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SYMPOSIUM ON BIOLOGICAL INTERACTIONS IN THE NORTH PACIFIC REGION AND ON FACTORS AFFECTING RECRUITMENT, DISTRIBUTION, AND ABUNDANCE OF NON-ANADROMOUS SPECIES
(held by the Standing Committee on Biology and Research at Tokyo, Japan, October 29 to 31, 1985)

VANCOUVER, CANADA, 1986
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PREFACE

This Bulletin is a compilation of papers presented at an International Groundfish Symposium held in Tokyo, Japan, October 29 to 31, 1985, under the auspices of the International North Pacific Fisheries Commission.

The symposium was the third such held by the Commission and topics under which papers were presented were:

(1) Biological interactions of fisheries resources in the North Pacific region; and

(2) Environmental and biological factors affecting recruitment, distribution, and abundance of non-anadromous species.

The full program is shown in the Table of Contents. The symposium was held under the general chairmanship of Dr. Ikuo Ikeda of Japan and was originally organized by a symposium committee with the following membership:

Ikuo Ikeda (Chairman) Fisheries Agency of Japan, Shimizu, Japan
R.J. Beamish Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada
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Attendance at the symposium was by invitation and approximately 75 people participated. Twenty (20) scientific papers and/or presentations were received from scientists of the three member nations of the Commission and Taiwan. Dr. Syoiti Tanaka, Ocean Research Institute of the University of Tokyo, reviewed and summarized the symposium.

Designated panel members initiated or guided discussions which took place on the two topics. No record was kept of the discussion, but authors benefited from the comments and questions by subsequently having an opportunity to revise their papers prior to final submission for publication. The organizing committee acted as an informal editorial board to review and coordinate the submissions.
In order to expedite publication of the papers presented at the symposium, the organizing committee and the Standing Committee on Biology and Research agreed that they would not undergo the usual rigorous and time-consuming peer review process traditional for Commission publications. In effect, this Bulletin then is a partial proceedings and has been approved for publication by the Commission.

Approval for publication by the Commission does not necessarily constitute endorsement of the views of the authors. Bulletins of the Commission are published separately in English and Japanese; accuracy of translation is the responsibility of the Secretariat. The original languages of papers in this Bulletin were English and Japanese.

C.R. Forrester, Executive Director, INPFC

and

Ikuo Ikeda, Chairman, Symposium Organizing Committee
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Topic</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREFACE</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF CONTRIBUTORS</td>
<td>vii</td>
</tr>
<tr>
<td><strong>TOPIC 1--BIOLOGICAL INTERACTIONS OF FISHERIES RESOURCES IN</strong></td>
<td></td>
</tr>
<tr>
<td><strong>THE NORTH PACIFIC OCEAN REGION.</strong></td>
<td>1</td>
</tr>
<tr>
<td>Wakabayashi, Kiyoshi. Interspecific feeding relationships</td>
<td>3</td>
</tr>
<tr>
<td>on the continental shelf of the eastern Bering Sea, with</td>
<td></td>
</tr>
<tr>
<td>special reference to yellowfin sole.</td>
<td></td>
</tr>
<tr>
<td>Kihara, Kohei and Allen M. Shimada. Fine structure of</td>
<td>31</td>
</tr>
<tr>
<td>demersal fish community and marine environment in the</td>
<td></td>
</tr>
<tr>
<td>eastern Bering Sea.</td>
<td></td>
</tr>
<tr>
<td>Livingston, P.A.; D.A. Dwyer; D.L. Wencker; M.S. Yang; and</td>
<td>49</td>
</tr>
<tr>
<td>G.M. Lang. Trophic interactions of key fish species in the</td>
<td></td>
</tr>
<tr>
<td>eastern Bering Sea.</td>
<td></td>
</tr>
<tr>
<td>Ware, D.M. and G.A. McFarlane. Relative impact of Pacific</td>
<td>67</td>
</tr>
<tr>
<td>hake, sablefish and Pacific cod on west coast of Vancouver</td>
<td></td>
</tr>
<tr>
<td>Island herring stocks.</td>
<td></td>
</tr>
<tr>
<td>Smith, Ronald L. and A.J. Paul. A theoretical energy budget</td>
<td>79</td>
</tr>
<tr>
<td>for juvenile walleye pollock in Alaskan waters.</td>
<td></td>
</tr>
<tr>
<td>Walters, Carl; M. Stocker; A.V. Tyler; and S.J. Westrheim.</td>
<td>87</td>
</tr>
<tr>
<td>Interactions between Pacific cod (<em>Gadus macrocephalus</em>) and</td>
<td></td>
</tr>
<tr>
<td>herring (<em>Clupea harengus pallasi</em>) in the Hecate Strat, British</td>
<td></td>
</tr>
<tr>
<td>Columbia.</td>
<td></td>
</tr>
<tr>
<td>Yeh, Shean-Ya and Loh-Lee Low. A Leslie matrix-differential</td>
<td>101</td>
</tr>
<tr>
<td>equation model for yield analysis of groundfish resources.</td>
<td></td>
</tr>
<tr>
<td>Kawai, Tomoyasu and Kimiko Isibasi. On the mechanism of</td>
<td>111</td>
</tr>
<tr>
<td>drastic changes in species composition of Japanese meritic</td>
<td></td>
</tr>
<tr>
<td>pelagic fish resources.</td>
<td></td>
</tr>
<tr>
<td>Sudo, Hiroyuki and Masanori Azeta. Species interrelationships</td>
<td>129</td>
</tr>
<tr>
<td>on food and habitat utilization in fishes of Shijiki Bay.</td>
<td></td>
</tr>
<tr>
<td>Kitano, Yutaka; Kozo Kitani; and Fumihiko Kato. Estimating</td>
<td>143</td>
</tr>
<tr>
<td>productivity of the pelagic ecosystem in the Japan Sea.</td>
<td></td>
</tr>
</tbody>
</table>
TOPIC 2—ENVIRONMENTAL AND BIOLOGICAL FACTORS AFFECTING RECRUITMENT, DISTRIBUTION, AND ABUNDANCE OF NON-ANADROMOUS SPECIES..... 153

Bailey, K.; R. Francis; and J. Schumacher. Recent information on the causes of variability in recruitment of Alaska pollock in the eastern Bering Sea: Physical conditions and biological interactions................................. 155

Deriso, R.B.; S.H. Hoag; and D.A. McCaughran. Two hypotheses about factors controlling production of Pacific halibut... 167

Tyler, A.V. and S.J. Westheim. Effects of transport, temperature, and stock size on recruitment of Pacific cod (Gadus macrocephalus)................................................................. 175

McFarlane, G.A. and R.J. Beamish. Production of strong year-classes of sablefish (Anoplopoma fimbria) off the west coast of Canada........................................................... 191

Royer, Thomas C. Temperature fluctuations in the northeast Pacific from 1954 to 1985 in response to El Nino/southern oscillations and longer period forcing......................... 203

Blackburn, James E. Predation by cod and pollock upon shrimp in the central and western Gulf of Alaska with speculation on predatory effects on other fishery resources........ 209

Kubodera, Tsunemi. Relationships between abundance of epipelagic squids and oceanographical-biological environments in the surface waters of the Subarctic Pacific in summer....................................................... 215

Kosaka, Sunao. Relation of the migration of Pacific sauries to oceanic fronts in the northwest Pacific Ocean............... 229

Shimazaki, Kenji. Distribution of the pelagic fish community around the Subarctic boundary in the North Pacific Ocean.. 247

Hara, Ichiro and Taisuke Watanabe. Distribution and survival of Japanese sardine and their relation to the Kuroshio................................................................. 265

SYMPOSIUM REVIEW — Syoiti Tanaka........................................................... 277
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TOPIC NO. 1

BIOLOGICAL INTERACTIONS OF FISHERIES RESOURCES
IN THE NORTH PACIFIC REGION

SESSION CO-CHAIRMEN

K. Bailey
K. Wakabayashi
INTERSPECIFIC FEEDING RELATIONSHIPS ON THE CONTINENTAL SHELF OF THE
EASTERN BERENG SEA, WITH SPECIAL REFERENCE TO YELLOWFIN SOLE

by
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ABSTRACT

In order to study interspecific feeding relationships of yellowfin sole on the continental shelf of the eastern Bering Sea, stomach content weights for flounders and walleye pollock were compiled based on samples collected at trawl survey stations in July 1970 and in June 1971. In addition, stomach contents of Pacific cod and sculpins collected at trawl stations from May to July in 1975 and in 1976, which were described in unpublished reports, were used. Published reports on food habit of fishes, crabs, asteroids, mammals, and birds relating to yellowfin sole are also cited.

The principal prey items of yellowfin sole were bivalves, polychaetes, echiurids, and benthic amphipods. These prey items were also consumed by Alaska plaice, rock sole, eelpouts, king and tanner crabs, starfishes, etc. It was estimated from daily rate of food consumption, stomach contents, and predator biomass in the major area of distribution of yellowfin sole that the consumption of those common prey by each predator was relatively low compared to that by yellowfin sole. The consumption of yellowfin sole and each predator may be slight. The aggregate amount consumed by those competitive predators could be equivalent or exceed that for yellowfin sole. It is still uncertain whether yellowfin sole competes heavily with the complex of those predators.

Though there were no data on larvae and fry consumed, yellowfin sole were preyed upon mainly by walleye pollock, Pacific cod, and plain sculpin. Other predators were Pacific halibut, warby sculpin, mammals, and birds. Based on rate of food elimination or daily rate of food consumption and percentage in stomach contents of predators, the consumption of yellowfin sole by these species, except for birds for the six-month period when yellowfin sole are distributed on the inner shelf, was roughly estimated to be 2 to 3% of the apparent biomass. That estimate is more than the recent annual average commercial catch of 93,000 t.

INTRODUCTION

The yellowfin sole, Limanda aspera (Pallas), is a small-sized flounder distributed widely in northern waters of the North Pacific. In the eastern Bering Sea, the species inhabits 100 to 250 m depths in dense concentrations in winter and areas on the continental shelf shallower than 100 m in much less density in summer. Feeding occurs mainly in May to November and is much less active in winter.

According to Japan-U.S. cooperative trawl surveys, the yellowfin sole is the second most abundant species following walleye pollock which has both a pelagic and demersal nature. The yellowfin sole biomass has been estimated to be at a high level of about 2 million t or more since 1979. Therefore, it is considered that abundant yellowfin sole could have a very important role in the ecosystem of the eastern Bering Sea shelf and greatly affect biomasses and distributions of its prey benthos, competitors, and possibly predators.

The purpose of this report is to analyze feeding habits, competitors, and the predators of yellowfin sole on the continental shelf of the eastern Bering Sea. The following data were used: (1) stomach contents of flounders and walleye pollock sampled from the same catch at trawl stations in 1970 and 1971, (2) stomach contents of Pacific cod and sculpins collected in 1975 and 1976 (previously described in unpublished reports), and (3) published feeding data. The degree of competition and predation on yellowfin sole are examined based on stomach content data and biomass estimates.

Detailed numerical data on population numbers and stomach contents by length class used in the analyses could not be shown in this report, but are available upon request.

MATERIALS

Fish samples were collected at trawl stations on the continental shelf of the eastern Bering Sea during surveys conducted by the Far Seas Fisheries Research Laboratory (FSFRL). Flounders and walleye pollock were sampled in July 1970 and June 1971 and Pacific cod and sculpins were collected during May to July in 1975 and 1976. Figure 1 shows distributions of trawl stations and catch rates of yellowfin sole. Outlines of the surveys and station data on haul and catch by species have been

In order to have wide coverage of the survey area, sampling was conducted at about every other station. At each sampling station, 30 fish per species were collected for all flounders and about 20 to 30 kg for each species of codfishes and the sculpin complex. Samples were frozen to be brought back to the laboratory.

After thawing, fork length in mm (equal to total length in small-sized flounders) and body weight in g were recorded. Stomachs were removed at pharynx and pylorus portions following determination of sex. Flounder stomachs were assessed with 10:1 freshwater-formaldehyde mixture. Each prey item in the stomach was weighed to 0.1 g for each stomach. When contents were digested and taxa not determined, they were classified as digested matter. The other fishes category included unidentified fish and fish other than those known by taxon. The same applied to other crustaceans, etc. Empty stomachs described those with less than 0.05 g of solids or only water or mucus.

The numbers of stomachs sampled by species and by year are shown in Table 1. Examinations were made by the author and other staff of the North Pacific Groundfish Resources Section of FSFRL for species other than Pacific cod and sculpins which were examined under the direction of the author by Sekiya (1978) and Hosoki (1978).

