” of a fish community.

**Methods**

Often a single species precautionary approach is based on simplest single species considerations—production models. Thus as a starting point for a multispecies precautionary approach, it is possible to choose the simplest form of multispecies model (equation 1).

Since any real ecosystem persists in nature for a sufficiently long time, even the simplest model describing it should have at least one stable equilibrium point; for example:

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1(a_1 - bx_1 - cx_2) - F_1x_1 \\
\frac{dx_2}{dt} &= x_2(a_2x_1 - M) - F_2x_2
\end{align*}
\]

where

- \(x_1\) is abundance of a prey species;
- \(x_2\) is abundance of a predator species;
$a_1$ and $b$ are parameters of growth of a prey population in existence of limiting factor (if there are no predators in the system, the prey population grows according to logistics law);

$c x_2$ is a mortality rate attributable to the predators (described by a “Volterra term”);

$a_2 x_1$ is a predator population growth rate in terms of reproduction rate, proportional to the number of prey individuals;

$M$ is the predator natural mortality rate; and

$F_1$ and $F_2$ are the fishing mortality rates for the prey and predator species respectively.

It follows from equation (1) that predator species go extinct in the absence of the prey species.

If the community is not exploited, equilibrium of equation (1) gives:

$$X_{10} = \frac{M}{a_2}; X_{20} = \frac{D}{a_2 c}.$$  

The solution is positive if:

$$D = a_1 a_2 - b M > 0. \quad (2)$$

It is assumed that equation (2) is always true in this analysis.

If the fishing mortality rate is constant over time, the equilibrium point of system (1) (equilibrium stock abundance) has coordinates:

$$X_{10} = \frac{M}{a_2}; X_{20} = \frac{D - (a_2 F_1 + b F_2)}{a_2 c}.$$  

For point $(X_{10}, X_{20})$ to lie in a positive quadrant it is necessary that the fishing mortality rates (the parameters of control on our community) meet the condition

$$a_2 F_1 + b F_2 < D \quad (4)$$

Research into the stability of an equilibrium point $(X_{10}, X_{20})$ on the I method by Ljapunov has shown that under condition (4) and $b > 0$ this point is asymptotically stable. As model (1) is a special case of a model by Kolmogoroff (1972), we obtain an additional feature of the equilibrium point: if the following condition is met

$$0.25 b^2 (M + F_2) + b a_2 (a_2 + F_2) > a_2^2 (a_1 - F_1)$$

it is a steady node; otherwise, a stable focal point. Thus, as parameters $b$, $F_1$ and $F_2$ increase (until condition (4) is broken) the system is damped. At
$b = 0$ a condition of stability is broken (system (1) is now the elementary set of V. Volterra’s equations the solution of which is undamped oscillations).

**Results**

Using fishing mortality rates \{F_1, F_2\} as coordinates, Fig. 1 shows the region (triangle MON together with its boundaries ON and OM) corresponding to an area of allowable management of the two-species community, as derived from condition (4) and $F_1 \geq 0$, $F_2 \geq 0$. The equation for line MN is obtained by changing (4) from an inequality to an equality and solving for $F_1$:

$$F_1 = \frac{D}{a_z} - \frac{F_2 b}{a_z}$$

*(5)*

**Fishing Strategies for a Prey Population**

Let us assume that in managing a fishery of a prey population we neglect any effort of the predator on the prey population; we consider it to be isolated. Then using accepted terminology (ICES 1996) $F_1 = a_1$ is a maximum (limiting) value of prey fishing mortality named $F^*_{1\text{crash}}$, and maximum sustainable yield (MSY) corresponds to a value $F^*_{1\text{MSY}} = 0.5 a_1$ (point S in Fig. 1). The manager expects to obtain the catch $\text{MSY}^* = \frac{a_1^2}{4a_2}$. Sign * means that the formula concerns a model of an isolated population.

However, since the predators exist, the maximum intensity of fishing on the prey species is reduced. If the predators are not fished, $F^*_{1\text{crash}} = D/a_2 < a_1$ (on equation [2]), and with the increase of $F_2$, $F^*_{1\text{crash}}$ linearly decreases according to equation (5). The line MN represents a scenario in which fishing mortality rates $F_1$ and $F_2$ are such that the fishery results in the extinction of the predator population (i.e., $X_{20r} = 0$). That is an example of limiting the crash line in a community management area corresponding to a collapse of the community structure.

Stable annual yield of the prey species in a year is given by

$$Y_{10} = F_1 X_{10} = \frac{F_1(M + F_2)}{a_z}$$

The function $Y_{10}$ ($F_1$, $F_2$) has no maximum in a positive area of argument and increases with increasing $F_1$ and $F_2$ up to the intersection with a plane perpendicular to the plane \{F_1,F_2\} and passing through the line MN.

There are two possible cases, as follows.
In this case point S lies inside the allowable area, maximum sustainable yield of the prey population on line MN is given by \( \text{MSY}_1 = \frac{a_1^2}{4b} \), with the corresponding coordinates \( F_1 = 0.5a_1 \) and \( F_2 = \left( a_1a_2/2b - M \right) \). This is indicated as point Q on the boundary of allowable control area (Figs. 1 and 2a). Thus point Q is not a target point but rather a crash point with respect to the predator population. For prey species point Q could look like a target point, but fishing control corresponding to point Q is unallowable because it results in the extinction of the predator species. To manage the fishery using a precautionary approach, it is necessary to select the management strategy so as to save the predator species. It means, that instead of a point Q it is necessary to select a point lying inside area ONM. The precise choice of a management reference point depends on inter alia the relative value (biological or economic) of both species as well as on agreement between managers. For example, if a 90% control criterion were adopted the line MN would have to be shifted parallel to itself to pass through point \( F_1 = 0.9D/A_2 \). The shifted line (dashed line on Fig. 1) would obviously be included in the new allowable area of control. A point \( Q_{pr} \) on the this dashed line corresponds to the target point of the prey fishery.

**Case 1: \( a_1/2 < D/a_2 \)**

In this case point S lies inside the allowable area, maximum sustainable yield of the prey population on line MN is given by \( \text{MSY}_1 = \frac{a_1^2}{4b} \), with the corresponding coordinates \( F_1 = 0.5a_1 \) and \( F_2 = \left( a_1a_2/2b - M \right) \). This is indicated as point Q on the boundary of allowable control area (Figs. 1 and 2a). Thus point Q is not a target point but rather a crash point with respect to the predator population. For prey species point Q could look like a target point, but fishing control corresponding to point Q is unallowable because it results in the extinction of the predator species. To manage the fishery using a precautionary approach, it is necessary to select the management strategy so as to save the predator species. It means, that instead of a point Q it is necessary to select a point lying inside area ONM. The precise choice of a management reference point depends on inter alia the relative value (biological or economic) of both species as well as on agreement between managers. For example, if a 90% control criterion were adopted the line MN would have to be shifted parallel to itself to pass through point \( F_1 = 0.9D/A_2 \). The shifted line (dashed line on Fig. 1) would obviously be included in the new allowable area of control. A point \( Q_{pr} \) on the this dashed line corresponds to the target point of the prey fishery.
Figure 2. Sustainable yield for the prey species $Y_{10}$ (a) and for the predator species $Y_{20}$ (b) in the allowable area of management for Case 1: $a_1 = 0.5; b = E^{-11}; c = 5E^{-10}; a_2 = 5E^{-11}; M = 0.2; D = 2.3E^{-11}$.
Case II: $a_1/2 > D/a_2$ (i.e., $M < a_1a_2/b < 2M$)

In this case point $S$ (the point corresponding to a level MSY for an “isolated” population) lies outside the allowable area of control. It means that an attempt to manage the prey population using the conventional MSY criterion for an isolated population will result in the extinction of the predator population; i.e., the destruction of the community even in the complete absence of a predator fishery! This case is most dangerous for a multispecies fishery system. The greatest value of the yield of the prey species is equal to $DM/a_2^2$ and is reached in a point $M$ in Fig. 1 ($F_1 = D/a_2$, $F_2 = 0$). For a precautionary approach a point corresponding to a smaller $F_1$ value should be chosen (with possible $F_1$ values up to $F_1 = 0.9D/a_2$).

**Fishing Strategies for a Predator Population**

In a steady state of community the yield of the predator species is given as

$$Y_{20} = F_2Y_{20} = \frac{F_2(D - a_2F_1 - bF_2)}{a_2c} \quad (6)$$

For fixed $F_1$, the predator yield is maximized at

$$F_2 = \frac{(D - a_2F_1)}{2b} \quad (7)$$

represented by the line $ML$, which is inside the allowable control area and is a median of angle $OMN$. By substituting equation (7) into equation (6), we receive $Y_{20}$ as a function of $F_1$ as shown below:

$$Y_{20}^* = \frac{(D - a_2F_1)^2}{4a_2bc}$$

This surface is shown in Fig. 2b.

For any fixed $F_1$ the line $ML$ gives both levels of predator fishing mortality rate $F_{2MSY}$ and of maximum predator yield. Predator yield is maximized at $F_1 = 0$ at point $L[F_1=0, F_2 = D/2b]$ on the boundary of the allowable area. We obtain an expected conclusion: the maximum yield of the predator population can be found in a lack of prey fishing. Point $L$ is therefore a target reference point for the predator population. An example of a precautionary point may be taken as $L_{pr} = 0.9D/2b$.

In Fig. 2 functions $Y_{10} (F_1, F_2)$ and $Y_{20} (F_1, F_2)$ are built for the model (equation 1) parameter values that satisfied the Case 1 condition ($a_1/2 < D/a_2$): $a_1 = 0.5; a_2 = 5E-11; b = E-11; c = 5E-10; M = 0.2; D = 2.3E-11$. 