BIOMASSES AND POPULATION NUMBERS OF MAJOR SPECIES OF FISH AND INVERTEBRATES AND THEIR FOOD HABITS

Biomass and population number

Many species of fish and invertebrates inhabit the inner continental shelf in summer. Table 2 shows the estimated biomass and population number by species or species group in the major area of distribution of yellowfin sole (the area encompassed by solid lines in the upper left panel of Fig. 1), determined from the 1979 Japan-U.S. cooperative trawl survey. As the estimates were obtained using an area-swept method with the assumption that the trawl gear catches all individuals in an area swept, they may be underestimated.

Degrees of underestimation are considered to be relatively large for those fishes which tend to be distributed off bottom and for small-sized or slender-shaped fishes, but the values may provide a quantitative yardstick of species encountered. In addition to the above species, epifauna such as gastropods and ophiuroids and infauna such as bivalves and polychaetes inhabit the area constituting the benthic community. Zooplankton bears relation to the benthic community as detritus or prey and marine mammals and seabirds bear relation as predators.

Stomach content composition

Flounders--The stomach content compositions in weight for flounders by year are shown in Fig. 2 and Appendix Table 1. Though compositions varied by year, they clearly showed differences among species. Among small-sized flounders with a small mouth, the yellowfin sole, Alaska plaice, rock sole, and longhead dab mostly preyed upon benthos. Yellowfin sole were highly omnivorous. Major prey items of this species were bivalves, polychaetes, ophiuroids, and amphipods. The principal four prey items in the report. Yellowfin sole preyed also upon fishes and zooplankton. The other three small-mouthed flounders preyed mostly upon polychaetes. Unlike the above four species, the major prey of starry flounder was sand lance followed by bivalves. The flathead sole, a small-sized flounder with a relatively large mouth, preyed chiefly upon fishes, shrimps (Macrura) and ophiuroids in 1970 and codfishes in 1971. The large flounders, Greenland turbot, arrowtooth flounder, and Pacific halibut, and Pacific halibut upon fishes consisting mainly of codfishes which was quite unlike the habits of small-sized flounders except for flathead sole.

The stomach content composition by 5 cm length class for yellowfin sole, Alaska plaice, rock sole, longhead dab, flathead sole, and Pacific halibut, where sample sizes were relatively large, are shown in Fig. 3. Even within the same species, stomach contents often varied substantially by size class. Percentages of polychaetes, amphipods (tending to increase in longhead dab), and ascidians tended to decrease with increase in predator size or tended to be high at a certain size and to decrease as the size became larger. On the other hand, percentages of bivalves, sand lances, and echinoids tended to increase with size. Zooplankton only appeared in stomachs of small individuals.

Codfishes--The major prey of walleye pollock less than 20 cm in fork length was zooplankton such as euphausiids and copepods (Fig. 4 and Appendix Table 2). In stomachs of pollock larger than 20 cm, the percentage of zooplankton dropped and those of pollock pollock and other fishes increased. Based on material collected in 1970, Takahashi and Yamaguchi (1972) showed that percentages of copepods and euphausiids in stomachs decreased and those of walleye pollock and other fishes increased with an increase in predator size.

The major prey item of Pacific cod was fishes and mainly walleye pollock. Other prey items which appeared at a considerable percent level were benthic crustaceans. Unlike walleye pollock, the percentage of zooplankton in stomach contents of Pacific cod was nearly zero.
As with flounders and walleye pollock, stomach contents showed a tendency to change with size of Pacific cod (Fig. 5).

Sculpins—The mouth opening of sculpins is relatively large for their length with the exception of the spectacled sculpin. The bigmouth sculpin, great sculpin, warty sculpin, and plain sculpin are relatively large-sized, the spinyhead sculpin and yellow Irish lord are medium-sized, and other sculpins are small. The stomach contents of sculpins are shown in Fig. 6 and Appendix Table 3.

The major prey items of threaded sculpin, warty sculpin, and plain sculpin, all of which appear in the main waters inhabited by yellowfin sole in June and July, were polychaetes, crabs (mainly tanner crabs), and fishes (mainly smelts), respectively. The warty sculpin and plain sculpin belong to the same genus and their sizes are similar but stomach contents, however, varied substantially between them.

Sculpins other than the above three species inhabit mainly areas deeper than about 100 m. The major prey item of bigmouth sculpin, great sculpin, and spinyhead sculpin was fishes and the great sculpin also frequently preyed upon tanner crabs. Yellow Irish lord and thorny sculpin preyed mainly upon crustaceans such as jacapods and shrimps. Unlike the above, the major prey item of blackfin sculpin and spectacled sculpin was infauna and zooplankton, respectively.

Total weight of stomach contents by prey item for each population

To provide a quantitative yardstick of dietary overlap for prey and predation on yellowfin sole, the products of population number and stomach content weight by prey item per fish are shown in Table 3 as the total weight of stomach contents. Data by length class were used for the calculation of item available. The table covers only those fishes distributed in the area inhabited by yellowfin sole in June and July and whose total percentage of the principal four prey items of yellowfin sole in their stomachs was relatively high or whose stomachs contained flounders. The values for species whose sampling year differed from that of yellowfin sole were obtained using the average weight of their prey items in stomachs.

COMPETITION FOR PREY

Similarity in stomach contents

Stomach contents of yellowfin sole were not very similar to those of other flounders (Fig. 2). This was true even for samples from the same location. The major prey items of codfishes and sculpins were also different from those of yellowfin sole. However, the aggregate percentage of the principal four prey items of yellowfin sole, that is, bivalves, polychaetes, echiuroids, and amphipods in stomachs was 86% for Alaska pollock, 60% for rock sole, and 69% for longhead dab in the 1970 sample and 92%, 77%, and 93%, respectively, in the 1971 sample, similar to 66% in 1970 and 75% in 1971 for yellowfin sole. For threaded sculpin, values were 72% in 1975 and 82% in 1976.

Total weight of the principal four prey items in stomachs of each population

The total weight of the principal four prey items in stomachs of each population was an average of 8,600 t for yellowfin sole, 19% of that level for Alaska pollock, 12% for rock sole, 1% for longhead dab, 5% for walleye pollock, 9% for Pacific cod, and 5% for threaded sculpin (Table 3). Thus, the consumption of the major prey items of yellowfin sole by fishes other than yellowfin sole is thought to be relatively low compared to that by yellowfin sole. However, when all the species were combined, the aggregate stomach contents weight of the principal four prey items accounted for an average of 55% of that for yellowfin sole. The weights of polychaetes and amphipods consumed by fishes other than yellowfin sole in 1970 were 113% and 95%, respectively, of that for yellowfin sole and in 1971 accounted for 65% and 46%. The above suggests that the major prey items of yellowfin sole are also consumed substantially by other fishes.

Food habits of other species

Fishes—Other than the species discussed so far, benthos feeders with relatively large biomass are eelpouts and polychaetes. The former preyed on amphipods and the latter preyed on echinoderms, gastropods, small-sized bivalves, crustaceans such as shrimps, and fishes (Feder and Jewett 1981). Tanner crabs prey mainly upon polychaetes, ophiuroids, crustaceans, mollusks, and cirripods.

Invertebrates—Prey items of red king crab are polychaetes, echinoderms, medium-sized gastropods, small-sized bivalves, crustaceans such as shrimps, and fishes (Feder and Jewett 1981). Tanner crabs prey mainly upon polychaetes, ophiuroids, crustaceans, mollusks, and cirripods.

The major prey items of starfishes are shrimps, clypeasteroids (sand dollars), echinoids (sea urchins), bivalves, and polychaetes (Feder and Jewett 1981); the two latter are very similar to yellowfin sole.

Mammals—Frost and Lowry (1981) reported on stomach contents of cetaceans, Harry and Hartley (1981) on those of northern fur seal, and Lowry and Frost (1981) on those of seals and walrus. Among mammals, gray whale prey mainly upon benthiic amphipods, polychaetes, and shrimps; bearded seal and walrus prey mainly upon bivalves. Their major prey items are similar to those of yellowfin sole. However, their consumption of
major prey items of yellowfin sole is considered to be small since gray whale and bearded seal mainly inhabit northern waters in summer and bearded seal and walrus feed upon prey individuals that are larger than those taken by fishes (Laevastu and Larkins 1981).

**Estimated food consumption**

In order to estimate the degree of predation on the major prey items of yellowfin sole by species, including those lacking data on stomach content weight, the daily food consumption was calculated using daily rate of food consumption per body weight shown in Laevastu and Larkins (1981) and biomass (Table 2). The daily food consumption of the principal four prey items was obtained as the product of daily food consumption and total percentage of the four items in stomach contents (Table 4).

The daily food consumption of the principal four prey items by yellowfin sole was estimated to be 15,500 t. The highest consumption by other species was observed for starfishes, followed by tanner crabs, Alaska pleace, red king crab, rock sole, and eelpouts. Of these, consumption by starfishes, crabs, and eelpouts may be underestimated because their aggregate percentage of principal four prey items was assumed to be 100% though no stomach content compositions were available.

Assuming that the amount of predation on the common prey species reflects the degree of competition, yellowfin sole are considered to compete for prey with other species in the above order of species. Although the amount of predation by each species is not substantial compared to that by yellowfin sole, the consumption by all the other species combined amounts to 17,800 t, i.e. more than the 15,500 t by yellowfin sole.

**PREDATION ON YELLOWFIN SOLE**

**Occurrence of flounders in stomachs**

Fishes--Fish which had flounders in their stomachs were Pacific halibut, Pacific cod, walleye pollock, warty sculpin, plain sculpin, great sculpin, bigmouth sculpin, and spinyhead sculpin (Figs. 2 to 5). Among them, the first five are found on the inner shelf, the habitat of yellowfin sole, and thus possibly prey upon the species.

Total weight of flounders in stomachs (Table 3) showed predation on flounders to be highest by plain sculpin (380 t of stomach contents) followed by walleye pollock (440 t), Pacific cod (340 t), Pacific halibut (33 t), and warty sculpin (5 t).

Seabirds--Predation on flounders was observed in red-faced cormorant, pelagic cormorant (Peder and Jewett 1981), and common murre (Ogi 1982). However, the consumption of yellowfin sole by birds is considered to be small since (1) red-faced cormorant has a habit of feeding close to its nest, (2) pelagic cormorant appear in the southern Bering Sea only in winter (Hunt et al. 1981), and (3) dependence of predation on flounders is very low in common murre.

**Marine mammals--**Predation on flounders by mammals is reported for beluga whale (Frost and Lowry 1981), harbor seal, ribbon seal, bearded seal (Lowry and Frost 1981), and northern fur seal (Harry and Hartley 1981). However, the amount of their predations on flounders is considered to be low since the major prey of mammals are pelagic and semi-demersal fishes and many seals appear in the southern Bering Sea only in winter.

**Estimated amount of predation**

Jones (1974) reported on rate of elimination of food from stomachs of gadoids in the Atlantic Ocean. The rate of elimination per hour, Rh (g/h), at water temperature of 6°C can be expressed as,

\[ Rh = 0.0095 \cdot Sw^{0.46} \cdot Bw^{0.44} \]

where, Sw is stomach contents weight (g) per fish and Bw is average body weight.

The extent of predation on flounders during six months on the continental shelf was estimated as shown in Table 5 using Rh value, population number, and percentage of flounders in Table 2. Flounders in millions, values by length class were used when available and, lacking data on rate of elimination for sculpins and Pacific halibut, the equation for cods was applied for those species. The amount of predation on flounders was also estimated in Table 5 using daily rate of food consumption reported in Laevastu and Larkins (1981) and biomass (Table 2).

The amounts of predation on flounders calculated by these methods were high for walleye pollock, Pacific cod, and plain sculpin as also noted from the total weight of stomach contents in Table 3. The estimated total predation on flounders by all fishes examined was 169,500 t by the Jones’ method and 89,000 t by the Laevastu and Larkins’ method. The biomass of yellowfin sole accounts for 79% of that for all flounders (Table 2). Assuming that the predation is proportional to biomass, the extent of predation on yellowfin sole would become 134,000 and 70,000 t, respectively.

Laevastu and Larkins (1981), using numbers of inhabiting marine mammals and stomach contents, estimated amount of predation on flounders in an ecosystem simulation model. The estimate was 53,400 t per year in the Bering Sea east of 170°W. If this is apportioned in proportion to biomass of each flounder, the predation on yellowfin sole would become 42,000 t. Since yellowfin sole migrate to deeper waters in winter, the value is
thought to be close to that during their six-month period in shallow waters.

Thus, the amount of predation on yellowfin sole by fishes and mammals during the six-month period of June to November on the inner shelf of the eastern Bering Sea was roughly estimated to be 176,000 t or 112,000 t. These values correspond to about 9% or 6% of the yellowfin sole biomass in 1979, estimated to be 1,949,100 t, and both are more than the average commercial catch of 93,000 t during the 1979 to 1982 period.