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**Ecosystem Approaches for Fisheries Management**

155
The Problem of Maximization of Economic Profit

Consideration of the problem of optimal control on a community as a whole warrants investigation of the problem of maximization of economic profit of a two-species fishery in an equilibrium state and during a set time period (for example, one year) inside the allowable area of control MON. In the simplest form, economic profit can be expressed as the function:

\[ P(F_1, F_2) = \frac{A_1 F_1 (M + F_2)}{a_2} + \frac{A_2 F_2 (D - a_2 F_1 - b F_2)}{c a_2} - B_1 F_1 - B_2 F_2 \]  

(8)

where parameters \( A_1 \) and \( A_2 \) are profit per unit yield of populations I and II, respectively; and \( B_1' \) and \( B_2' \) are the respective expenses per unit of fishing effort \( E \). Assuming the fishing mortality rate is proportional to fishing effort, i.e., \( F_i = q_i E \), (\( i = 1, 2 \)) where the \( q_i \) is a constant factor, we have \( B_i = B_i' / q_i \) and \( B_2 = B_2' / q_2 \). Equation (8) may be written in a polynomial form

\[ P(F_1, F_2) = k_1 F_1 + k_2 F_2 - k_3 F_1 F_2 - k_4 F_2^2 \]  

(9)

where

\[ k_1 = A_1 X_{10} - B_1 \]
\[ k_2 = A_2 X_{20} - B_2 \]
\[ k_3 = -A_1 / a_2 + A_2 / c \]
\[ k_4 = A_2 b / c a_2 \]

In this case, \( X_{10} \) and \( X_{20} \) are the coordinates of an equilibrium point of the unexploited system (equation 2) (at \( F_1 = F_2 = 0 \)), and therefore \( k_1 \) and \( k_2 \) are profits per unit of fishing mortality rate in this "initial" equilibrium point. If the fishery is cost effective at this point, \( k_1 \) and \( k_2 \) are positive constants. The sign of \( k_3 \) can be either: for example, if \( (A_2/c) >> (A_1/a_2) \), then the predator population is more valuable, then \( k_3 > 0 \), and vice versa.

Analysis of the function of two variables (equation 9) shows that it has neither a maximum nor a minimum, so that its greatest value is achieved on the boundary of the allowable area. The function \( P \) on each of the boundary lines is given by the following functions of one argument

\[ P_1 \text{ (on line ON)} = k_2 F_2 - k_4 F_2^2 \]
\[ P_2 \text{ (on line OM)} = k_1 F_1 \]
\[ P_3 \text{ (on line MN): substituting } F_1 = D / a_2 - F_2 b / a_2 \text{ in equation (9), we obtain the function of } F_2 \]

\[ P_3(F_2) = F_2^2 \alpha_2 + F_2 \alpha_1 + \alpha_0 \]  

(10)
where

\[ \alpha_2 = -A_1 \frac{b}{a_2^2} \]
\[ \alpha_1 = A_1 \frac{(D - bM)}{a_2^2} + B_1 \frac{b}{a_2} - B_2 \]
\[ \alpha_0 = \left( \frac{A_1 M}{a_2^2} - B_1 \right) \frac{D}{a_2} \]

The constant term \( \alpha_0 \) is equal to a value of function \( P \) at point M. The value \( P \) at point N is equal \((-B_2D/b) < 0\), i.e., at this point the fishery is unprofitable. In a point \( \{ F_1 = 0, F_2 = 0 \} \) \( P = 0 \).

It is necessary to consider four separate cases:

1. \( k_1 > 0, k_2 > 0 \).

On line ON (with zero fishing on the prey species) \( P_1(F_2) \) is maximized at the point R \( \{0, k_2/2k_4\} \) which lies left of point L \( \{0, D/2b\} \), because \( k_2/2k_4 = D/2b - B_2/2k_4 \). The value of \( P \) at this point is \( k_2^2 /4k_4 \).

On line OM, \( P_2(F_1) \) increases with increasing \( F_1 \), so that on this line the greatest value of the profit occurs at point M and is equal to \( k_1D/a_2 \).

On line MN, \( P_3(F_2) \) has a maximum at \( F_2 = -\alpha_1 /2\alpha_2 \) (point U), provided \( \alpha_1 > 0 \), and max \( P_3 = \alpha_0 - \alpha_1^2 /4\alpha_2 > P \) (at point M).

If the condition \( \alpha_1 > 0 \) holds, it is therefore necessary to calculate and compare the value of the function \( P \) at each of the points U and R since profit is maximized at one of these two points. If this condition does not hold, the value of \( P \) at points M and R should be compared.

2. \( k_1 < 0, k_2 > 0 \). The fishery for the prey species is not cost effective.

On line MN, \( P < 0 \). On line ON maximum occurs at point R.

3. \( k_1 > 0, k_2 < 0 \). The fishery for the predator species is not cost effective, the greatest value \( P \) occurs at point M.

4. \( k_1 < 0, k_2 < 0 \). The fishery for either of the two species is unprofitable.

The task of maximizing the summed yield of two species, given that they have different economic values, can easily be solved by substituting zeros in place of \( B_1 \) and \( B_2 \) in the profit function. From equation (9) it follows that the factors \( k_1 \) and \( k_2 \) are now positive, so that it is fair to assume that conclusions of case 1 hold. Now

\[ \alpha_2 = -A_1 \frac{b}{a_2^2} ; \alpha_1 = A_1 \frac{(D - bM)}{a_2^2} \]
\[ \alpha_0 = A_1 \frac{M D}{a_2^2} \]

Point U will therefore coincide with point Q, and point R with point L. Using 90% criterion for \( F \) rates, precautionary management points now correspond to points \( Q_{pr}, M_{pr} \) and \( R_{pr} \), so that the values of \( P \) at these points should be compared. For example, point U will change to the corresponding precautionary point \( U_{pr} = \{0.9F_1(Q), 0.9F_2(Q)\} \) and so on. Thus

\[ P(U_{pr}) = A_1 \frac{(D^2 - M^2 b^2)}{(2ba_2^2)}; \]
\[ P(R_p) \equiv A_2 D^2 / (4 b c a_2) \]. (Sign \( \equiv \) arose from \( 0.9^2 \equiv 0.8 \)).

The choice of optimal control strategy will depend on the relation between both the biological and the economic (\( A_1 \) and \( A_2 \)) parameters.

**Discussion**

A simplified single predator-single prey model is considered in this paper, whereas the structure of real ecosystems is obviously much more complicated. At a shortage of prey species the predator switches to another prey; i.e., the risk of its extinction is not so high. There are more advanced models of community. For example, Collie and Spencer (1994) applied more complicated function in a predator-prey model to describe the predation: if in a set of equations (equation 1) the food consumption rate is proportional to prey number \( a_i x_i \), these authors apply function \( g x_i A x_i ^{2} / (A^2 + x_i^2) \), which takes into account the existence of threshold prey abundance \( A \) and level of saturation corresponding to maximum ration. These authors also described a natural mortality by quadratic function taking into account the interspecies competition of a predator and (or) cannibalism. The obtained model for different relations among parameters of a model has one or two steady equilibrium points in the positive quadrant. Outcomes of research of a model are very interesting: with changing parameter values or increasing \( F \) for prey population, the population number can “slide” from one equilibrium state to another.

Collie and Spencer (1994), to simplify the analysis, did not consider predator fishing; but if to the right side of the equation for a predator we add the term \( -F x_i \), it is simply to show (for example, with help of the analysis of isoclines) that the area of parameters for which there is the lower equilibrium state of a prey is narrowed; i.e., fishing for predators stabilizes prey population fluctuations and promotes the stabilization of its abundance near the top level of an equilibrium.

Incorporation of alternative prey into a two-species predator-prey model (Spencer and Collie 1995) does model more realistically but complicates an analysis.

Besides the prey-predator relation, it is interesting to consider other types of interspecies relations such as competition for some common resource. The task of optimizing a fish community with two competing species according to the Gause model (Gause 1935, Gause and Witt 1935) has previously been considered (Bulgakova 1970). Competition is manifest only in an environment with limited resources and hence a logistics growth model was used for each population. The set of equations describing an exploited community of this sort has the form:

\[
\frac{dX_i}{dt} = \frac{X_i a_i}{K_i} (K_i - X_i - b_j X_j) - F_i X_i, \quad i = 1, 2 \tag{11}
\]
where $K_i$ is the maximum abundance of species $i$ in the absence of a competing species. Competition parameters $b_i$ mean that in terms of the competition interaction $X_j$ individuals of species $j$ are equivalent to $b_iX_j$ individuals of species $i$ (i.e., they consume the same amount of resource limiting development of the species).

Further details pertaining to the analysis of this system are presented by Bulgakova (1970). We describe here only the main features of the results. The area of allowable control for the system (equation 11) is shown in Fig. 3. The line $F_{1\text{crash}}$ is the line where $X_{10} = 0$; i.e., the prey population goes extinct. The line $F_{2\text{crash}}$ is similarly a boundary where the predator species goes extinct. For this model, the allowable area is bounded by two crash lines! It is clear from this figure that an increase in $F_2$ allows an increase in the allowable $F_1$ value.