**DISCUSSION**

Based mainly on stomach contents and biomass, interspecific feeding relationships of yellowfin sole were analyzed. The results are shown in a schematic diagram in Fig. 7. The diagram does not include small yellowfin sole which inhabit very shallow waters and for which no data were obtained.

The competition of yellowfin sole with other species was analyzed based on consumption of the major prey items of yellowfin sole in a broad area. However, high consumption indicates only a possibility of competition when the amount of prey is limited because some segregations in habitat of yellowfin sole and possible competitors were observed in that area. In addition, all common preys were regarded as having the same quality to each predator in the analysis, but selectivity could be different among prey items and also predators. Moreover, each prey category included plural species and a predator could feed selectively on some prey species differently from other predators.

It is estimated that the biomass of yellowfin sole in the eastern Bering Sea was at the lowest level around 1972, shortly after the sampling of flounder stomachs, followed by a rapid increase to a level of or exceeding about 2 million t in recent years (Wakabayashi 1985b). In addition, biomasses of rock sole and Alaska plaice, which are possible competitors for yellowfin sole, are estimated to be increasing in recent years. Examination of biological data on growth, etc. of these flounders may provide useful information on presence or absence of competition.

The degree of predation on yellowfin sole was calculated based on amount of predation estimated from rate of food elimination or daily rate of food consumption, biomass, and percentage of flounders in stomach contents. It is very difficult to estimate those rates. In addition, they are considered to vary substantially by site, day, and month. It is possible that the percentage of flounders in stomachs has changed in accordance with the considerable increase in biomass of flounders in recent years. Further, stomach contents of Pacific cod were obtained mainly from fish taken on the outer shelf, whereas flounders were distributed than on the inner shelf and the biomass of eelpouts may be underestimated. Therefore, the calculated amount of predation should be considered as a very rough estimate.

The interspecific relationships presented here apply to the period when yellowfin sole inhabit waters shallower than about 100 m. Different relationships may exist during wintering and migration in spring and autumn. The degree of predation by Pacific halibut which migrates past yellowfin sole may increase as Novikov (1960) pointed out. Observations throughout the year are important to completely understand the influence of other species upon the biomass of yellowfin sole.

**ACKNOWLEDGEMENTS**

The author wishes to express his sincere gratitude to the following staff of the Far Seas Fisheries Research Laboratory for their help during the course of this study: Dr. Takashi Sasaki, Mr. Yoshiya Takahashi (Present: Nansen Regional Fisheries Research Laboratory), Mr. Hirotsume Yamaguchi (Tohoku Regional Fisheries Research Laboratory), and Dr. Shiro Chikuni (FAO) participated in the troublesome work of examining stomach contents: Mr. H. Yamaguchi also processed pollock data; Dr. Keiichi Mito gave invaluable suggestions on rate of food elimination; Drs. Ikuo Ikeda, Keiuke Okada (Japan Marine Fishery Resource Research Center), T. Sasaki, Kazuyuki Teshima, and K. Mito reviewed the manuscript.

**REFERENCES**


Table 1. Stomach samples collected during the PFSRL\(^a\) trawl surveys on the continental shelf of the eastern Bering Sea.

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<td>Number of</td>
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<td>stomachs</td>
<td>interval (m)</td>
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\(^a\)Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan.
\(^b\)Survey period of July 2 to August 2.
\(^c\)Survey period of May 30 to June 30.
\(^d\)Sampling period of May 4 to June 6 for threaded sculpin, warty sculpin, and plain sculpin. Sampling period of May 4 to July 3 for other species.
\(^e\)Sampling period of May 13 to June 10 for threaded sculpin, warty sculpin, and plain sculpin. Sampling period of May 13 to July 14 for other species.
Table 2. Biomass and population number estimates of species or species groups on the continental shelf of the eastern Bering Sea, based on Japan-U.S. cooperative trawl survey in 1979.\textsuperscript{a}

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\textsuperscript{a}Estimates from Bakkala et al. (1985) or computer outputs for the area shown in Fig. 1, except population number of crabs, which are from Otto (1981) for the area south of 58°N.

\textsuperscript{b}Larger than 200 mm in fork length.
| Prey item     | Yellowfin sole | Alaska pollock | Rock sole | Flathead sole | Longhead sole | Starry flounder | Pacific halibut | Walleye pollock | Pacific cod | Warty sculpin | Plain sculpin | Threaded sculpin | Subtotal H |
|--------------|----------------|----------------|-----------|---------------|---------------|-----------------|-----------------|----------------|-------------|---------------|---------------|----------------|----------------|------------|
| Smelts       | 61.2           | 106.4          |           | 19.3          | 357.5         | 398.5           | 12.0            | 12.0           | 12.0        | 12.0          | 12.0          | 12.0           | 5,532.2   |
| Codfishes    | 176.6          | 601.8          | 1,300.5   | 5,911.6       | 29.4          | 414.9           | 10,809.1        | 11,695.3       | 3,410.8     | 93.8          | 48.6          | 444.9          | 61,254.5 |
| Sand lances  | 65.8           | 570.5          | 2.4       | 473.1         | 412.0         | 63.9            | 59.5            | 59.5           | 59.5        | 59.5          | 59.5          | 59.5           | 1,580.5   |
| Flounders    | 83.5           | 442.8          | 1,779.3   | 26.0          | 333.3         | 217.4           | 150.0           | 150.0          | 150.0       | 150.0         | 150.0         | 150.0          | 1,695.1   |
| Other fishes | 837.8          | 2,238.3        | 75.4      | 1,479.3       | 417.4         | 313.2           | 313.2           | 313.2          | 313.2       | 313.2         | 313.2         | 313.2          | 10,415.1 |
| Amphipoda    | 1,179.1        | 401.7          | 32.0      | 473.1         | 412.0         | 63.9            | 59.5            | 59.5           | 59.5        | 59.5          | 59.5          | 59.5           | 3,077.0  |
| Mysidacea    | 3.5            | 0.0            | 0.3       | 0.3           | 0.3           | 0.3             | 0.3             | 0.3            | 0.3         | 0.3           | 0.3           | 0.3            | 1.7       |
| Euphausiacea | 344.2          | 7.0            | 17.7      | 1.7           | 3.0           | 150.0           | 150.0           | 150.0          | 150.0       | 150.0         | 150.0         | 150.0          | 150.0     |
| Macrura      | 232.3          | 30.4           | 32.0      | 473.1         | 412.0         | 63.9            | 59.5            | 59.5           | 59.5        | 59.5          | 59.5          | 59.5           | 3,077.0  |
| Brachyura    | 222.7          | 0.8            | 1.5       | 313.2         | 313.2         | 313.2           | 313.2           | 313.2          | 313.2       | 313.2         | 313.2         | 313.2          | 3,077.0  |
| Hermit crabs | 395.4          | 5.8            | 8.2       | 17.6          | 19.8          | 17.6            | 17.6            | 17.6           | 17.6        | 17.6          | 17.6          | 17.6           | 176.0     |
| Other crustacea | 10.6         | 0.1            | 0.2       | 17.6          | 19.8          | 17.6            | 17.6            | 17.6           | 17.6        | 17.6          | 17.6          | 17.6           | 176.0     |
| Polychaeta   | 2,637.4        | 732.9          | 100.4     | 4.2           | 8.6           | 257.2           | 257.2           | 257.2          | 257.2       | 257.2         | 257.2         | 257.2          | 2,637.4  |
| Cephalopoda  | 0.12           | 0.0            | 0.5       | 0.5           | 0.5           | 0.5             | 0.5             | 0.5            | 0.5         | 0.5           | 0.5           | 0.5            | 0.5       |
| Bivalvia     | 2,662.5        | 19.2           | 138.3     | 2.8           | 40.3          | 6.7             | 6.7             | 6.7            | 6.7         | 6.7           | 6.7           | 6.7            | 70.4      |
| Gastropoda   | 81.2           | 2.0            | 0.0       | 0.5           | 0.5           | 0.5             | 0.5             | 0.5            | 0.5         | 0.5           | 0.5           | 0.5            | 0.5       |
| Ophiuroidea  | 249.5          | 21.0           | 6.0       | 84.8          | 84.8          | 84.8            | 84.8            | 84.8           | 84.8        | 84.8          | 84.8          | 84.8           | 84.8      |
| Holothurioidea | 44.0           | 1.5            | 5.0       | 21.0          | 21.0          | 21.0            | 21.0            | 21.0           | 21.0        | 21.0          | 21.0          | 21.0           | 21.0     |
| Clypeasteroidea | 238.2         | 3.5            | 16.2      | 0.1           | 1.3           | 1.3             | 1.3             | 1.3            | 1.3         | 1.3           | 1.3           | 1.3            | 1.3      |
| Echiura      | 1,649.3        | 109.2          | 31.5      | 2.4           | 2.8           | 49.1            | 49.1            | 49.1           | 49.1        | 49.1          | 49.1          | 49.1           | 49.1     |
| Ascidiae     | 101.1          | 45.8           | 29.3      | 0.7           | 0.7           | 0.7             | 0.7             | 0.7            | 0.7         | 0.7           | 0.7           | 0.7            | 0.7      |
| Sand, mud    | 568.1          | 42.2           | 0.0       | 0.2           | 39.5          | 1.1             | 1.1             | 1.1            | 1.1         | 1.1           | 1.1           | 1.1            | 1.1      |
| Others       | 1,018.2        | 30.0           | 79.8      | 2.5           | 2.5           | 2.5             | 2.5             | 2.5            | 2.5         | 2.5           | 2.5           | 2.5            | 2.5      |
| Digested matter | 461.2         | 30.6           | 17.7      | 2.6           | 3.0           | 0.1             | 0.1             | 0.1            | 0.1         | 0.1           | 0.1           | 0.1            | 0.1      |
| Total        | 12,433.1       | 1,775.1        | 2,014.6   | 424.8         | 169.8         | 124.4           | 858.3           | 16,012.7       | 1,653.0     | 8,636.2       | 561.4         | 61,254.5       | 61,254.5 |
| Sub-total    | 7,729.1        | 1,521.0        | 1,115.5   | 44.5          | 9.5           | 465.1           | 734.9           | 734.9          | 465.1       | 465.1         | 465.1         | 465.1          | 4,600.1  |

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<td>14.3</td>
<td>1,070.7</td>
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<td>Other crustacea</td>
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<td>0.0</td>
<td>6,101.4</td>
<td>6,104.1</td>
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<td>Polychaeta</td>
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<td>719.6</td>
<td>10.1</td>
<td>139.1</td>
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<td>605.4</td>
<td>2,947.6</td>
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<tr>
<td>Cephalopoda</td>
<td>62.0</td>
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<td>5.2</td>
<td>304.0</td>
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<td>186.2</td>
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<td>70.9</td>
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<td>10.0</td>
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<td>10.4</td>
<td>23.0</td>
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<td>Holothuroidea</td>
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<td>e</td>
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<td>Clypeasteroidea</td>
<td>90.0</td>
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<td>0.6</td>
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<td>Echiurida</td>
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<td>76.7</td>
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<td>Ascidiae</td>
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<td>64.1</td>
<td>26.1</td>
<td>0.2</td>
<td>11.8</td>
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<td>102.2</td>
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<td>Sand, mud</td>
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<td></td>
<td></td>
<td>0.1</td>
<td>0.1</td>
<td>1.1</td>
<td>2.7</td>
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<td>Others</td>
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<td>6.8</td>
<td>12.4</td>
<td>1.0</td>
<td>0.9</td>
<td>1.6</td>
<td>240.3</td>
<td>271.0</td>
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<td>Digested matter</td>
<td>82.2</td>
<td>13.3</td>
<td>0.7</td>
<td>1.7</td>
<td></td>
<td>4.9</td>
<td>83.2</td>
<td>103.8</td>
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<tr>
<td><strong>Total</strong></td>
<td>12,648.3</td>
<td>1,880.9</td>
<td>1,239.0</td>
<td>454.0</td>
<td>165.0</td>
<td>798.7</td>
<td>58,032.9</td>
<td>62,570.5</td>
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<td>9,479.3</td>
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<td>34.9</td>
<td>145.4</td>
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<td>1,809.7</td>
<td>4,705.1</td>
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...continued
Table 3. Continued.

a (Stomach contents weight per individual) x (population number), calculated by size class. Average weight of 1975 and 1976 shown in Appendix Table 1 or 2 is used for Pacific cod and sculpins.

b For species other than yellowfin sole.

c For the principal four prey items of yellowfin sole, that is, Amphipoda, Polychaeta, Bivalvia, and Echiurida.

d Walleye pollock, Pacific cod, and sculpins combined.

e Included in Others, if any.
Table 4. Estimates of daily food consumption of the principal four prey items of yellowfin sole by species in the eastern Bering Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Daily food requirements (%)</th>
<th>Biomass (t)</th>
<th>Daily food consumption (t)</th>
<th>Principal four preys Consumption (%)</th>
<th>Principal four preys Consumption (t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>1.16</td>
<td>1,949,100</td>
<td>22,600</td>
<td>68.7</td>
<td>15,500</td>
</tr>
<tr>
<td>Alaska plaice</td>
<td>1.16</td>
<td>237,300</td>
<td>2,800</td>
<td>89.8</td>
<td>2,500</td>
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<tr>
<td>Rock sole</td>
<td>1.16</td>
<td>174,000</td>
<td>2,000</td>
<td>67.2</td>
<td>1,300</td>
</tr>
<tr>
<td>Longhead dab</td>
<td>1.18</td>
<td>33,600</td>
<td>400</td>
<td>77.3</td>
<td>310</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>1.50</td>
<td>1,871,900</td>
<td>28,100</td>
<td>1.5</td>
<td>420</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>1.42</td>
<td>611,800</td>
<td>8,700</td>
<td>4.4</td>
<td>380</td>
</tr>
<tr>
<td>Threaded sculpin</td>
<td>1.44</td>
<td>14,000</td>
<td>200</td>
<td>79.2</td>
<td>160</td>
</tr>
<tr>
<td>Eelpouts</td>
<td>1.44</td>
<td>84,800</td>
<td>1,200</td>
<td>100f</td>
<td>1,200</td>
</tr>
<tr>
<td>Poachers</td>
<td>1.44</td>
<td>27,400</td>
<td>400</td>
<td>100f</td>
<td>400</td>
</tr>
<tr>
<td>Tanner crab</td>
<td>0.97</td>
<td>363,000</td>
<td>3,500</td>
<td>100f</td>
<td>3,500</td>
</tr>
<tr>
<td>Red king crab</td>
<td>0.97</td>
<td>199,200</td>
<td>1,900</td>
<td>100f</td>
<td>1,900</td>
</tr>
<tr>
<td>Starfishes</td>
<td>1.11</td>
<td>513,600</td>
<td>5,700</td>
<td>100f</td>
<td>5,700</td>
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<tr>
<td><strong>Sub-total</strong></td>
<td></td>
<td></td>
<td></td>
<td><strong>17,800</strong></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Daily rate per body weight, from Laevastu and Larkins (1981).

\(^b\) From Table 2 (Bakkala et al. 1985).

\(^c\) (Food requirement) x (biomass).

\(^d\) Total percentage of the principal four prey items of yellowfin sole in stomach contents, from Table 3.

\(^e\) (Daily food consumption) x (share of four preys).

\(^f\) Stomach contents composition not available.

\(^g\) For species other than yellowfin sole.
Table 5. Estimates of flounders consumption for six months by each predator on the continental shelf of the eastern Bering Sea.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Year</th>
<th>Stomach contents(^a) (g/indiv.)</th>
<th>Body weight(^b) (g)</th>
<th>Daily food consumption</th>
<th>Flounders Consumption(^f) (t/6 months)</th>
<th>Average (t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plain sculpin</td>
<td>1975</td>
<td>24.37</td>
<td>439</td>
<td>14.41</td>
<td>4,000</td>
<td>14.96</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>17.41</td>
<td>346</td>
<td>11.11</td>
<td>3,900</td>
<td>3.51</td>
</tr>
<tr>
<td>Warty sculpin</td>
<td>1975</td>
<td>30.51</td>
<td>503</td>
<td>16.96</td>
<td>890</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>32.11</td>
<td>587</td>
<td>18.59</td>
<td>830</td>
<td>0.27</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>1975</td>
<td>g</td>
<td>g</td>
<td>11.98</td>
<td>15,400</td>
<td>g</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>g</td>
<td>g</td>
<td>10.34</td>
<td>13,200</td>
<td>g</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>1970</td>
<td>g</td>
<td>g</td>
<td>5.82</td>
<td>35,400</td>
<td>g</td>
</tr>
<tr>
<td></td>
<td>1971</td>
<td>7.08</td>
<td>492</td>
<td>8.58</td>
<td>32,600</td>
<td>0.11</td>
</tr>
<tr>
<td>Pacific halibut</td>
<td>1970</td>
<td>g</td>
<td>g</td>
<td>15.18</td>
<td>690</td>
<td>g</td>
</tr>
<tr>
<td></td>
<td>1971</td>
<td>g</td>
<td>g</td>
<td>9.85</td>
<td>450</td>
<td>0</td>
</tr>
<tr>
<td><strong>Sub-total</strong></td>
<td></td>
<td></td>
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</table>

...continued
**Table 5. Continued.**

Laevastu and Larkins' method

<table>
<thead>
<tr>
<th>Predator</th>
<th>Year</th>
<th>Daily food requirement (%)</th>
<th>Biomass (t)</th>
<th>Daily food consumption (t)</th>
<th>Flounders</th>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Share (%)</td>
</tr>
<tr>
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<td>1975</td>
<td>1.44</td>
<td>122,100</td>
<td>1,800</td>
<td>14.96</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>1.44</td>
<td></td>
<td></td>
<td>3.51</td>
</tr>
<tr>
<td>Warty sculpin</td>
<td>1975</td>
<td>1.44</td>
<td>26,300</td>
<td>380</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>1.44</td>
<td></td>
<td></td>
<td>0.27</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>1975</td>
<td>1.42</td>
<td>611,800</td>
<td>8,700</td>
<td>2.10</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>1.42</td>
<td></td>
<td></td>
<td>0.25</td>
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<tr>
<td>Walleye pollock</td>
<td>1970</td>
<td>1.50</td>
<td>1,871,900</td>
<td>28,100</td>
<td>1.43</td>
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<tr>
<td></td>
<td>1971</td>
<td></td>
<td></td>
<td></td>
<td>0.11</td>
</tr>
<tr>
<td>Pacific halibut</td>
<td>1970</td>
<td>1.16</td>
<td>58,100</td>
<td>670</td>
<td>3.80</td>
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<tr>
<td></td>
<td>1971</td>
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</table>

Sub-total: 89,000

---

*aAverage weight of stomach contents per fish, Sw.
*bAverage weight of fish from which stomachs were collected, Bw, except Pacific cod, walleye pollock for 1970, and Pacific halibut for which species values were estimated using length-weight relationships.
*cRd = 0.228 x Sw** 0.46 x Bw** 0.44, from Jones (1974), where ** indicates exponential.
*dCd = Rd x (Biomass)/Bw or Cd = Rd x (Population number).
*ePercentage of flounders in stomach contents, Rf.
*fCd x Rf x 180.
*gCalculated using data by length class.
*i(Biomass) x (Daily food requirement).
Fig. 1. Distributions of trawl survey stations shown as ranking of catch rate (kg/30 min. trawled) of yellowfin sole in the eastern Bering Sea in 1970, 1971, 1975, and 1976. The area encompassed with solid lines is where biomass estimates shown in Table 2 were obtained.
Fig. 2. Stomach content weight compositions (%) for flounders, collected on the continental shelf of the eastern Bering Sea in 1970 and 1971. See Appendix Table 1 for details. Yellowfin sole data are from Wakabayashi (1985a).
Fig. 3. Stomach content weight compositions (%) by length class (mm) for flounders collected on the continental shelf of the eastern Bering Sea in 1970 and 1971. See Fig. 2 for abbreviations. Yellowfin sole data are from Wakabayashi (1985a).
Fig. 3. Continued.
Fig. 4. Stomach content weight compositions (%) for walleye pollock by length category and for Pacific cod, collected on the continental shelf of the eastern Bering Sea in 1970 and 1971 or 1975 and 1976. See Fig. 2 for abbreviations and Appendix Table 2 for details and data sources.
Fig. 5. Stomach content weight compositions (%) by length class (mm) for Pacific cod collected on the continental shelf of the eastern Bering Sea in 1975 and 1976. See Fig. 2 for abbreviations. Source: Original data used in Sekiya (1978).
Fig. 6. Stomach content weight compositions (%) for sculpins collected on the continental shelf of the eastern Bering Sea in 1975 and 1976. See Fig. 2 for abbreviations and Appendix Table 3 for details. Source: Hosoki (1978).
Fig. 7. Schematic diagram of interspecific feeding relationships with reference to yellowfin sole on the continental shelf of the eastern Bering Sea. Arrows indicate flow of matter. Bold-faced and underlined species are key ones for yellowfin sole. Minor species are excluded.
## Appendix Table 1. Stomach contents (g), by prey item, per individual for flounders collected on the continental shelf of the eastern Bering Sea in 1970 and 1971.

<table>
<thead>
<tr>
<th>Prey Item</th>
<th>Yellowfin solea</th>
<th>Alaska pollock</th>
<th>Rock sole</th>
<th>Longhead dab</th>
<th>Starry flounder</th>
<th>Flatehead sole</th>
<th>Greenland turbot</th>
<th>Arrowtooth flounder</th>
<th>Pacific halibut</th>
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<tr>
<td>Smelts</td>
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<td></td>
<td></td>
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<td></td>
<td>0.5086</td>
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<td>Codfishes</td>
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<td>0.3864</td>
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<td>4.9478</td>
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<td>1.4296</td>
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<td>Flounders</td>
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<td></td>
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<tr>
<td>Other fishes</td>
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<td>0.1005</td>
<td>0.8625</td>
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<td>Amphipoda</td>
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<td>0.0057</td>
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<td>Nysitaceae</td>
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<td>0.0571</td>
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<td>Hermit crabs</td>
<td>0.0314</td>
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<td>0.0013</td>
<td>0.0004</td>
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<tr>
<td>Other crustacea</td>
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<td>0.0004</td>
<td>0.0004</td>
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<td>0.0205</td>
<td>0.0059</td>
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<tr>
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...continued
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<th>Rock sole</th>
<th>Longhead dab</th>
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<th>Flathead sole</th>
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<sup>a</sup>From Wakahayashi (1985a).
Appendix Table 2. Stomach contents (g), by prey item, per individual for walleye pollock by length category and Pacific cod, collected on the continental shelf of the eastern Bering Sea in 1970 and 1971 or 1975 and 1976.

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Appendix Table 2. Continued.

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<sup>a</sup>Prepared by Mr. H. Yamaguchi (Tohoku Regional Fisheries Research Laboratory, Hachinohe).

<sup>b</sup>From original data used in Sekiya (1978).
Appendix Table 3. Stomach contents (g), by prey item, per individual for sculpins, collected on the continental shelf of the eastern Bering Sea in 1975 and 1976.a

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<th>Great sculpin</th>
<th>Yellow Irish lord</th>
<th>Spinyhead sculpin</th>
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...continued
### Appendix Table 3. Continued.

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| Total       | 3.7628           | 32.1375       | 17.4087       | 146.1548      | 6.7046           | 4.9034           | 195.0964        | 1.0237         | 3.0535          | 0.8378            |
| Sample size | 200              | 112           | 1.113         | 21            | 219              | 89               | 14              | 612            | 43              | 147               |
| Number of empty stomachs | 2          | 1             | 56            | 1             | 6                | 9                | 3               | 105            | 3               |                   |
| Rate of empty stomachs (%) | 1.0        | 0.9           | 5.0           | 4.8           | 2.7              | 10.1             | 21.4            | 17.2           | 7.0             | 2.0               |
FINE STRUCTURE OF DEMERSAL FISH COMMUNITY AND MARINE ENVIRONMENT
IN THE EASTERN BERING SEA

by
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Tokyo University of Fisheries, Tokyo, JAPAN

and

Allen M. Shimada
Northwest and Alaska Fisheries Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
7600 Sand Point Way N.E.
Seattle, Washington 98115

ABSTRACT

The eastern Bering Sea demersal community, partitioned into 111 fish and 123 invertebrate species and species groups, was examined by recurrent group analysis (Fager 1957, 1963). Research bottom-trawl composition during summers 1979-84 together with sex and body length categories for walleye pollock (Theragra chalcogramma), Pacific cod (Gadus macrocephalus), yellowfin sole (Limanda aspera), and Pacific halibut (Hippoglossus stenolepis) were incorporated in this study. Community structure separated into 20, 24, 17, 19, 24, and 20 recurrent groups in each respective year.

First recurrent groups included pollock (males 31-55 cm, females >56 cm), Pacific cod (males >51 cm, females 55-60 cm), opilio tanner crab (Chionoecetes opilio), flathead sole (Hippoglossoides elassodon), starfish (Asteridae), and skates (Rajidae). Second groups included yellowfin sole (both sexes 11-35 cm), the sturgeon poacher (Agonus aciperenurus), and other variable species. The location of persistent community complexes was observed in 100-200 m depths between St. Matthew Island and the Pribilof Islands. Other community groups were found between the 30-50 m isobaths extending from Nunivak Island to Cape Vane and Constantine. Although the results indicate a relative constancy of key species in core group membership, other species associations were found to vary both temporally and spatially.