For an “isolated” prey population MSY$_1$ is reached at point U such that $F_1 = 0.5a_i$. In the presence of the competitor (the second population) MSY$_1$ increases with increasing $F_2$ and occurs on the line AR. The max $Y_{10}$ corresponds to point R that lies on the crash line for the second population. It implies that control of this sort results in the displacement of the second

Figure 3. The area of available management for two competing species (unshaded area).
Figure 4. Sustainable yield for two competing species for $K_1 = K_2 = 100$; $a_1 = 1.5$; $a_2 = 2$; $b_1 = 0.5$; $b_2 = 0.8$. 
species and therefore in a collapse of ecosystem structure. To avoid displacing the second species with the first species, it is necessary to select a point of control that lies inside the allowable area on the line AR (on the dashed line), i.e., point $\text{R}_{pr}$. The functions $Y_{10}$ and $Y_{20}$ for model (equation 11) are represented in Figs. 4a and 4b as functions of $F_1$ and $F_2$.

**Conclusions**

1. The management strategy chosen for an exploited prey-predator fish community should be selected on the basis of the relationship between the parameters of this community. It is important to determine whether this community corresponds to case 1 or case 2 as described in the text. A different precautionary approach has to be applied for different community types.

2. For a solution of the problem of optimal control it is useful to construct an area of allowable control using as coordinates the fishing mortality rates of the species in the community.

3. Consideration of interspecies interaction suggests that the effect of fishing can be very risky to a community because the fishing of one species can result, for example, in the extinction of the predators in the system. Certainly, we considered a simplified single-predator single-prey model. At a shortage of prey species the real predator switches to another prey; i.e., the risk of its extinction is not so high.

4. The model (equation 1) may serve to illustrate the need to elaborate on the theory of a precautionary approach to community management.

5. Fishing on a population corresponding to lower trophic level without considering the influence of predators on them is unacceptable. It is necessary to expect that there are a number of predators on the same prey population in the natural ecosystem that increase the pressure on the prey.

**Acknowledgments**

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References


Consumption and Harvest of Pelagic Fishes and Squids in the Gulf of Maine–Georges Bank Ecosystem

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Abstract
The fish biomass on the continental shelf off the eastern United States and Canada has shifted toward the pelagic community in the 1990s. Biological interactions play a major role in the structure and function of this dynamic ecosystem and thus a greater understanding of these mechanisms can provide a basis for better fisheries management. Low-frequency monitoring of predator diet compositions, such as the current program at the Northeast Fisheries Science Center, can provide a basis for conclusions on the impact of biological interactions on this or similar ecosystems. This study provides estimates of consumption by 12 species of piscivorous fish on Atlantic mackerel (Scomber scombrus), Atlantic herring (Clupea harengus), butterfish (Peprilus triacanthus), sand lance (Ammodytes sp.), short-finned squid (Illex illecebrosus), and long-finned squid (Loligo pealei) during 1977-1997. Results suggest that total consumption by these predatory fish is significant when compared to landings, ranging from 1.5 million to 3.0 million t per year. Predation on pelagic fish and squids appears to be an important and large component of the overall system dynamics of this ecosystem. Consumption of pelagic fish and squids by predatory fish appears to equal or exceed landings in most years from 1977-1997. In several cases, notably for long-finned squid, herring, and butterfish, consumption also exceeds the current MSY for these stocks.
Introduction

The Georges Bank–Gulf of Maine ecosystem in the Northwest Atlantic found along eastern Canada and the United States has undergone significant changes in biomass and relative abundance of fishes during 1970-1997 (Clark and Brown 1977, Mayo et al. 1992, Fogarty and Murawski 1998). Traditionally important fisheries on groundfish (i.e., gadids and flounders), and pelagic species experienced major declines associated with large increases in foreign and domestic fishing effort throughout the 1970s and 1980s (Fig. 1). Following these reductions, formerly underutilized species such as goosefish, white hake, and spiny dogfish became important sources of landings in the 1990s, which then resulted in declines of these stocks. Concurrently, lack of interest by commercial fleets allowed for recovery of the herring and mackerel stocks present in this ecosystem; such that the community is now dominated by pelagic species.

Reported landings of herring and mackerel reached 470,000 t and 437,000 t in 1968 and 1973, respectively, and both stocks collapsed several years later (NEFSC 1996, 1998). Stock rebuilding of these species was complete by the mid-1990s and current biomass for both is on the order of 1-3 million t (NEFSC 1998). Previous research indicated that these species and several other pelagic fish and squids comprise major portions of the diets of piscivorous fish, seabirds, and marine mammals in this ecosystem (Cohen et al. 1982, Bowman and Michaels 1984, Overholtz et al. 1991a).

Understanding the interactions that occur in this pelagic complex should be important for understanding and managing this dynamic system. Future single species and multispecies management regimes for this region may benefit greatly from an increased understanding of the role that biological interactions play in the region (Larkin 1996). Previous research and analysis of diet composition data of piscivorous fish from the region of the Gulf of Maine to Cape Hatteras suggests that predation on pelagic fishes and squids may be one of the more important areas for investigation of biological interactions in this ecosystem. Prior studies suggest that piscivorous fish consumed more biomass than the current harvest of many pelagic species (Cohen et al. 1982, Overholtz et al. 1991a,b). Current fishery management in the United States is focused on sustainable levels of fishing as mandated in the recent revision of the Magnuson-Stevens Fishery Conservation and Management Act. Consumption of fish by predators may in many cases exceed the maximum sustained yield (MSY) of various stocks, with significant overlap of size distributions between commercial landings and predators.

The objective of this research was to utilize the time-series of diet compositions of 12 important predatory fish collected on bottom trawl surveys during 1977-1997 in the area from Maine to North Carolina, to produce estimates of consumption of the more important pelagic species, namely: Atlantic mackerel, Atlantic herring, butterfish, sand lance, short-
finned squid, and long-finned squid. We contrasted fish consumption with commercial landings and current estimates of MSY. Estimates of individual and total consumption for the entire set of predators were produced. We also quantified and discussed various sources of uncertainty.

**Methods**

**Input Data and Analysis**

Diet composition data from spring and autumn research survey cruises for 1973-1990 were analyzed to determine a list of significant predators of Atlantic mackerel, Atlantic herring, sand lance, butterfish, and short-finned and long-finned squid. A set of 12 piscivorous fish was chosen based on percentage of pelagic prey in the diets and consistency over time (Table 1). Data were also analyzed in 5 cm intervals to determine appropriate lengths of predators where the fishes and squids began to comprise a significant portion of the diets. Cutoff lengths for predators averaged about 30 cm and ranged from 20 to 40 cm.

Sample sizes of stomachs were examined, and too few samples were available to use a calendar year approach for most predators. Data from
Table 1. Number of samples (N), minimum and maximum predator length (MIN_LEN, MAX_LEN), mean predator fork length (MEAN_LEN), standard error of predator length (SE_LEN), average total stomach content (AVE_STOM, g), and standard error of total stomach contents (SE_STOM) by species based on data from 1973-80 and 1981-1990 bottom trawl surveys from all areas.

<table>
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<tr>
<th>S NAME</th>
<th>N</th>
<th>MIN_LEN</th>
<th>MAX_LEN</th>
<th>1973-1980 MEAN_LEN</th>
<th>SE_LEN</th>
<th>AVE_STOM</th>
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*Squalus acanthias*  
*Raja ocellata*  
*Merluccius bilinearis*  
*Gadus morhua*  
*Pollachius virens*  
*Urophycis chuss*  
*Urophycis tenuis*  
*Urophycis regia*  
*Paralichthys dentatus*  
* Pomatomus saltatrix*  
*Cynoscion regalis*  
*Lophius americanus*
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<th>SE_LEN</th>
<th>AVE_STOM</th>
<th>SE_STOM</th>
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Figure 2. Average spring and autumn bottom temperature during 1968-1997 for the region from Maine to Cape Hatteras, North Carolina.

Figure 3. Mean number of fish per tow and 95% CI from research bottom trawl surveys for 12 species of predatory fish during 1973-1997.
Figure 4. Coefficient of variation (CV) of mean survey abundance for 12 species of predatory fish during 1973-1997.

1977-1997 were aggregated on 2-year intervals for all predators except spotted hake, bluefish, and weakfish which were averaged over 5-year intervals. Interval length was based on having at least 50-75 stomachs available in each season (i.e., spring and autumn). We assumed that spring data would serve as a proxy for winter and autumn for the summer periods of the year.

Bottom temperature data were obtained for the same research survey cruises during 1977-1997. Average profiles for the entire region from the Gulf of Maine to Cape Hatteras, North Carolina, were calculated using methods developed by Holzwarth and Mountain (1992) to interpolate between stations and regions (Fig. 2).

Estimates of annual predator biomass and abundance were obtained from spring and autumn bottom trawl surveys during 1977-1997 (Fig. 3). Survey catch per tow in numbers were trimmed to account for each predator cutoff length and area swept abundance for the entire survey region was estimated. Coefficients of variation in the trawl survey abundance estimates averaged 20-40% for most species with occasional values at 50% or greater in specific years (Fig. 4). For species with virtual population analysis (VPA) available an average catchability coefficient (q) was calculated
Figure 5. A: Total stock numbers from virtual population analysis (VPA) and survey q method (Survey) for summer flounder during 1982-1997. B: Total stock numbers from VPA and survey q method for Georges Bank cod during 1978-1997.
from age-specific results appropriate for each predator cutoff length. This average q was divided into area swept numbers to produce a virtual population estimate for each year. This method appears to produce useful results similar to current VPAs (Fig. 5), and is necessary for estimating predator numbers during years prior to the first year in the VPA. For species without a current VPA, weighting coefficients from Clark and Brown (1977) were applied in the same manner to produce estimates of population numbers. Exceptions to this were spiny dogfish and winter skate where area swept numbers were used. Spiny dogfish are very vulnerable to bottom trawl survey gear and following the same procedures used in the assessment for this stock (NEFSC 1998), an area swept estimate of numbers was used in this analysis. The estimate for winter skate was also based on an estimate of area swept numbers, but lacking any collaborative analysis, an estimate based on night tows (higher vulnerability) was used. Since availability to survey gear can be influenced by numerous factors in any given year, large, but not actual changes in average number and weight per tow may occur, resulting in very abrupt interannual variability in bottom trawl time series data. To compensate for this type of problem we used LOWESS (Cleveland 1979) smoothing methods to produce estimates of predator biomass. This approach is consistent with the current methodology applied in the spiny dogfish assessment (NEFSC 1998). Predator numbers used to estimate consumption are shown in Fig. 6.