The influence of bottom water temperature, a significant abiotic environmental index, on community structure was also noted during the study period.

INTRODUCTION

The marine community comprising many species is considered to be formed through individual organism response to changes in the environment. Studies of community structure are important in understanding biological relationships between prey, predator, and competitor within the ecosystem. Furthermore, it is necessary to examine the relative contribution of both biotic and abiotic factors in order to better know the mechanism of community formation.

This paper attempts to describe a more precise classification for the eastern Bering Sea demersal community by elucidating its internal biological structure in finer detail with linkage to the abiotic environment.

MATERIALS AND METHODS

Sample composition of demersal fish and invertebrates, together with bottom water temperatures, were obtained from annual National Marine Fisheries Service crab-groundfish trawl surveys of the eastern Bering Sea shelf. These surveys were conducted between the months of May and August from 1979 to 1984 (Table 1). Characteristics of the vessels and trawl gear employed each year can be found in various data reports of the Northwest and Alaska Fisheries Center (Bakkalas et al. 1982, 1985). Procedures for sampling research trawl catches have been described in detail by Halliday (1985). Generally, bottom tows of 30 minutes duration were made.

Table 1. Time period, number of hauls and species categories examined during surveys from 1979 to 1984.

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<td>314</td>
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<td>June 7-August 1</td>
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<td>June 5-August 27</td>
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at preprogrammed stations: each representing the center of a 20 x 20 nautical mile grid-square (Figure 1). Water temperatures were collected by expendable bathythermograph (XBT) following the retrieval of each tow.

An index of affinity between individual species, or combined species identifications (i.e. unidentified skates, unidentified starfish, etc.) was calculated following the method of Fager to determine recurrent group membership (Fager 1957, 1963). This index is expressed by the geometric mean of the proportion of joint occurrence and is corrected for sample size:

\[
\frac{J}{(N_aN_b)^{1/2}} - \frac{1}{2} (N_a)^{1/2}
\]

where \( J \) is the number of joint occurrences; \( N_a \) and \( N_b \) are the total number of occurrences of species A and B respectively. Species are assigned to each letter such that \( N_a < N_b \). The analysis is based on presence or absence of any one species in each trawl sample, and neglects relative abundance encountered between different sample locations. In this paper the number of occurrences of each species was defined to be the number of stations where it represents a recorded catch weight >0.045 kg. This is the minimum value carried in the NWAFIC computer data base.

Affinity indices were calculated for all possible species combinations. Species pairs having an index value equal or greater than 0.45 were regarded as having a significant affinity with each other. This definition indicates that species A and species B should be found together more than half of the geometric mean of their occurrences. Recurrent groups were then formed according to the requirements that all species within a group show significant affinity with all other group members, that each group include as many species as possible, and that each species may not be included in more than one group. Groups that satisfy these conditions represent the largest, most frequent, separate units within which all inclusive species form a constant component of a common biological environment (Fager 1957).

The results of this paper also incorporated an analysis of four principal groundfish species classified by sex and body length: pollock males (9 classes), pollock females (9), pollock unsexed (9), Pacific cod males (9), Pacific cod females (9), Pacific cod unsexed (9), yellowfin sole males (8), yellowfin sole females (9), yellowfin sole unsexed (7), and Pacific halibut unsexed (8).

![Figure 1. Survey area and fixed trawl stations occupied each summer from 1979 to 1984.](image)
RESULTS AND DISCUSSION

1. Structure of Communities

The total number of recurrent groups formed between 1979 and 1984 were 28, 24, 17, 19, 24, and 20 (Appendix). Major species found in the first groups having the largest number of species were pollock, Pacific cod, opilio Tanner crab, flathead sole, and skates. Other species were included, but not consistently between all years. The categories of pollock and Pacific cod found were significant: more pollock (males 31-55 cm, females >56 cm), and Pacific cod (males >51 cm, females 55-60 cm). Group One membership was particularly large in 1981 and again in 1984. Greenland turbot (Reinhardtius hippoglossoides) was a core member in most years, with the exception of 1983 and 1984.

The principal species of second recurrent groups were yellowfin sole of both sexes (11-35 cm) and the sturgeon poacher. Group Two membership was more variable between years than for the first group. Longhead dab (Limanda proboscidea), rock sole (Lepidopsetta bilineata), a neptunid snail (Neptunea heros), and capelin (Mallotus villosus) tended to form the main components of the second, third, and fourth recurrent groups.

Species that rarely co-occur with others in an affinity pair, and thus form single-species associations were juvenile pollock (both sexes <20 cm), young Pacific cod (unsexed 21-35 cm and both sexes >56 cm), juvenile yellowfin sole (both sexes <10 cm), and Pacific halibut (unsexed for all length categories).

There are several notable points to be made from the analysis. Pollock of both sexes (>41 cm) often were members of first recurrent groups. Male pollock (21-40 cm) were also commonly found. juvenile pollock (<20 cm) coexisted with large pollock in 1979 and 1983. Male Pacific cod (>41 cm) were frequent members of first groups, but were replaced by Pacific cod (31-50 cm) in 1979, 1980, and 1982. Large and medium cod of both sexes were found in 1979 and 1980. In other years large and medium Pacific cod males were noted in the group. Both cod sexes (<30 cm) coexisted with the neptunid snail (N. heros) each year, excluding 1980 and 1984. Juvenile yellowfin sole (both sexes 6-15 cm) were found with the telmessus crab (Telmessus cheiragonus) in all six years. Yellowfin sole males (6-10 cm) and females (7-10 cm) often co-occurred with rainbow smelt (Osmerus mordax). Yellowfin sole (both sexes 15-20 cm) formed the same association with sturgeon poachers in all years.

2. Abiotic Marine Environment

This study also considered bottom water temperature as one readily obtained parameter of the abiotic marine environment (Figure 2). Mean temperature changed over a two year cycle, declining between 1979 and 1984 (Figure 3). The warmest year encountered was 1979 and the coldest in 1984. In the temperature series, northwest continental shelf water was typically 1-2°C less than southeast water. This trend reversed itself in 1982 when the southeast region was colder.

In 1979 the intrusion of the 2°C isopleth, an indicator of cold bottom water, was not strong enough of a line formed by St. Matthew and Nunivak Islands at 60°N latitude but continued to the outer northwest shelf. A relatively sharp front was observed between warm coastal water (12°C) extending from Nunivak Island to Cape Newenham. Alaskan Stream Extension Water was found to extend from the outer shelf edge onto the central shelf (Kihara 1982). In 1980 cold water (<2°C) persisted over the middle shelf, but coastal waters were warm. In 1981 warmer 3-7°C water was observed throughout the southeast shelf below 58°N latitude. Cold bottom temperatures less than 0°C were found in the northwest region and water below 2°C was observed well inside Bristol Bay during 1982. Coastal areas were also much colder than in other years. In 1983 warm temperatures were found north of Unimak Island and colder water dominated west of Nunivak Island representing temperatures lower than 0°C. The coldest year in the series was 1984 when water temperatures lower than -1.0°C were noted between St. Matthew and Nunivak Islands. The Cold Shelf Water also extended well into the southeast shelf, as evidenced by the well developed 2°C isotherm inside central Bristol Bay.

3. Distribution of Recurrent Groups

The distributions of major species associations are shown in Figure 4. First recurrent groups were found on the outer shelf south of St. Matthew Island between 100-200 m where 1-4°C bottom temperatures were consistently observed each year. Second groups composed principally of yellowfin sole (both sexes 11-35 cm), sturgeon poachers, and other intermittent species were found in 2-5°C water over 30-50 m isobaths between Nunivak Island, Cape Newenham, and Cape Constantine. However, in 1981 and 1983; these two species formed the foundation of the third recurrent group but retained their characteristic spatial distribution (Appendix and Figure 4). During 1981 this pair was found with longhead dab, red king crab
Figure 2. Distributions of bottom water temperatures in the eastern Bering Sea during summers from 1979 to 1984 (°C).
Figure 3. Variations of mean bottom water temperature of overall, south-east, and northwest shelf regions of the eastern Bering Sea during summers from 1979 to 1984. Regions are divided by AB line in Figure 2.

(Paralithodes camtschatica), and a neptunid snail (Neptunea ventricosa) south of Cape Newenham. In 1983 yellowfin sole and sturgeon poachers were associated with male Pacific cod (43 cm), a neptunid snail (Neptunea heros), capelin, and Pacific herring (Clupea harengus pallasi). This group was found southwest of Nunivak Island in depths less than 50 m.

Pollock smaller than 20 cm (both sexes) form single-species associate groups and distributed themselves in 100-200 m depths from St. Matthew Island to the Pribilof Islands; excepting 1979, 1982, and 1983 when bottom water temperatures were found between 1-4°C. In 1983 this group was found near St. Matthew Island within a 1.00°C temperature regime. Juvenile pollock were associated with wintled eelpout (Lycodes palearis) between St. Matthew Island and the Pribilof Islands in 1982. In 1979 they were part of the first recurrent group.

Male pollock larger than 51 cm were first recurrent group members in most years. In the 1979 analysis, they formed an associate group with gastropods in 2-3°C temperatures between 60-100 m near St. Matthew Island, and in 4-5°C water east of the Pribilof Islands. Large pollock males combined with small Pacific cod (both sexes) and the neptunid snail (N. heros) as the third 1982 recurrent group. Their distribution was in cold 1-2°C water of the central shelf.

Pacific cod larger than 66 cm (both sexes) formed a single-species group in 1979 and were generally found on the outer shelf between Unimak Island north to the Pribilof Canyon. In the same area, Pacific cod males (56-65 cm) and females (56-60, >66 cm) formed the seventh recurrent group in 1980. Water temperature in this area was typically near 4°C.

Yellowfin sole smaller than 10 cm (both sexes) were found with different species by year. These included rainbow smelt, telmessus crab, and whitespotted greenling (Hexagrammos stelleri). This composite group was found in warm coastal waters between Nunivak Island and Cape Constantine.

4. Community Structure and Marine Environment

It has been noted that temporal community structure and spatial patterns are affected by changes in the abiotic marine environment of the eastern Bering Sea (Kihara 1983a, 1983b). This paper attempts to further clarify the influence of water temperature against change in more detailed bottom community structure. Correlations were made between bottom temperature and the sex and size categories of four groundfish species. These were examined on the hypothesis that even a single abiotic factor can influence the habitat area of species either directly or indirectly. The resulting distribution patterns of each member species then forms the basis for demersal community structure.

Catch compositions were found to differ in species mix and in sex-size categories by trawl location. Flathead sole, opilio tanner crab, and Alaska pollock (Pleuronectes quadrituberculatus) were encountered over a broad area covering more than 70% of the continental shelf. Yellowfin sole (males 21-30 cm, females 21-35 cm), pollock (both sexes 41-55 cm), and rock sole inhabit 50-60% of the shelf. Yellowfin sole (males 6-15 cm, females 7-15 and 36-43 cm) were distributed in a more restricted area covering less than 24% of shelf area.

The correlation between inhabited areas (i.e. the number of sample locations where species were found) and mean bottom temperature were: pollock males 31-35 cm (NW region temp. r=0.92, p<0.01), pollock females 31-35 cm (NW region temp. r=0.95, p<0.01) and females 36-40 cm (NW region temp. r=0.87, p<0.05). Each had a significant positive correlation. Pollock males larger than 56 cm (NW region temp. r=0.84, p<0.05); yellowfin sole females 21-25 cm (NW region temp. r=0.83, p<0.05); females 26-30 cm (NW region temp. r=0.85, p<0.05); 31-35 cm females (NW region temp. r=0.83, p<0.05). All had significant negative correlation with temperature as did Alaska plaice and capelin.

It is also suggested that medium pollock of both sexes expand their habitat in years when the northwest shelf region is relatively warm. Large male pollock were found in a rather narrow habitat area. There was no significant correlation between mean bottom temperature and the habitat of large female pollock, yellowfin sole (except
Figure 4. Distributions of major recurrent groups of the eastern Bering Sea during summers from 1979 to 1984. Numbers indicate recurrent group numbers (Appendix).
medium-size females), and Pacific cod of both sexes (all size categories). Significant correlation was found between capelin and bottom temperatures observed from the northwest shelf, and between Alaska plaice and overall shelf temperatures.

As yet there is no satisfactory hypothesis offered to explain why some species demonstrate independence from temperature while others appear to be temperature dependent. To some extent other factors of their biotic environment may have greater weight in determining distribution. These may include species-specific physiological requirements, time of spawning, pelagic or demersal ontogeny, semi-demersal and benthic life history strategies, as well as prey-predator-competitor relationships.

On the assumption that mutual coexistence in time and space between two or more species implies some community structure, it is evident that such associations are also affected by abiotic parameters. One other comparison made by this study was the correlation between such species coexistence, represented by the index of affinity, and mean temperature. Coexistence within the same species of different sex and size categories is also affected by the environment. For instance, pollock of different sex and size respond to variations in bottom water temperature (Figure 5). This observation suggests cannibalism by larger pollock on smaller pollock of different sex and size is affected by their abiotic environment.

Significant negative correlation with bottom temperature was found between the index of affinity for female pollock (>56 cm) and opilio tanner crab, which are core members of the first recurrent group, as well as for rock sole. There were no other significant correlations between the coexistence of other core species of the first recurrent groups and temperature. Significant negative correlations were found in the index of affinity between yellowfin sole (females 16-20 cm) and sturgeon poachers, which are principal members of the second recurrent group, and for longhead dab and capelin (Table 2).

Although rock sole distribution was independent of bottom temperature variation, it became a member of the first recurrent group by changing its relationship with opilio tanner crab and pollock females (>56 cm), which taken together were found to be temperature dependent between 1982 and 1984. The habitat of Greenland turbot, arrowtooth flounder (Atheresthes stomias) which are pollock predators, and Alaska plaice are dependent upon bottom temperature variability. These species also co-occur with core species of the first recurrent groups independently through temperature shifts.

The combination of capelin, whose habitat is dependent on water temperature in the northwest shelf region, was noted with yellowfin sole (16-20 cm) of both sexes and sturgeon poachers, whose habitat is dependent on southeast shelf temperature variation. Capelin was a member of the second recurrent group in all years except the relatively warm years of 1979 and 1981. The high index of affinity between longhead dab with yellowfin sole and sturgeon poachers depended on bottom temperatures of the southeast shelf. There were no significant correlations found with a neptunid snail (N. heros), rock sole, and sculpins (Cottidae), which were principal...
<table>
<thead>
<tr>
<th>Species pair</th>
<th>Temperature of shelf region</th>
<th>Correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pollock F &gt;56 cm Rock sole</td>
<td>Overall shelf</td>
<td>r = -0.87, p &lt; 0.05</td>
</tr>
<tr>
<td>Opilio tanner crab Rock sole</td>
<td>Overall shelf</td>
<td>r = -0.85, p &lt; 0.05</td>
</tr>
<tr>
<td>Yellowfin sole F 16-20 cm Longhead dab</td>
<td>Southeast shelf</td>
<td>r = -0.88, p &lt; 0.02</td>
</tr>
<tr>
<td>Yellowfin sole M 16-20 cm Capelin</td>
<td>Southeast shelf</td>
<td>r = -0.97, p &lt; 0.01</td>
</tr>
<tr>
<td>Yellowfin sole F 16-20 cm Capelin</td>
<td>Overall shelf</td>
<td>r = -0.97, p &lt; 0.01</td>
</tr>
<tr>
<td>Sturgeon poacher Capelin</td>
<td>Southeast shelf</td>
<td>r = -0.92, p &lt; 0.01</td>
</tr>
<tr>
<td>Pollock M 36-40 cm Myxocephalus sculpin</td>
<td>Overall shelf</td>
<td>r = 0.81, p &lt; 0.05</td>
</tr>
</tbody>
</table>

F: Female, M: Male

co-occurring Group Two, members, and bottom temperature.

It is suggested that significant associations were formed among core species of each recurrent group through the changing relationship between rock sole, longhead dab, and capelin; acting dependently with the abiotic parameter of temperature. Community structures formed by these major associations and other intermittent species members, independent of bottom temperature, was also found to shift spatially. The relationship of co-occurrence is thought to be based on other factors, including biotic relationships and the requirements of specific life history strategies.

While it is also important to consider the mechanism of community formation from the aspect of predator-prey and competitor linkages, physical environment influences should also be addressed. For example, the pairing of known pollock predators with pollock was found to have significant correlation with bottom temperature (Figure 6). The habitat of thorny sculpins (Tecus spiniger) with southeast bottom temperature was found to be significant (r = 0.84, p < 0.02). The relationship between this species and pollock was found to correlate differently with temperature and pollock size categories. Coexistence with 21-25 cm pollock males (overall temp. r = 0.81, p < 0.05); < 20 cm pollock females (overall temp. r = 0.81, p < 0.05); 21-25 cm females (overall temp. r = 0.95, p < 0.01); and females 26-30 cm (overall temp. r = 0.86, p < 0.05) were significant from 1979 to 1984. The pairing of bigmouth sculpin (Hemipterus bolini) and pollock females (36-40 cm) was variable according to the shift in temperatures of the overall shelf (r = -0.81, p < 0.05). The pairing of spinyhead sculpins (Dasycottus setiger) with 26-30 cm pollock females (r = 0.82, p < 0.01); 31-35 cm males (r = 0.82, p < 0.05) and 46-50 cm males (r = 0.88, p < 0.025) correlate with northwest shelf bottom temperature. Large sculpins (Myxocephalus spp.) were found with 36-40 cm male pollock depending on observed variability in temperature of the overall shelf (r = 0.81, p < 0.05).

Many papers have discussed pollock prey, predators, and competitors (Mito 1974; Smith et al. 1984; Dwyer 1985, and Livingston et al. 1985). Flathead sole, skates, and large Pacific cod are known predators of pollock and opilio tanner crab which were found to coexist in the first recurrent group. Large sculpins (Myxocephalus spp.) which consume pollock often co-occur with members of the first and second groups. Other pollock predators, thorny sculpin and bigmouth sculpin are other group members. Capelin, a prey of pollock, is a major member of Group Two (Appendix).

Such results indicate that environmental water temperature, an easily
obtained abiotic parameter, affects the association of predator and prey to some degree. It is therefore prudent to examine whether additional abiotic parameters affect the location and mutual existence of observed associations in order to clarify the demersal ecosystem.

This study has determined which species appear to be dependent or independent of the effects of the abiotic marine environment. This was based on a relationship of co-occurrence measured by an index of affinity and its correlation with bottom temperature. Further work is required to add other environmental parameters including salinity, water mass structure, and water transport properties. The successful interpretation of observed species associations rests on food habit studies leading to improved understanding of eastern Bering Sea demersal ecosystem processes.

ACKNOWLEDGEMENTS

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LITERATURE CITED


Appendix. Community structures of demersal species of the eastern Bering Sea during summers from 1979 to 1984. Recurrent group numbers are listed along the left margin of each diagram. Connections between groups are shown by mean indices of affinity. Figures in parentheses are body length (cm). M: male, F: female, MF: male and female, ?: unknown sex.
TROPHIC INTERACTIONS OF KEY FISH SPECIES
IN THE EASTERN BERING SEA

by

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ABSTRACT

The food habits of six key fish predators in the eastern Bering Sea are examined: Walleye pollock, Theragra chalcogramma; Pacific cod, Gadus macrocephalus; Greenland turbot, Reinhardtius hippoglossoides; arrowtooth flounder, Atheresthes stomias; yellowfin sole, Limanda aspera; and flathead sole, Hippoglossoides elassodon. We use a variety of feeding strategies and prey types. Differences in their diets by size, season, and area are outlined, discussed, and compared with other studies. Diet overlap among size groups of these key predator species is calculated to determine the degree of diet similarity at the individual fish level. Preliminary calculations of population consumption by each key fish species are performed using existing data regarding diet composition, evacuation rates, stomach content weights, and population size of key predator species. The potential impact on prey populations common to these key predator species is discussed.

INTRODUCTION

Marine fisheries management advice is often derived from fish population assessment data and models. Most single-species population models require estimates of natural mortality rates by age of commercial fish and invertebrate species. In addition, multispecies ecosystem models are now being considered more seriously for providing information which may be useful in providing fishery management advice (Mercer 1982). The main link between species in multispecies models is through predation mortality which is the major component of natural mortality. Thus, both single- and multispecies models require accurate species-specific estimates of natural (or predation) mortality.

The purpose of many current trophic interaction studies, such as the programs developed for the North Sea by the International Council for the Exploration of the Sea (ICES), Georges Bank in the Northwest Atlantic by the Northeast Fisheries Center, and for the eastern Bering Sea by the Northwest and Alaska Fisheries Center (NWFSC), is to define key species which are major sources of predation mortality and to estimate the degree of predation mortality on commercial stocks by each of these key species. Several types of food habits data need to be collected in order to estimate predation mortality. Estimating the proportions by weight of major prey categories in a key predator's diet is one of the most basic but most important types of data analysis performed on food habits data for input to multispecies models because it is the primary method for partitioning predation mortality among species. Calculation of the daily ration for each key predator species is also necessary for models which require estimates of the rate of food consumption by each species.

The purpose of this paper is to show preliminary results from the data collection efforts of the Trophic Interactions Program of the Northwest and Alaska Fisheries Center. The Trophic Interactions Program has designated six fish species which are thought to be major predators of commercial fish or crabs in the eastern Bering Sea. These key fish species are: walleye pollock, Theragra chalcogramma; Pacific cod, Gadus macrocephalus; Greenland turbot, Reinhardtius hippoglossoides; arrowtooth flounder, Atheresthes stomias; yellowfin sole, Limanda aspera; and flathead sole, Hippoglossoides elassodon. The seasonal and size-related food habits of these predators will be discussed and compared with other studies. Diet overlap among size groups of these key predator species will be calculated to determine the degree of diet similarity. Preliminary calculations of population consumption which will eventually lead to estimates of natural mortality by each key fish species will be performed using existing data regarding diet composition, daily ration, and population size of key predator species. These results should enable some discussion of potential impacts of key predator species on commercially important prey populations.
METHODS

Sample Collection and Processing

Specimens were collected during the period of 1981 through 1984 in the eastern Bering Sea by U.S. Fishery observers aboard foreign fishing vessels and by U.S. scientists aboard research vessels participating in resource assessment surveys of the area. Stomachs of walleye pollock, Pacific cod, Greenland turbot, arrowtooth flounder, yellowfin sole and flathead sole were taken from bottom and midwater trawl samples of variable tow duration. Table 1 summarizes the dates and number of samples collected for each species.

Individual fish were first checked for signs of regurgitation, i.e., food items in mouth or gill rakers or flaccid stomachs and were discarded if any such signs were noted. Stomachs from the remaining fish were excised and placed individually into cloth bags with a specimen label containing fish fork length, sex, and station information. All samples were preserved in a 10:1 seawater to formalin mixture.

Stomachs were analyzed individually in the laboratory. Prey items were identified to the lowest practical taxon and damp weight to the nearest milligram and number of each prey taxon were recorded. Length measurements of fish and crab prey were taken when enough remained of the items to permit measurement.

Data Analysis

Samples were divided among four seasons which were defined as follows:

- Spring: 15 March-14 June
- Summer: 15 June-14 September
- Autumn: 15 September-14 December
- Winter: 15 December-14 March

Food habits information for each species was separated into two length strata for description of size related feeding trends. The choice of length categories varied for each species depending upon the length at which fish tended to change feeding behavior.

Based on a review of dietary overlap measures (Cailliet and Barry 1979; Linton et al. 1981), Schoener’s (1970) index was chosen because it was found to measure overlap accurately over most of the range of potential overlap (Linton et al. 1981). Schoener’s index, \( C_{xy} \), is calculated as:

\[
C_{xy} = 1.0 - 0.5 \sum \frac{P_{xi} - P_{yi}}{P_{xi} + P_{yi}}
\]

where \( P_{xi} \) and \( P_{yi} \) are the estimated proportions by weight of prey \( i \) in the diets of species \( x \) and \( y \), respectively. The index ranges from 0 which indicates no dietary overlap to a maximum overlap of 1 when all prey items are found in equal proportions. Taxonomic grouping to the family level was employed for Schoener’s index calculations.