The biomass of pelagic fish and squids varied considerably during 1973-1997. Butterfish, long-finned squid, and short-finned squid were generally more abundant during the 1970s, showed some decline in the 1980s, but did not fluctuate to any great degree during the entire period (Fig. 7). Sand lance on the other hand were very abundant during the late 1970s and early 1980s, but declined to very low abundances thereafter. Mackerel and herring, stocks that were heavily fished, were very low through the mid-1970s and early 1980s, but increased greatly during the 1990s (Fig. 7).

**Estimation of Consumption**

Many approaches to estimating consumption are available in the literature, but we chose the approach developed by Eggers (1977), Elliot and Persson (1978), and Pennington (1985) that utilizes the relationship between average stomach contents and gut evacuation rate as:

\[
C = 24RS^\gamma
\]  

(1)

where \( C \) is consumption, 24 is the number of hours in a day, \( S \) is the mean stomach weight per 24-hour period per fish predator, \( \gamma \) is a derived constant (usually assumed equal to 1), and \( R \) is the evacuation rate, where:

\[
R = \alpha e^{\beta T}
\]  

(2)
where $\alpha$ and $\beta$ are fitted constants and $T$ is temperature. Values for parameters in these two equations were obtained from the literature after a review of methods and estimates from various analyses (Tyler 1970, Jones 1974, Kioeboe 1978, Durbin et al. 1983). The alpha and beta parameters in equation 2 were assumed to equal 0.004 and 0.115, respectively, conservative values for teleost fishes from Durbin et al. (1983). Since results are tied closely to the choice of values for these two important parameters, a sensitivity analysis was completed for both the alpha and beta parameters over a range of temperature values. As expected, evacuation rates change minimally, but detectably, over a range of assumptions for the alpha parameter (Fig. 8 top). The beta parameter has a much more pronounced impact on evacuation rates resulting in large and dramatic increases in $R$, as expected due to the exponential effect of this parameter (Fig. 8 bottom).

Stomach content data for 1977-1980 were estimated in grams per stomach while data collected during 1981-1997 were estimated in volumetric units (cubic centimeters per stomach). We used a conversion of 1.1 g per 1.0 cc of stomach material in the current analysis. Data for estimating the
Figure 7. Survey biomass prey species 1973-1997. Biomass (kg) of Loligo, Illex, butterfish, mackerel, herring, and sand eels from research bottom trawl surveys during 1973-1997.
average stomach content in predators were obtained from spring and au-
tumn bottom trawl surveys during 1977-1997. Stomach content data were
averaged across 2-year periods for all predators except spotted hake, blue-
fish, and weakfish, which were averaged across 5-year blocks. Percent
composition data were based only on predators with prey (all prey types)
in their stomachs. The percentage of empty stomachs by year and season
is poorly estimated in the current database due to regurgitation and other
factors.

Although our primary focus is on the Gulf of Maine–Georges Bank
region, we assumed homogeneity for the entire region and thus have a
course spatial resolution for these initial estimates of consumption. The
pelagic prey studied in this analysis change their distribution on a sea-
sonal basis and this should be reflected in the spring and autumn ap-
proach we developed. We assumed that fishery-independent trawl surveys
collect both pelagic prey and their predators consistently across the time
series.

Results

Total Consumption

Total annual consumption (all prey) by the 12 species of predatory fish
averaged 1.5 million t per year and ranged between 1.3 million and 2.9
million t per year during 1977-1997 (Fig. 9). Total annual consumption by
individual predators was lowest for goosefish and summer flounder and
highest for spotted hake, silver hake, and spiny dogfish, but varied with
predator abundance in any given year. Consumption estimates by indi-
vidual predators demonstrate a gradient across 3 orders of magnitude,
mainly reflective of predator size and abundance. For example, total con-
sumption by spiny dogfish averaged 619,000 t per year and ranged from
113,000 to 890,000 t per year during 1977-1997 (Fig. 10). Total annual
consumption for bluefish averaged 108,000 t per year and ranged from
16,000 to 167,000 t per year during this same period (Fig. 10). Goosefish
total annual consumption averaged 14,000 t per year and ranged from
3,600 to 61,000 t per year during 1977-1997 (Fig. 10).

Consumption of Pelagics

Consumption of pelagic fishes and squids generally tracked levels of prey
abundance, particularly for herring, mackerel, and sand lance (Fig. 11).
Predation on sand lance reached very high levels in the late 1970s and
early 1980s coincident with the collapse of mackerel and herring and the
large biomass of sand lance present at this time (Fig. 11). As the mackerel
stock began to recover in the early 1980s, predation increased, reaching
89,000 t in 1988 (Fig. 11). Consumption of herring averaged 200,000 t
Figure 8. (Top) Results of sensitivity analysis with $\alpha = 0.004$ and $\beta$ ranging from 0.001 to 0.5 over temperatures from $-2^\circ$ to $20^\circ$ C. (Bottom) Results of sensitivity analysis with $\beta = -0.1$ and $\alpha$ ranging from 0.001 to 0.1 over temperatures from $-2^\circ$ to $20^\circ$ C.
during the 1990s, reaching well over 300,000 t in several years (Fig. 11). Consumption of *Illex* and *Loligo* averaged 24,000 t and 46,000 t, respectively, during 1977-1997, but remained relatively constant over this period, with a minor peak during the late 1970s and early 1980s for *Illex* (Fig. 11). Predation on butterfish was more variable, but with the exception of a few years, was relatively low when compared to the other species (Fig. 11).

**Unidentified Fish**

The proportion of unidentified fish in the diets of these predators varied over 1977-1997, but generally represented a large amount of biomass, on the order of several hundred thousand t per year. This component of the predator diet averaged 292,000 t annually and ranged between 170,000 and 436,000 t per year (Fig. 12).

**Consumption vs. Available Biomass of Mackerel and Herring**

Consumption of mackerel during 1977-1997 generally followed mackerel biomass until 1989, when a sharp decline occurred ($r = 0.21$) (Fig. 13 top). The reduction in mackerel consumption by piscivorous fishes continued through 1993 in spite of large increases in mackerel biomass (Fig. 13 top). Consumption of herring was relatively low during 1977-1988, and then
Figure 10. Total consumption by spiny dogfish, bluefish, and goosefish during 1977-1997.
increased rapidly as herring biomass began to increase after 1989 (Fig. 13 bottom). Consumption of herring remained high during 1989-1996 with the exception of sharp drop during 1993-1994 (Fig. 13 bottom). Overall consumption of herring by the 12 predators was positively correlated ($r = 0.61$) with herring biomass, increasing substantially in the 1990s (Fig. 13 bottom).

**Consumption and Fishing**

Recent changes in the Sustainable Fisheries Act (SFA) have meant that maximum sustained yields are again an important biological reference point for fish stocks; MSYs for the pelagic fishes and squids in this analysis were recently reevaluated (NEFMC 1998). The MSY for mackerel and herring are on the order of 300,000 t, while averaging only about 20,000 t for butterfish, *Illex*, and *Loligo* (NEFMC 1998).
Commercial landings of prey species during 1973-1997 ranged over 2 orders of magnitude (Fig. 14). Squid and butterfish landings were relatively constant and low, except for *Illex* in the mid-1970s. Herring and mackerel landings were very large in the early to mid-1970s and then dropped to much lower values thereafter (Fig. 14). There is no commercial fishery on sand lance.

Consumption of *Loligo* exceeded landings in all years during 1977-1997 (Fig. 15 top). Mackerel consumption and landings were similar during this period and both were well below the MSY for this stock (Fig. 15 middle). Annual herring landings averaged 82,000 t during 1977-1997, ranging from 36,000 to 120,000 t per year (Fig. 15 bottom). Consumption by predators was below 50,000 t during 1977-1987 and then increased dramatically in the 1990s, ranging from 100,000 to 270,000 t (Fig. 15 bottom). Consumption by piscivorous fish in recent years approaches the estimated MSY for the herring complex (Fig. 15 bottom).
Figure 13. (Top) Consumption of mackerel by 12 species of predatory fish and average mackerel VPA biomass during 1977-1994. (Bottom) Consumption of herring by 12 species of predatory fish and average herring VPA biomass during 1977-1996.
Figure 15. Consumption of (top) Loligo, (middle) mackerel, and (bottom) herring by 12 species of predatory fish and commercial landings during 1977-1997.
Discussion

Results from this analysis suggest that the magnitude of total consumption by these predatory fish is large, ranging from 1.5 million to 3.0 million t during 1977-1997. Predation on pelagic fish and squids is an important and large component of the overall dynamics of this Northeast shelf ecosystem. In many instances that diet composition data collected during bottom trawl surveys follows prey abundance rather closely. For example, during the collapse of the herring and mackerel stocks in the mid-1970s, the consumption of these species dropped and a surge in sand lance abundance and consumption occurred (Fogarty et al. 1991). Similarly, mackerel from the large 1982 year class were present in many predators in 1983 and 1984 as sand lance were declining very rapidly in abundance and importance in predator diets. Stock rebuilding of the herring complex in the 1990s was also apparent in predator diets as percentages increased considerably during this period.