Table 1.—Stomach sampling dates, areas, and depths for size groundfish species in the eastern Bering Sea and the respective sample sizes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sampling dates</th>
<th>Area</th>
<th>Depth interval (m)</th>
<th>No. stomachs 1/</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greenland turbot</td>
<td>Aug-Sep 1982</td>
<td>Outer shelf, slope</td>
<td>60-200+</td>
<td>932 (499)</td>
</tr>
<tr>
<td>(Reinhardtus hippoclentus)</td>
<td>Jul-Nov 1983</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>or (Hippoglossoides)</td>
<td>Jun-Nov 1984</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arrowtooth flounder</td>
<td>May-Nov 1983</td>
<td>Outer shelf, slope</td>
<td>65-200+</td>
<td>1618 (713)</td>
</tr>
<tr>
<td>(Atheresthes stomias)</td>
<td>Mar-Oct 1984</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific cod</td>
<td>Sep-Oct 1982</td>
<td>Middle-outer shelf, slope</td>
<td>30-200+</td>
<td>667 (30)</td>
</tr>
<tr>
<td>(Gadus macrocephalus)</td>
<td>Nov-Dec 1983</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flathead sole</td>
<td>Sep 1982</td>
<td>Middle-outer shelf, slope</td>
<td>45-125</td>
<td>381 (81)</td>
</tr>
<tr>
<td>(Hippoglossoides elassodon)</td>
<td>Jun-Sep 1984</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellowfin sole</td>
<td>Sep 1982</td>
<td>Inner, middle, outer shelf</td>
<td>25-125</td>
<td>1000 (500)</td>
</tr>
<tr>
<td>(Limanda aspera)</td>
<td>Feb-Sep 1984</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>Jul-Nov 1981</td>
<td>Inner, middle, outer shelf</td>
<td>35-200</td>
<td>2857 (493)</td>
</tr>
<tr>
<td>(Theragra chalcoforma)</td>
<td>Jan-Dec 1982</td>
<td></td>
<td></td>
<td>7455 (2316)</td>
</tr>
</tbody>
</table>

1/ Total number of stomachs sampled. Number of empty stomachs in parentheses.
Daily ration was calculated for each species by using the Elliott and Persson (1978) model which assumes an exponential, temperature-dependent evacuation rate, R. If stomach samples are collected at intervals of t hours, the mean stomach content weight as a percentage of fish weight, \( S_i \), in each interval i is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978) the daily ration in terms of percentage body weight, \( IC_i \), can then be evaluated by the following expression:

\[
IC = \frac{Rt}{1 - \exp(-Rt)} \sum_{i=1}^{m} S_i (1 - \exp(-Rt)) = 24S R
\]

where \( S = \frac{tS_i}{m} \). The general relationship between R and temperature T was found by Durbin et al. (1983) to be of the following form:

\[
R = a \times e^{1.15T}
\]

where the intercept a is a parameter which is thought to change with prey type and can be estimated from gastric evacuation rate experiments. Estimates of a for euphausiids, pollock and squid prey consumed by walleye pollock were revised from data presented in Dwyer (1984); where a equals 0.0078 for euphausiids prey, 0.0143 for fish prey, and 0.0079 for squid prey. Values for a are not available for the other key predators so one of the above-mentioned values was used for each predator depending on which prey item dominated a particular predator’s diet. Average bottom temperatures for the eastern Bering Sea during each of the four seasons were estimated from Ingraham (1983).

Population consumption estimates were calculated using the following formula modified from Mehl and Westgard (1983):

\[
C_{ijk} = DR_{ij} \times D_i \times B_j \times P_{ijk}
\]

where \( C_{ijk} \) is the consumption (weight) of prey k during season i by predator j; \( DR_{ij} \) is the daily ration, as the fraction of body weight consumed per day of predator j in season i; \( D_i \) is the number of days in season i; \( B_j \) is the biomass of predator j; and \( P_{ijk} \) is the proportion (by weight) of prey k consumed by predator j in season i.

SEASONAL AND SIZE-RELATED FEEDING BEHAVIOR OF KEY PREDATORS

Flathead sole

Figure 1 shows the percentages by weight of main food items consumed by flatheadsole sampled during summer in the eastern Bering Sea. Flathead sole less than 25 cm in length consumed mostly small crustaceans such as mysids, gammarid amphipods, and crangonid shrimp. Other invertebrates consumed were polychaetes and brittle stars. Commercially important crustaceans such as pandalid shrimp and Tanner crab constituted about 7% of the diet by weight. Some walleye pollock were also consumed.

Larger flathead sole (>25 cm) consumed mainly brittle stars and walleye pollock. Small amounts of Pacific cod and other fish were also eaten.

Yellowfin sole

Figure 2 shows the percentages by weight of main food items consumed by yellowfin sole sampled during spring and summer in the eastern Bering Sea. The diet of both size groups of yellowfin sole was dominated by bivalves. Small amounts of
other invertebrates such as polychaetes were also present in the diet.

The summer diet for both size groups, however, contained only small amounts of bivalves. Other invertebrates such as polychaetes and echiurid worms were major prey as were crustaceans such as euphausiids and crangonid shrimp. Small amounts of fish such as Pacific cod and walleye pollock were also consumed by yellowfin sole. The spring diet was composed wholly of benthic prey while the summer diet, although mostly benthic, also included pelagic prey items.

Winter samples were also obtained but 86% of the 152 stomachs sampled were empty. The remaining stomachs contained marine worms, unidentified decapods, and Tanner crab.

**Arrowtooth flounder**

There was little seasonal variation in the diet of arrowtooth flounder (Figure 3). The main food item of both size groups in spring, summer, and autumn was fish. In most cases, pollock constituted at least 40% by weight of the diet. In spring, however, other fish such as zoarcids were a major dietary component. Cephalopods (mostly squid) were present in the diet of both size groups of arrowtooth flounder in all three seasons. Other prey items included euphausiids and pandalid and crangonid shrimp.

**Greenland turbot**

Figure 4 shows the main food items consumed by Greenland turbot sampled in spring, summer, and autumn in the eastern Bering Sea. There appeared to be little seasonal variation in diet except for a decrease in the percentage of squid in the diet during summer. Squid, mostly *Berryteuthis* sp., along with pollock and other fish were the most dominant prey items by weight in the diet of Greenland turbot. Other fish consumed were mostly deep-water fishes of the families Bathylagidae and Myctophidae. Zoarcids and cottids were also present in the food. Only small incidental amounts of crustaceans and other invertebrates were consumed.

Some differences seem evident in prey type consumed between the two size groups of Greenland turbot. Turbot <60 cm in length consumed mostly squid and small amounts of fish. Larger turbot (>60 cm) consumed mostly pollock and smaller amounts of squid and other fish.

**Pacific cod**

Figure 5 shows the main categories of food consumed by Pacific cod sampled during all four seasons in the eastern Bering Sea. Crustaceans, crab and fish constituted the major portion of the cod’s diet by weight. Most of the crab consumed was Tanner crab (*Chionoecetes* spp.) and the major identifiable fish prey were pollock and pleuronectids. Cod also consumed a variety of invertebrates including crangonid and pandalid shrimp, amphipods, squid, polychaetes, and small epibenthic crustaceans.

In general, cod exhibited size-related feeding trends. Cod <55 cm in length consumed mostly crustaceans and invertebrates and only smaller amounts of fish (<30% by weight of the diet). Larger cod consume mostly fish (60-90% by weight of the diet) and only small amounts of crustaceans.

There appeared to be some seasonal trends in prey types consumed. In winter and spring, small cod consumed crustaceans which were mainly euphausiids (13% by weight) and crangonid and hippolytid shrimps. In summer and autumn however, crustaceans consumed by smaller cod were mostly Tanner crab (30-45% by weight). King crab (*Paralithodes* sp.) were consumed only in the spring by large cod. In spring and summer, cod of both size groups consumed fish which appeared to be fishery discards, up to 10% by weight of the diet consisted of these fish.

**Walleye pollock**

Figure 6 shows the major prey items consumed by pollock during all four seasons in the eastern Bering Sea. Euphausiids, copepods, pandalid shrimp, pollock, and unidentified gadids formed the major portion of the diet. Larger pollock (>40 cm) tended to consume more fish than did smaller pollock.

Fairly strong seasonal trends were observed in the diet of both size groups of pollock. In spring, the diet of both sizes of pollock was dominated by euphausiids. Pollock also consumed small amounts of copepods, fish, and other invertebrates. In summer, small pollock consumed mostly copepods (47% by weight) and euphausiids while pollock >40 cm in length ate mostly juvenile pollock. Euphausiids and copepods were still present in small amounts in the diet of large pollock during summer. Both size groups of pollock consumed juvenile pollock during autumn. The winter diet consisted mostly of fish: myctophids (12% by weight) and unidentified gadids (20% by weight) for pollock <40 cm and mostly juvenile pollock prey (64% by weight) for large pollock predators.
Figure 3.--Percentages by weight of main food items consumed by two size groups of arrowtooth flounder during spring, summer, and autumn in the eastern Bering Sea.

Figure 4.--Percentages by weight of main food items consumed by two size groups of Greenland Turbot during spring, summer, and autumn in the eastern Bering Sea.

Figure 5.--Percentages by weight of main food items consumed by two size groups of Pacific cod during spring, summer, autumn, and winter in the eastern Bering Sea.

Figure 6.--Percentages by weight of main food items consumed by two size groups of walleye pollock during spring, summer, autumn, and winter in the eastern Bering Sea. (Adapted from Dwyer 1984).
SEASONAL DIET OVERLAP OF KEY PREDATORS

Diet overlap among key predators was calculated using equation (1) for each season. The results of these calculations are shown in Figures 7-10. Overlap values were grouped into three categories to represent low (0 to <30%), intermediate (30 to <60%), and high (60 to 100%) levels of diet overlap (Langton and Bowman 1980).

Spring

Diet overlap between most species was low during spring (Fig. 7). Intermediate overlap levels occurred between both sizes of arrowtooth flounder because both groups consumed large amounts of Zoarcidae. Large arrowtooth flounder had intermediate diet overlap with both size groups of Greenland turbot and large Pacific cod because all these groups had walleye pollock as a dominant prey item in the diet. There was intermediate diet overlap between the two Greenland turbot size groups due to their common prey of squid. High overlap was observed between the two yellowfin sole size groups as both diets were dominated by clams. Both sizes of walleye pollock consumed mostly euphausiids which resulted in a high overlap value.

Summer

More dietary overlap was observed in summer (Fig. 8). Yellowfin sole diets had intermediate overlap with flathead sole, small cod (common prey were polychaetes and crangonid shrimp), and with pollock due to joint euphausiid consumption. Large pollock, cod, Greenland turbot, and both sizes of arrowtooth flounder had intermediate to high diet overlap among each other because of their common consumption of juvenile pollock.

Autumn

Most key species groups had intermediate overlap during autumn (Fig. 9). Small cod had low overlap with most groups because its diet was the only one for which the major prey was Tanner crab. Intermediate to high diet overlaps occurred between all other groups. Again, this was mostly due to the common dominant prey item of juvenile pollock.

Winter

Diet information in winter was only available for Pacific cod and walleye pollock (Fig. 10). Large cod and both pollock size groups had intermediate to high diet overlap between each other due to their common consumption of pollock or other fish. Since small cod consumed polychaetes, euphausiids, and some fish they had intermediate diet overlap with all groups except large pollock whose main food was juvenile pollock.

![Figure 7](image-url) -- Diet overlap of key fish predators during spring in the eastern Bering Sea calculated using Schoener’s index.
Figure 8.--Diet overlap of key fish predators during summer, in the eastern Bering Sea calculated using Schoener's Index.

Figure 9.--Diet overlap of key fish predators during autumn in the eastern Bering Sea calculated using Schoener’s Index.