Interestingly, mackerel, although very abundant now, appear to be less important than herring in the diets of piscivorous fish. This may be related to predator preference or availability of these prey fish to predators. Mackerel grow rapidly and are probably only vulnerable for the first several years of their life history, unless affected by mechanisms such as density dependence (Overholtz et al. 1991b). Herring, except at very large sizes (> 30 cm), seldom grow out of the window of predation vulnerability and are subject to predation by fish over most of their life history. Predation may be positively related to the available biomass of mackerel and herring, but consumption of mackerel appears to have declined in conjunction with major increases in herring biomass, at least for this set of predators.

Several issues need to be addressed in the design of future fish stomach sampling regimes to address some of the possible uncertainties encountered in this analysis. The percentage of empty stomachs in the current database may be in excess of actual values encountered in other ecosystems (Daan 1973, Bowman 1976). The problem of unidentified fish in the stomachs is very important because these are likely the same small pelagics of interest to this study. This means that consumption on these species of fish may be underestimated in the current analysis. Daan (1973) was able to closely examine digested fish to provide positive identification of the remains. This can be done by examining hard parts such as otoliths, skeletal structure, musculature, and other forensic approaches. Clearly this is an area for further investigation.

It appears that low-frequency monitoring of predator diet compositions such as the current program can provide an adequate database for drawing conclusions concerning the impact of biological interactions. If predators change their preference for different food items based on several factors, it may be necessary to establish a long-term monitoring program to document patterns, instead of extrapolating results from one or
two intensive sample periods. On the other hand, intense seasonal sampling may be necessary to fully elucidate stomach content and diet composition of key predators. Several years of intense seasonal sampling would provide important information for a comparison with the current low-frequency monitoring program. This would improve our knowledge base on the seasonal mean and variance of stomach content data and diet compositions. It would also confirm if extrapolations to half-year intervals based on spring and autumn sampling are valid.

Our results may underestimate consumption since we choose to use relatively conservative parameters in our estimation. The sensitivity analysis we conducted indicates that consumption estimates are very dependent on the choice of parameters. Further work in this important area would allow for more precise statements about the impacts of predation.

Finally, consumption of pelagic fish and squid by predatory fish appears to equal or exceed landings in most years from 1977 to 1997. In several cases, notably for *Loligo*, herring, and butterfish, consumption also exceeds the current value of MSY for these stocks. Length compositions of mackerel in landings and predators do not overlap to any great degree because most of the commercial fishery is centered on age 3+ fish. However, for herring, butterfish, *Loligo*, and *Illex*, there is probably some overlap between the fishery and predators. This means that to an extent the fishery and predators are competing for the same fish.

**Acknowledgments**

We would like to thank D. Mountain for providing the temperature profiles used in the analysis. We also thank the many seagoing personnel who collected the stomach content data during the 1970s, 1980s, and 1990s.

**References**


Multispecies Interactions in the Georges Bank Fish Community

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Abstract
Dramatic shifts in the species composition of the Georges Bank fish community have occurred during the past 30 years. The bottomfish community, once dominated by cod, haddock, and flounder, shifted to lower-value species such as skates and dogfish. Herring and mackerel declined during the 1960s and 1970s, but have since recovered to record levels. These shifts are attributed primarily to high fishing pressure, but predation is the largest source of pre-recruit mortality, and is also considered important in controlling the dynamics of the fish community. Prior studies have identified the important predators as cod, silver hake, and spiny dogfish. Herring, mackerel, silver hake, and yellowtail flounder all experience high predation mortality, especially in the first and second years of life. To construct dynamic production models of the Georges Bank fish community, we aggregated the dominant species into four groups: gadoids, flatfishes, pelagics, and elasmobranchs. Inclusion of species interactions in the dynamic models was based on statistical fits to the biomass data and groundtruthed with known species interactions. The most important interactions are predation of gadoids and elasmobranchs on pelagics and apparent competition between gadoids and elasmobranchs. Equilibrium yields of each group depend on the abundances and hence the exploitation rates of the other species. Harvest strategies are simulated for both the multispecies model and the corresponding single-species equations, to illustrate the sensitivity of medium-term projections to species interactions.

Introduction
The Georges Bank fish community has undergone profound shifts in abundance and species composition during the past 3 decades (Fogarty and Murawski 1998). From 1963 to 1993 the principal groundfish species (cod,
haddock, yellowtail flounder) were progressively depleted, first by distant-water fleets and then by domestic fisheries. The principal pelagics (herring and mackerel) initially declined due to high exploitation, and subsequently recovered to record abundance levels as exploitation was reduced. Dogfish and skates, which have experienced low exploitation until recent years, increased to maximal levels in 1990 and have since begun to decline. The end result was a shift in community structure from demersal groundfish to pelagics and elasmobranchs.

Were these shifts in community structure independent responses to fishing? If so, single-species management approaches should be sufficient to prevent overfishing and to rebuild depleted stocks. Or, did trophic interactions contribute to the shift in species composition? Did predation contribute to the decline of the groundfish stocks, and does it delay their recovery from overfishing? What caused the dramatic increase in elasmobranchs and, more recently, the pelagic species? To the extent that multispecies interactions occur, their effects may need to be considered in restoring the Georges Bank fish community to a more desirable and valuable species composition (Sissenwine and Cohen 1991, Fogarty and Murawski 1998).

Several lines of evidence support the importance of species interactions in the Georges Bank fish community. A biomass-dynamics model, fit to the aggregate biomass of fish species, indicated that, although the species composition of the fish community may change, aggregate yield is limited by community-level density dependence (Brown et al. 1976). The Georges Bank energy budget is relatively tight in the sense that most of the production at lower trophic levels can be accounted for by predation at higher trophic levels (Sissenwine et al. 1984). By including a juvenile fish component in the energy budget, Sissenwine et al. (1984) demonstrated that the largest source of mortality of prerecruit fish is predation by other fish. Hence predation can potentially affect the survival of prerecruit fish and/or the growth and production of predator populations.

The feeding habits of the Georges Bank fish species have been analyzed in conjunction with the National Marine Fisheries Service (NMFS) bottom trawl survey (Grosslein et al. 1980). This food habits database has been used to calculate diet overlap by Langton (1982) and as input to age-structured multispecies models of the fish community by Overholtz et al. (1991). These authors found that predation mortality rates were highest on the youngest ages of fish and that predation mortality varied during the 5 years of their analysis. Multispecies virtual population analysis (MSVPA) is a form of age-structured multispecies analysis that relates changes in diet composition to changes in the abundances of prey and predator species (Sparre 1991). A nine-species MSVPA of the Georges Bank fish community from 1978 to 1992 was performed by Tsou and Collie (In press). The important predators were cod, silver hake, dogfish, and skates, whereas the important prey species were herring, mackerel, silver hake, and yellowtail flounder. The MSVPA confirmed the high levels of preda-
tion mortality on age-0 and age-1 fish. The biomass of prey species consumed was of the same order as the commercial harvest.

Other types of multispecies analysis have been performed with the NMFS trawl survey data. Fogarty and Brodziak (1994) aggregated the survey data into gadids, flatfishes, skates, other groundfish, and small pelagics to reduce the complexity of the multispecies system. Lagged correlations between the aggregate indices revealed inverse relationships between species groups that are known from food-habits data to interact (e.g., flounder and skates). This correlation structure was used to select the terms of a multivariate time-series model.

In this study we aggregated biomass and landings data from 1963 to 1993 of 10 biologically or commercially important species on Georges Bank into four groups. These data were used to fit single and multispecies biomass-dynamics models. Unlike cohort-based methods, biomass-dynamics models can be applied to species for which age-composition data are lacking. The multispecies model parameter estimates identify and quantify the strongest species interactions. We explore how species interactions cause biological reference points to vary as other species are exploited. Finally, the single and multispecies model fits are used to simulate population trajectories and to evaluate management strategies. The results of this study can help evaluate the ability of single-species models to be used to successfully manage species that interact strongly with one another.

**Methods**

Ten fish species were selected for this study based on their commercial and/or trophic importance (Table 1). We compiled biomass and landings data for these 10 species for the years 1963-1993. This time period corresponds to the start of the autumn trawl survey in 1963 up until 1994 when catch reporting requirements were changed and consistent landings estimates are not yet available for all species. Sand lance (*Ammodytes* spp.) and squid (*Loligo pealei* and *Illex illecebrosus*) are important as prey of other fishes, but were not included in this study because biomass estimates for these taxa are not available.

Biomass and landings data were compiled from the most recent stock assessments, where available (Table 1). For species with age-structured assessments, we summed ages 2 and older, as age 2 corresponds roughly to the age of recruitment and maturity for many of these species. Data for cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Pleuronectes ferrugineus*), herring (*Clupea harengus*), and mackerel (*Scomber scombrus*) were extracted from recent ADAPT runs. Historical virtual population analyses (VPA) were used to fill in the early years for herring and silver hake (*Merluccius bilinearis*), for which there is no recent stock assessment. Catch-survey analysis (CSA) was used to fill in the early years of cod and yellowtail flounder prior to the age-structured assessments.
Table 1. Sources of biomass and landings data.

<table>
<thead>
<tr>
<th>Method</th>
<th>Species</th>
<th>Years</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Winter flounder</td>
<td>1963-1993</td>
<td>q for yellowtail flounder</td>
</tr>
<tr>
<td></td>
<td>Winter skate</td>
<td>1963-1993</td>
<td>Fall survey area swept</td>
</tr>
<tr>
<td></td>
<td>Little skate</td>
<td>1963-1993</td>
<td>Fall survey area swept</td>
</tr>
</tbody>
</table>

To accomplish this we used the method of Collie and Sissenwine (1983) as implemented on a spreadsheet. The biomass of spiny dogfish (*Squalus acanthias*) has been estimated with a biomass-dynamics model (Northeast Fisheries Science Center [NEFSC] 1994). The biomass estimates of silver hake were updated to 1993 by regressing 1968-1987 VPA estimates on survey weight per tow. For the remaining species we used trawl survey indices scaled by appropriate catchability coefficients ($q$). The survey $q$ estimated for yellowtail flounder with CSA was used to scale the survey indices for winter flounder (*Pleuronectes americanus*). The Georges Bank trawl survey indices were based on survey strata 15-23. Landings data were compiled from the corresponding assessments or extracted from NMFS catch tables. The statistical areas corresponding to Georges Bank are 522-525, 551, 552, 561, and 562. The tables of biomass and landings estimates are available from the authors.

Several of these fish species migrate (herring, mackerel, and dogfish) and are assessed over a wider geographic area than Georges Bank. For these species, we used the trawl survey data to calculate the proportion of the species total biomass found on Georges Bank each year. We used spring survey data to map the spatial distributions of these species because the spring survey data are considered the best index of their abundance and are therefore used for stock assessment. The estimated proportions on Georges Bank were quite variable because of the high spatial variability in...
mean catch per tow. We therefore chose to use the mean proportions on Georges Bank across years to scale the total biomasses and catches of herring, mackerel, and dogfish. This proration preserves the temporal trends for these species but scales their abundance to that of species resident on Georges Bank.

The biomasses and landings of the 10 fish species were aggregated into four groups to simplify the model and to reduce the number of interaction terms that would need to be estimated. The groups were primarily taxonomic: gadoids (cod, haddock, silver hake), flatfishes (yellowtail flounder, winter flounder), pelagics (herring, mackerel), and elasmobranchs (spiny dogfish, winter skate, little skate). We expect the species in each group to have similar rates of increase and similar ex-vessel prices. Some of the species also have similar exploitation histories (e.g., haddock and silver hake) and similar feeding habits (e.g., yellowtail and winter flounders). In fitting the biomass-dynamics model we treated each aggregate group as a “species.”

Correlation analyses were conducted on the aggregate biomass data to determine at which time lags the potential interactions were the strongest. A 2-year time lag was selected for the biomass-dynamic models because it approximates the age of recruitment and maturity of many of these species. Lags greater than 2 years reduced the apparent correlation between taxonomic groups and would result in fewer observations for model fitting.

The biomass-dynamics model consists of delayed-difference equations of the form:

\[ G_{t+1} = G_t + rG_{t-1} - \frac{r}{k} G_{t-1}^2 - Y_t \pm \text{species interaction terms.} \quad (1) \]

This equation applies to gadoids \((G, g)\) and there are three equivalent equations for flatfishes \((F, f)\), pelagics \((P, p)\), and elasmobranchs \((E, e)\). Equation (1) is a discrete form of the Schaefer model with rate of increase \(r\), carrying capacity \(k\) and commercial landings \(Y\). The species interaction terms can represent competition or predation. A competition term, with competition coefficient, \(c_{ge}\):

\[ -c_{ge} G_{t-1} E_{t-1}. \]

represents the negative effect of elasmobranchs on gadoids. We investigated three types of predator functional response:

Type I  
\[ d_{gp} G_{t-1} P_{t-1}, \]

Type II  
\[ \frac{d_{gp} G_{t-1} P_{t-1}}{1 + a_{gf} F_{t-1} + a_{gp} P_{t-1}}, \text{ and} \]


Type III
\[ \frac{d_{gp} G_{t-1} P_{t}^{2}}{1 + a_{gf} F_{t-1}^{2} + a_{gp} P_{t-1}^{2}}. \]

The \( d_{gp} \) coefficients represent the positive effect of pelagics on gadoids. The \( a \) coefficients combine search time and probability of capture and represent the suitability of each prey type to the predator. Complementary negative terms represent the effects of predators on the prey. By specifying the \( t-1 \) lag for the biomass variables, we assume that the important trophic interactions occur during the first year of life and recruitment occurs at age 2.

A hierarchical set of models was fit that differed in complexity and hence number of parameters to estimate. To identify the most important subset of interaction terms, we fitted process-error versions of the single-species (no interactions) and Type-I equations (linear interactions). “Leaps and bounds” regressions were performed to identify which subset of interaction terms minimized Mallow’s Cp statistic (Statistical Sciences 1991). Once the important interaction terms had been identified, non-linear estimation was used to fit observation-error versions of the biomass-dynamics models. The biomass values for the first 2 years of each species group were used as starting values and therefore assumed to be measured without error. The remaining biomass values were estimated by minimizing the sum of squares objective function:

\[ \sum_{i=1}^{4} \sum_{t=2}^{T} (\ln B_{i,t} - \ln \hat{B}_{i,t})^2 \]

where \( B_{i,t} \) is the observed biomass of group \( i \) in year \( t \) and \( \hat{B}_{i,t} \) is the predicted biomass. Due to some missing values in 1963 we had a total \( (T) \) of 30 years of data and four species groups. The nonlinear estimation was performed with AD Model Builder (Otter Research 1994).

The Type-I model was fitted with those species interactions that were consistent with food-habits data and gave a low Cp statistic. To determine the important interaction terms in the Type II and III models we started with the single-species fit and added in the terms identified in the Type-I fits one at a time. The term that caused the largest reduction in the sum of squared residuals was added in each step. As terms were included, we tested opposite interactions regardless of whether they were significant in the single-species fits.

The goodness of fit of the alternative model forms was compared with \( F \)-tests and the Akaike Information Criterion (AIC). The AIC is defined as:

\[ \text{AIC} = -2 \ln L + 2p, \]

where \( \ln L \) is the log likelihood evaluated at the maximum likelihood estimates and \( p \) is the number of model parameters (Quinn and Deriso 1999).
Equilibrium analyses were performed to calculate the single-species biological reference points, $h_{\text{msy}}$, the exploitation fraction for maximum sustainable yield. Equilibrium yields were calculated by simulating the system of equations for 600 years. Response surfaces were plotted to investigate the sensitivity of each species group equilibrium yield to the exploitation rate and hence equilibrium biomass of the other groups. These biological reference points and sensitivities were used to guide simulations of the multispecies fish community.

**Results**

Biomass estimates of the 10 fish species are first compared to check for consistent patterns within taxonomic groups (Fig. 1). Haddock and silver hake were the dominant gadoids in the 1960s, but were fished down by distant-water fleets in the late 1960s (Fogarty and Murawski 1998). Cod was less abundant in the 1960s, reaching its peak biomass in the 1970s. All three gadoids had declined to low levels by the late 1980s. The variability in flounder biomass in the 1960s is due to variability in the survey indices from which these biomass estimates were calculated. Yellowtail flounder biomass declined sharply in the 1970s and collapsed to very low levels in the late 1980s. Winter flounder biomass has less of a trend, but also declined to low levels by 1990.

The biomasses of herring and mackerel were scaled by the proportions found on Georges Bank in the spring trawl survey; the mean proportions were 0.121 for herring and 0.126 for mackerel. Herring biomass declined in the late 1960s, again due to high catches by distant-water fleets. During the 1980s herring was virtually absent from Georges Bank and present at low levels in the rest of the Gulf of Maine (NEFSC 1996). Since then herring biomass has increased to record high levels. Fluctuations in mackerel biomass are less dramatic than for herring, but mackerel has also increased to record high biomass levels. Spiny dogfish biomass was also scaled by the mean proportion found on Georges Bank in the spring survey (0.124). Dogfish abundance increased almost monotonically from 1963 to 1993. The skate data are minimum biomass estimates based on area swept calculations from the autumn trawl survey data. Winter skate biomass increased to a maximum in 1986 and by 1993 had declined to values as low as those seen in the 1970s. Unlike the other two elasmobranchs, there was apparently no concurrent increase in the abundance of little skate.

The aggregate biomass and landings data (Fig. 2) reflect the abundance patterns of the component species. Gadoid abundance declined sharply in the late 1960s and more gradually from 1975 to 1985. The corresponding decreases in flatfish biomass occurred in the early 1970s and the early 1980s, about 5 years later than the gadoids. The exploitation rate of flatfishes (landings per biomass) appears to have been very high in 1975 and in several of the years since 1985. By applying the catchability
Figure 1. Biomass of 10 fish species on Georges Bank. The biomass units used throughout this paper are thousand metric tons (kt).
coefficient for yellowtail flounder to winter flounder, we may have underestimated flounder biomass. On the other hand, the Georges Bank yellowtail flounder stock did sustain high levels of fishing mortality before collapsing (NEFSC 1997). The relatively high harvests of pelagics in the early 1970s contributed to their decline. Harvests since then have remained low while the biomass of pelagics increased rapidly to record levels. Elasmobranchs have low fecundities and therefore cannot sustain high exploitation rates. Low catches in the 1980s may have contributed to peak biomass levels, whereas increased harvests in the 1990s may partially explain the downturn in abundance.

The single-species biomass-dynamics models reproduce the general abundance patterns of the four groups (Fig. 2). The pelagic carrying capacity ($k_p$) cannot be estimated reliably from these data because of the near exponential increase in pelagic biomass in recent years. In all model fits $k_p$ was fixed at 1,000 kt. (The biomass units used throughout this paper are thousand metric tons [kt].) The nonlinear model with Type-I interactions fit significantly better than the single-species models, according to the $F$-test and AIC (Table 2). The interactions identified in this fit were positive effects of flatfishes and pelagics on gadoids and negative effects of elasmobranchs and gadoids on flatfishes. Elasmobranchs had a
Table 2. Parameters of the single- and multispecies biomass-dynamics models with Type-I and Type-III predator functional responses.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Single-species</th>
<th>Type-I interactions</th>
<th>Type-III interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td>( r_g )</td>
<td>0.3110</td>
<td>0.1343</td>
<td>0.4106</td>
</tr>
<tr>
<td>( k_g )</td>
<td>1,323</td>
<td>356.7</td>
<td>1,208.2</td>
</tr>
<tr>
<td>( r_f )</td>
<td>0.6125</td>
<td>1.814</td>
<td>0.6371</td>
</tr>
<tr>
<td>( k_f )</td>
<td>97.25</td>
<td>85.22</td>
<td>92.99</td>
</tr>
<tr>
<td>( r_p )</td>
<td>0.3398</td>
<td>0.3627</td>
<td>0.781</td>
</tr>
<tr>
<td>( k_p )</td>
<td>1,000(^a)</td>
<td>1,000(^a)</td>
<td>1,000(^a)</td>
</tr>
<tr>
<td>( r_e )</td>
<td>0.2178</td>
<td>0.6166</td>
<td>0.3231</td>
</tr>
<tr>
<td>( k_e )</td>
<td>194.4</td>
<td>171.4</td>
<td>108.1</td>
</tr>
<tr>
<td>( d_{gf} )</td>
<td></td>
<td>0.001911</td>
<td></td>
</tr>
<tr>
<td>( d_{gp} )</td>
<td></td>
<td>0.001073</td>
<td>6.361×10(^{-5})</td>
</tr>
<tr>
<td>( c_{ge} )</td>
<td></td>
<td>2.99×10(^{-4})</td>
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</tr>
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\(^a\) Fixed value
\(^b\) \( p < 0.001\)
\(^c\) \( p < 0.05\)
negative effect on pelagics and pelagics had a small, reciprocal positive effect on elasmobranchs. Gadoids had a negative effect on elasmobranchs which could be interpreted as competition. When this model was simulated with no harvesting, the elasmobranchs and flatfishes both went extinct within 30 years, which suggests that the interaction terms may be statistically significant but not biologically realistic.

The model with Type-II interactions fit slightly better than the Type-I model but the reduction in sum of squares was not significant and the AIC was higher (not shown). The same species interaction terms were present in the Type-II model as in the Type-I model. When this model was simulated with no harvest, the flatfishes and elasmobranchs again were eliminated by the negative interactions. We rejected this model because it lacked biological realism and did not significantly improve the fit to the biomass data.

When fitting the Type-III model, the effect of pelagics on gadoids \( (d_{gp}) \) caused the largest reduction in the sum of squared residuals from the single-species fit. The final term added was the effect of elasmobranchs on gadoids \( (c_{ge}) \) which did not substantially reduce the sum of squares until it was included with the other interaction terms. The Type-III predation model fit significantly better than either the single-species or the Type-I model. Based on the \( F \)-tests and the low AIC score we accepted it as the best multispecies model (Table 2). The improvements in the fits over the single-species models are apparent for gadoids and pelagics in the 1970s (Fig. 2). The full equations of the Type-III model are:

\[
G_{t+1} = G_t + r_g G_{t-1} - \frac{r_g}{k_g} G_t^2 - Y_{g,t} - c_{ge} G_{t-1} E_{t-1} + \frac{d_{gp} G_{t-1} P_{t-1}^2}{1 + a_{gp} F_{t-1}^2 + a_{gp} P_{t-1}^2},
\]

\[
F_{t+1} = F_t + r_f F_{t-1} - \frac{r_f}{k_f} F_t^2 - Y_{f,t}.
\]

\[
P_{t+1} = P_t + r_p P_{t-1} - \frac{r_p}{k_p} P_t^2 - Y_{p,t} - \frac{c_{gp} G_{t-1} P_{t-1}^2}{1 + a_{gp} F_{t-1}^2 + a_{gp} P_{t-1}^2} - \frac{c_{ep} F_{t-1} P_{t-1}^2}{1 + a_{ef} F_{t-1}^2 + a_{ep} P_{t-1}^2},
\]

and

\[
E_{t+1} = E_t + r_e E_{t-1} - \frac{r_e}{k_e} E_t^2 - Y_{e,t} - c_{eg} E_{t-1} G_{t-1} + \frac{d_{gp} E_{t-1} P_{t-1}^2}{1 + a_{ef} F_{t-1}^2 + a_{ep} P_{t-1}^2}.
\]

A different set of interaction terms was included in this model than for the Type-I and Type-II models (Fig. 3). The gadoids and elasmobranchs operate as Type-III predators of pelagics, which is consistent with food-habits data. The gadoids and elasmobranchs have reciprocal negative interactions which can be interpreted as competition. Gadoids are not known to
feed on elasmobranchs, but elasmobranchs do prey on gadoids (Tsou and Collie 1998). The negative effect of elasmobranchs on gadoids could be interpreted as predation; we chose to retain the Type-I interaction so as not to estimate additional parameters. The interactions with flatfishes were not important in this model fit, so the flatfish model is essentially the same as the single-species fit (Fig. 2). However, flatfish biomass still influences the other taxa through the denominators of the predator functional responses. If flatfish biomass increases, the feeding rates on pelagics decline, which benefits the pelagics and negatively effects the gadoids and elasmobranchs.

The interaction terms have units of biomass per year and can therefore be directly compared with the annual yields (Fig. 4). High catches of gadoids account for the sharp decline in biomass in the late 1960s (Fig. 4a). After 1975 the interaction terms were about the same order of magnitude as the yield. From 1975 to 1985 the negative effect of elasmobranchs exceeded the positive effect of pelagics, which helps explain the decline in gadoid biomass during that period. The negative effect of gadoids on pelagics has exceeded the commercial yield since 1975 (Fig. 4b). Consumption by elasmobranchs increased over time, equaling the commercial harvest by the 1990s. With the combination of low harvest rates and low gadoid abundance in the 1980s, the pelagics appear to have escaped
Figure 4. Interaction terms for three species groups as estimated with the Type-III model.
predator control. The interaction terms for elasmobranchs generally exceeded the magnitude of the yield (Fig. 4c). The increase in elasmobranch biomass is partly explained by low harvesting in the 1970s. The increase in pelagic prey coupled with the decrease in gadoid competition explains the peak biomass in the late 1980s. Increased harvesting has probably caused the downturn in biomass in the 1990s.

Equilibrium yield surfaces illustrate the trade-offs among the harvest of gadoids, pelagics, and elasmobranchs. For a given species group (e.g., gadoids) equilibrium yield was calculated for pairwise combinations of harvest rates, with the harvest rates of the remaining two groups fixed at \( \frac{1}{2} h_{\text{msy}} \). Thus, in Fig. 5a, the flatfish and elasmobranch harvest rates were fixed at \( \frac{1}{2} h_{\text{msy}} \) and in Fig. 5b the flatfish and pelagic harvest rates were fixed at \( \frac{1}{2} h_{\text{msy}} \). Gadoid yield and the harvest rate for multispecies MSY (\( h_{\text{mmy}} \)) decrease as the pelagic harvest rate is increased because the gadoids prey on pelagics (Fig. 5a). Conversely, gadoid yields and \( h_{\text{mmy}} \) increase with increasing elasmobranch harvest rate because gadoids compete with elasmobranchs (Fig. 5b). The vertical contour lines correspond to regions in which the elasmobranchs have been eliminated.

The multispecies model predicts that pelagic yields would be maximized at higher harvest rates than the single-species \( h_{\text{msy}} \) (Fig. 6). Under the multispecies model the pelagics have a high rate of increase (\( r = 0.78 \)) but much of this productivity is consumed by predators. The fishery competes with the predators and must harvest at a high rate to maximize the pelagic yield. The harvest rate to maximize pelagic yield (~0.4) is quite insensitive to the gadoid and elasmobranch harvest rate. Pelagic yield is maximized at high gadoid harvest rates because gadoids prey on pelagics (Fig. 6a). Conversely pelagic yield is maximized with no harvesting of elasmobranchs (Fig. 6b). Although elasmobranchs prey on pelagics, they exert a large negative effect on gadoids, which also prey on pelagics.

Elasmobranch yield and \( h_{\text{mmy}} \) is maximized at high gadoid harvest rates because the two taxa compete. Thus Fig. 7a is the complement of Fig. 5b. Elasmobranch yields could be maximized by eliminating the gadoids, as indicated by the vertical contours in this plot. With lower levels of gadoid harvesting (e.g., \( \frac{1}{2} h_{\text{msy}} \)) elasmobranch harvest is maximized at harvest rates below its single-species \( h_{\text{msy}} \) (Fig. 7b). Elasmobranch yield and its \( h_{\text{mmy}} \) level decrease with increasing pelagic harvest rate because elasmobranchs prey on pelagics.

Harvest rates for maximum sustainable yield (MSY) differ considerably between the single-species (\( h_{\text{msy}} \)) and multispecies models (\( h_{\text{mmy}} \)). Multispecies MSY would be obtained by depleting the elasmobranchs to remove their consumption of pelagics and competition with gadoids. Flatfishes would be lightly harvested because their biomass indirectly benefits the pelagics. Yield of the pelagics and gadoids would thus be maximized. Interestingly, total yield under the multispecies model with all species harvested at the \( h_{\text{mmy}} \) levels (290 kt) exceeds the total yield of the single-species models with all species harvested at \( h_{\text{msy}} \) (213 kt). In the
Figure 5. Gadoid equilibrium yield (kt) obtained for pairs of harvest rates (solid contours). Broken lines indicate \( h_{\text{msy}} \) from single-species model. The combination of harvest rates used in the forward simulation (Fig. 8) is denoted with an X.
Figure 6. Pelagic equilibrium yield (kt) obtained for pairs of harvest rates (solid contours). Broken lines indicate $h_{my}$ from single-species model. The combination of harvest rates used in the forward simulation (Fig. 8) is denoted with an X.
Figure 7. Elasmobranch equilibrium yield (kt) obtained for pairs of harvest rates (solid contours). Broken lines indicate \( h_{\text{msy}} \) from single-species model. The combination of harvest rates used in the forward simulation (Fig. 8) is denoted with an X.
Figure 8. Result of 20-year simulations with single-species and multispecies models. The gadoid, flatfish, and elasmobranch harvest rates were set to $\frac{1}{2}h_{my}$ and the pelagic harvest rate was $h_{my}$. 
multispecies case, unproductive biomass (elasmobranchs) would be eliminated and the “surplus” production harvested as pelagics and gadoids.

We also solved for the harvest rates that would maximize the revenue from the multispecies fishery. From 1989 to 1993 the average prices in dollars per kilogram were 1.64 for gadoids, 2.54 for flatfishes, 0.23 for pelagics, and 0.21 for elasmobranchs (NEFSC 1995a). To maximize total revenues, elasmobranchs would be eliminated due to their low value and negative interactions with gadoids and pelagics. Pelagics would not be harvested at all because their production is more valuable when converted to gadoids. Revenues would thus be maximized by enhancing the sustainable yield of valuable gadoids and flatfishes.

Deterministic simulations were run with constant harvest rates to illustrate the differences between single-species and multispecies projections. In this example we simulated the rebuilding of the groundfish by setting the gadoid and flatfish harvest rates to $\frac{1}{2} h_{msy}$. The elasmobranch harvest rate was also set at $\frac{1}{2} h_{msy}$ based on the yield contours in Fig. 7b and concerns that harvesting has caused the recent downturn in biomass. The pelagic harvest rate was set at $h_{msy}$ to take advantage of high abundance levels.

With the single-species models, the gadoids and flatfishes are projected to recover in response to low harvest rates while the pelagics and elasmobranchs equilibrate slightly below their peak biomass levels (Fig. 8). The flatfish single-species and multispecies projections are virtually identical because there are no interaction terms in the flatfish equation. The multispecies model predicts that the other three taxa would oscillate toward different equilibria. Gadoid biomass increases rapidly to a peak in 2001 after which the pelagics become depleted. Elasmobranchs also decline until 2005 due to the increase in gadoids and decrease in pelagics. After 2005 flatfish biomass has increased, and because the flatfish group occurs in the denominator of the predation term, this decreases the predation rate on pelagics. This interaction reverses the decline in pelagic and elasmobranch biomass, allowing the system to converge toward the multispecies equilibrium.

**Discussion**

Our results provide evidence of trophic interactions between groups of fish species on Georges Bank. Unlike simpler correlative studies (e.g., Fogarty and Brodziak 1994), the multispecies biomass-dynamics model accounts for changes in biomass due to commercial catch. The estimated trophic interactions are the same order of magnitude as the catch and therefore large enough to influence the population dynamics. Before these results can be used in a management context, the assumptions underlying the multispecies model need to be critically examined.

One important assumption was the proration of the biomasses of migrant species, which was done to scale their abundances to those of the
species considered to reside on Georges Bank. However, these migrants are also subjected to processes that occur off Georges Bank. For herring, mackerel, and dogfish we must assume that the trophic interactions occurring off Georges Bank are either contained in the single-species terms of the model \((r, k)\) or that they have the same temporal trend as the interaction terms that are included in the model \((c, d)\). In extensions of this work it will be desirable to model the seasonal migration of these species and to include fish stocks residing in southern New England and the Gulf of Maine.

By aggregating the species taxonomically, we pooled some species with different feeding habits. Haddock, for example, feed primarily on benthic invertebrates and would not be expected to prey on herring or mackerel (Grosslein et al. 1980). One reason for aggregating by taxonomic group was that we expected related species to have more similar rates of increase \((r)\) and compensatory capacity \((k)\). Haddock’s feeding habits are similar to the flounders’ (Grosslein et al. 1980) but the flounders can sustain higher exploitation rates (NEFSC 1997). Pooling the species by aggregate groups was necessary to minimize the number of interaction terms to estimate. Even so, there is a risk of overparameterizing the biomass-dynamics model. The multispecies model appears to fit better than the single-species model (Table 2) but some of the parameters were estimated with low precision. These interaction terms were retained in the model based on known feeding habits and to maintain symmetry in the food web.

Type-III predator functional responses appeared necessary to obtain biologically realistic predator-prey dynamics. With Type-I and Type-II functional responses the flatfishes and elasmobranchs would go extinct even without harvesting. This process has been termed “self simplification” and is common when multispecies models are simulated under exploitation regimes differing from those when the data were collected (Walters et al. 1998). Type-III functional responses are considered appropriate for vertebrate predators (Murdoch and Oaten 1975) but they require estimation of more parameters \((a\) coefficients) than the Type-I response and the squared prey variables make it difficult to solve analytically for equilibrium levels or to conduct a stability analysis. Simulation is the most tractable way of examining the dynamic behavior of these equations. Under all the combinations of harvest rates we considered, the system of equations converged to a multispecies equilibrium. However, with four interacting species and a 2-year time delay, more complex dynamic behavior might be expected (e.g., Basson and Fogarty 1997).

The trophic interactions identified in our multispecies model are consistent with the NMFS food habits data and with previous multispecies analyses of the shelf fish community of the northeastern United States. The magnitudes of the interaction terms are consistent with Sissenwine and Cohen’s (1991) finding that the fish community consumes most of its own production. Herring and mackerel are known to be important prey of cod, silver hake, dogfish, and winter skate (Overholtz et al. 1991; Tsou
and Collie, In press). MSVPA estimates of the biomass of prey consumed by predator groups (Tsou and Collie, In press) may be analogous to the species interaction terms estimated in this study. MSVPA estimates of yellowtail founder consumption by gadoids and elasmobranchs were quite small (<0.2 kt per year) and may help to explain the lack of significant interaction terms for flatfishes in the Type-III biomass-dynamics model. Furthermore, the negative effect of elasmobranchs on pelagics as estimated by the biomass-dynamics model was quite similar (3-10 kt per year) to MSVPA estimates of elasmobranch consumption. Conversely, the biomass-dynamics model estimates of the negative effects of gadoids on pelagics were considerable larger than the MSVPA predation estimates. This difference may be because interaction terms in the biomass-dynamics model are estimates of the negative effect of predators on the recruited biomass of the prey, rather than direct consumption estimates.

It has been hypothesized that predation may have hastened the collapse of the gadoid stocks or that they may be stuck in a “predator pit” from which escape is possible only with very low exploitation rates (Spencer and Collie 1995). The negative effect of elasmobranchs on gadoids could be interpreted as predation, but MSVPA estimates of gadoid consumption by elasmobranchs were much smaller (1-7 kt per year) than the negative effect estimated with the biomass-dynamics model. Conversely, gadoids are not known to prey on elasmobranchs. We chose to interpret the reciprocal negative interaction between gadoids and elasmobranchs as competition, which is consistent with the diet overlap between these two groups (Grosslein et al. 1980). It is difficult to explain the steady increase in elasmobranch biomass without some concurrent change in their ecosystem. Cod and silver hake are known to be cannibalistic but the consumption of gadoids by gadoids in the MSVPA was low relative to the gadoid biomass (Tsou and Collie, In press). In the biomass-dynamics model, predation among the gadoids should be accounted for by the intraspecific terms ($r$ and $k$).

Biomass-dynamics models are not commonly used as primary stock-assessment methods (National Research Council 1998) but they are useful for elucidating medium and longer-term management strategies and for conducting bioeconomic analyses (Edwards and Murawski 1993). If we accept that trophic interactions occur among species groups, how should these multispecies interactions influence management advice? In our simulation (Fig. 8) the multispecies yield was less than the single-species yields at the same combination of harvest rates because some of the "surplus production" is consumed by predators. However, the management considerations extend beyond simply reducing our expectations of yield from the fish community. There are explicit trade-offs between harvesting the species groups which have different productivities and different economic values and are caught by different segments of the fishing fleet. Total multispecies yield could exceed the sum of the single-species yields if the less productive taxa were depleted (cf. Brander and Mohn 1991). Revenue
might be maximized by harvesting only the most valuable species (Clark 1985). We do not advocate a particular harvest strategy but have examined the trade-offs in yield to illustrate that the present pelagic-dominated fish community is less commercially valuable than the groundfish-dominated community of the 1960s and 1970s.

Despite evidence that trophic interactions are strong enough to influence fish population dynamics, our parameter estimates are highly uncertain. The best test of a model is its ability to predict “out of sample data” that were not used to estimate the model parameters. Such a test will be possible when biomass and landings data from after 1993 become available for all 10 species included here. Recent assessments of some of these species suggest that the community has started to shift back toward groundfish. The biomasses of cod, haddock, and yellowtail flounder have increased somewhat (NEFSC 1997), herring and mackerel biomasses have peaked since 1993, and elasmobranch biomass has declined. This response is consistent with the multispecies model.

Until a more definitive test is possible, the single-species and multispecies models should be considered as alternatives in an adaptive management design (Sainsbury 1991). Harvest strategies (combinations of harvest rates) should be sought that are expected to perform well regardless of which model is correct. An informative harvest policy will lead to different trajectories for the single- and multispecies models, allowing the alternatives to be distinguished more quickly. The harvest rates in Fig. 8 illustrate a policy which would allow the groundfish to recover while providing informative variation between the single- and multispecies population projections.

Acknowledgments

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