Figure 10.--Diet overlap of key fish predators during winter in the eastern Bering Sea calculated using Schoener’s Index.
Table 2--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for flathead sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>flathead sole</td>
<td>24-1</td>
<td>0.724 ± 0.000</td>
</tr>
<tr>
<td>24-3</td>
<td>1.030 ± 0.367</td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>0.349 ± 0.051</td>
<td></td>
</tr>
<tr>
<td>9-12</td>
<td>0.378 ± 0.023</td>
<td></td>
</tr>
<tr>
<td>summer</td>
<td>15-18</td>
<td>0.322 ± 0.011</td>
</tr>
<tr>
<td>15-18</td>
<td>0.337 ± 0.016</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.266 ± 0.039</td>
<td></td>
</tr>
<tr>
<td>18-21</td>
<td>0.391 ± 0.000</td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>0.450 ± 0.12</td>
<td></td>
</tr>
<tr>
<td>D.R. = 245 ± 0.12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for yellowfin sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>yellowfin sole</td>
<td>24-3</td>
<td>0.012 ± 0.014</td>
</tr>
<tr>
<td>9-12</td>
<td>0.371 ± 0.030</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.363 ± 0.057</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.036 ± 0.025</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.361 ± 0.020</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.428 ± 0.025</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.511 ± 0.030</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.453 ± 0.12</td>
<td></td>
</tr>
<tr>
<td>D.R. = 245 ± 0.12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for yellowfin sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>24-3</td>
<td>0.123 ± 0.014</td>
</tr>
<tr>
<td>3-6</td>
<td>0.240 ± 0.024</td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>0.138 ± 0.045</td>
<td></td>
</tr>
<tr>
<td>9-12</td>
<td>0.541 ± 0.024</td>
<td></td>
</tr>
<tr>
<td>temperature</td>
<td>12-15</td>
<td>0.379 ± 0.011</td>
</tr>
<tr>
<td>15-18</td>
<td>0.626 ± 0.055</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.006 ± 0.001</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.315 ± 0.042</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>1.528 ± 0.073</td>
<td></td>
</tr>
<tr>
<td>D.R. = 245 ± 0.14</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for yellowfin sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>24-3</td>
<td>0.396 ± 0.024</td>
</tr>
<tr>
<td>3-6</td>
<td>0.392 ± 0.024</td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>0.234 ± 0.012</td>
<td></td>
</tr>
<tr>
<td>9-12</td>
<td>0.379 ± 0.011</td>
<td></td>
</tr>
<tr>
<td>temperature</td>
<td>12-15</td>
<td>0.626 ± 0.055</td>
</tr>
<tr>
<td>15-18</td>
<td>0.081 ± 0.010</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.759 ± 0.063</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>1.858 ± 0.075</td>
<td></td>
</tr>
<tr>
<td>D.R. = 245 ± 0.16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for yellowfin sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>24-3</td>
<td>0.283 ± 0.082</td>
</tr>
<tr>
<td>6-9</td>
<td>0.653 ± 0.070</td>
<td></td>
</tr>
<tr>
<td>9-12</td>
<td>0.753 ± 0.040</td>
<td></td>
</tr>
<tr>
<td>12-18</td>
<td>0.217 ± 0.046</td>
<td></td>
</tr>
<tr>
<td>D.R. = 245 ± 0.14</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 7--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for yellowfin sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>24-3</td>
<td>0.252 ± 0.030</td>
</tr>
<tr>
<td>3-6</td>
<td>0.287 ± 0.046</td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>0.421 ± 0.013</td>
<td></td>
</tr>
<tr>
<td>9-12</td>
<td>0.567 ± 0.021</td>
<td></td>
</tr>
<tr>
<td>temperature</td>
<td>12-15</td>
<td>0.336 ± 0.007</td>
</tr>
<tr>
<td>15-18</td>
<td>0.036 ± 0.010</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.398 ± 0.036</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>0.451 ± 0.033</td>
<td></td>
</tr>
<tr>
<td>D.R. = 245 ± 0.11</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 8--Mean stomach content weight as percent body weight (%BW) and standard error of mean and daily ration (D.R.) calculations for yellowfin sole.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>24-3</td>
<td>0.000 ± 0.000</td>
</tr>
<tr>
<td>6-9</td>
<td>0.242 ± 0.043</td>
<td></td>
</tr>
<tr>
<td>9-12</td>
<td>0.035 ± 0.004</td>
<td></td>
</tr>
<tr>
<td>12-18</td>
<td>0.035 ± 0.004</td>
<td></td>
</tr>
<tr>
<td>D.R. = 145 ± 0.02</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Population consumption or the amount of prey consumed by a predator population in the eastern Bering Sea was calculated during all four seasons using equation (4). Calculations were performed on key predator species groups within a season if there was sufficient information regarding diet composition during that season and if a daily ration estimate was available or could be estimated from another season's daily ration value.

The total annual consumption of walleye pollock and Tanner crab prey by key predator populations is shown in Tables 8-11. Pollock and Tanner crab were consumed during all four seasons. More
Table 4.—Mean stomach content weight as percent body weight (% W) and standard error of mean and daily ration (D.R.) calculations for arrowtooth flounder.

<table>
<thead>
<tr>
<th>Arrowtooth</th>
<th>Flounder</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (% W)</th>
<th>S = 1.256</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-3</td>
<td>5</td>
<td>0.181 ± 0.081</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>2</td>
<td>0.040 ± 0.028</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>5</td>
<td>0.199 ± 0.039</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>1</td>
<td>0.318 ± 0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp 2.5°C</td>
<td>4</td>
<td>0.000 ± 0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a-0.0143</td>
<td>1</td>
<td>5.834 ± 0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-0.0191</td>
<td>2</td>
<td>2.928 ± 1.727</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>13</td>
<td>0.545 ± 0.115</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.R. × 24SR = 0.58</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5.—Mean stomach content weight as percent body weight (% W) and standard error of mean and daily ration (D.R.) calculations for Greenland turbot.

<table>
<thead>
<tr>
<th>Greenland</th>
<th>Turbot</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (% W)</th>
<th>S = 0.910</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-3</td>
<td>35</td>
<td>0.020 ± 0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>14</td>
<td>0.224 ± 0.041</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>31</td>
<td>0.220 ± 0.030</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>8</td>
<td>0.001 ± 0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp 1.8°C</td>
<td>4</td>
<td>0.089 ± 0.009</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a-0.0079</td>
<td>33</td>
<td>3.192 ± 0.402</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-0.0096</td>
<td>20</td>
<td>2.072 ± 0.201</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>20</td>
<td>1.672 ± 0.180</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.R. × 24SR = 0.74</td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Greenland</th>
<th>Turbot</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (% W)</th>
<th>S = 1.737</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-3</td>
<td>32</td>
<td>1.329 ± 0.086</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>19</td>
<td>1.732 ± 0.146</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>30</td>
<td>2.843 ± 0.115</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>12</td>
<td>3.019 ± 0.084</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp 1.8°C</td>
<td>9</td>
<td>0.503 ± 0.072</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a-0.0143</td>
<td>18</td>
<td>0.766 ± 0.052</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-0.0176</td>
<td>26</td>
<td>0.337 ± 0.039</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>26</td>
<td>0.411 ± 0.033</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.R. × 24SR = 0.58</td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Greenland</th>
<th>Turbot</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (% W)</th>
<th>S = 1.712</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-3</td>
<td>11</td>
<td>3.260 ± 0.294</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>12</td>
<td>2.480 ± 0.271</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>18</td>
<td>3.370 ± 0.219</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>12</td>
<td>0.663 ± 0.066</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp 1.8°C</td>
<td>12</td>
<td>1.382 ± 0.078</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a-0.0143</td>
<td>19</td>
<td>0.894 ± 0.113</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-0.0176</td>
<td>26</td>
<td>0.133 ± 0.054</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>23</td>
<td>1.998 ± 0.093</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.R. × 24SR = 0.75</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Greenland</th>
<th>Turbot</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (% W)</th>
<th>S = 1.316</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-3</td>
<td>22</td>
<td>0.508 ± 0.036</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>18</td>
<td>2.334 ± 0.203</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>12</td>
<td>1.295 ± 0.307</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td>12</td>
<td>2.292 ± 0.437</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp 1.8°C</td>
<td>9</td>
<td>1.585 ± 0.364</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a-0.0079</td>
<td>17</td>
<td>0.635 ± 0.129</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-0.0096</td>
<td>40</td>
<td>0.778 ± 0.060</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>15</td>
<td>0.986 ± 0.118</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.R. × 24SR = 0.31</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Greenland</th>
<th>Turbot</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (% W)</th>
<th>S = 1.690</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-3</td>
<td>13</td>
<td>0.084 ± 0.023</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>22</td>
<td>0.887 ± 0.664</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-9</td>
<td>24</td>
<td>0.190 ± 0.019</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td>16</td>
<td>0.635 ± 0.071</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp 1.8°C</td>
<td>13</td>
<td>4.977 ± 0.262</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a-0.0143</td>
<td>23</td>
<td>0.411 ± 0.042</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-0.0176</td>
<td>48</td>
<td>1.345 ± 0.956</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21-24</td>
<td>7</td>
<td>4.942 ± 0.732</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.R. × 24SR = 0.71</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6.-- Mean stomach content weight as percent body weight (%BW ± standard error of mean) and daily ration (D.R.) calculations for Pacific cod.

<table>
<thead>
<tr>
<th>Time</th>
<th>Total no. of fish</th>
<th>Mean stomach content weight (%BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific</td>
<td></td>
<td></td>
</tr>
<tr>
<td>cod ≥55 cm</td>
<td>6-12</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>12-18</td>
<td>43</td>
</tr>
<tr>
<td>Autumn</td>
<td>18-24</td>
<td>12</td>
</tr>
<tr>
<td>Temp 3.0°C</td>
<td>a=0.0143</td>
<td>R=0.0202</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>S = 2.754</td>
<td>D.R. = 24SR = 1.33</td>
</tr>
<tr>
<td>Pacific</td>
<td></td>
<td></td>
</tr>
<tr>
<td>cod &lt;55 cm</td>
<td>4-8</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>8-12</td>
<td>22</td>
</tr>
<tr>
<td>Spring</td>
<td>12-16</td>
<td>14</td>
</tr>
<tr>
<td>Temp 2.5°C</td>
<td>a=0.0143</td>
<td>R=0.0104</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>S = 1.250</td>
<td>D.R. = 24SR = 0.31</td>
</tr>
</tbody>
</table>

Table 7.--Summary of daily ration estimates expressed as percent body weight daily (%BW/D) of key predators by size group and season in the eastern Bering Sea.

<table>
<thead>
<tr>
<th>Season</th>
<th>Flathead sole</th>
<th>Yellowfin sole</th>
<th>Arrowtooth flounder</th>
<th>Greenland turbot</th>
<th>Pacific cod</th>
<th>Walleye pollock</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;25 &lt;25</td>
<td>&lt;25 &lt;25</td>
<td>&lt;25 &lt;40</td>
<td>&lt;60 &lt;60</td>
<td>&gt;55 &gt;55</td>
<td>&lt;40 &gt;40</td>
</tr>
<tr>
<td>Spring</td>
<td>-- --</td>
<td>.11 .13</td>
<td>.58 .68</td>
<td>.22 .74</td>
<td>.31 --</td>
<td>.22 .27</td>
</tr>
<tr>
<td>Summer</td>
<td>.12 .12</td>
<td>.13 .11</td>
<td>.61 .63</td>
<td>.58 .75</td>
<td>-- --</td>
<td>.41 .46</td>
</tr>
<tr>
<td>Autumn</td>
<td>-- --</td>
<td>-- --</td>
<td>-- --</td>
<td>.31 .71</td>
<td>-- 1.33</td>
<td>.36 .29</td>
</tr>
<tr>
<td>Winter</td>
<td>-- --</td>
<td>-- --</td>
<td>.02 .12</td>
<td>-- --</td>
<td>-- --</td>
<td>.04 .26</td>
</tr>
</tbody>
</table>

1/ From Dwyer (1984).
Table 8.—Estimates of population level consumption of commercially important prey items, walleye pollock and Tanner crab, during spring by key predators in the eastern Bering Sea using daily ration, diet population biomass estimates. (BRWD = percent body weight daily). (Where 1/100 x (2/100 x (3) x 3) x 91.25 = (4); and 91.25 is the number of days per season.)

<table>
<thead>
<tr>
<th>Predator</th>
<th>Daily ration (BRWD)</th>
<th>Pollock consumption (% total stomach content weight)</th>
<th>Crab consumption (% total stomach content weight)</th>
<th>Predator biomass (1000 t)</th>
<th>Population consumption of pollock (1000 t)</th>
<th>Population consumption of crab (1000 t)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1)</td>
<td>(2a)</td>
<td>(2b)</td>
<td>(3)</td>
<td>(4a)</td>
<td>(4b)</td>
</tr>
<tr>
<td>Yellowfin sole</td>
<td>&gt;25 cm</td>
<td>0.11</td>
<td>--</td>
<td>--</td>
<td>1580.62/</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>&gt;25 cm</td>
<td>0.16</td>
<td>--</td>
<td>--</td>
<td>1720.0</td>
<td>--</td>
</tr>
<tr>
<td>Arrowtooth flounder</td>
<td>&lt;40 cm</td>
<td>0.58</td>
<td>--</td>
<td>--</td>
<td>44.52/</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>&gt;40 cm</td>
<td>0.88</td>
<td>39.56</td>
<td>--</td>
<td>44.5</td>
<td>14.14</td>
</tr>
<tr>
<td>Greenland turbot</td>
<td>&lt;60 cm</td>
<td>0.21</td>
<td>10.65</td>
<td>--</td>
<td>62.42/</td>
<td>1.37</td>
</tr>
<tr>
<td></td>
<td>&gt;60 cm</td>
<td>0.74</td>
<td>61.12</td>
<td>--</td>
<td>62.4</td>
<td>25.75</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>&lt;55 cm</td>
<td>0.31</td>
<td>--</td>
<td>10.38</td>
<td>243.02/</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>&gt;55 cm</td>
<td>0.66       /</td>
<td>17.45</td>
<td>6.07</td>
<td>757.0</td>
<td>79.55</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>&lt;40 cm</td>
<td>0.22       /</td>
<td>1.02</td>
<td>0.03</td>
<td>6090.02/</td>
<td>12.47</td>
</tr>
<tr>
<td></td>
<td>&gt;40 cm</td>
<td>0.27</td>
<td>1.99</td>
<td>--</td>
<td>4604.0</td>
<td>22.57</td>
</tr>
<tr>
<td><strong>Season total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>155.75</strong></td>
<td><strong>35.17</strong></td>
</tr>
</tbody>
</table>

2/ 1982 U.S.-Japan cooperative trawl survey data from Bakkala (1984a) assuming 50% of the biomass is <40 cm.
3/ 1982 U.S.-Japan cooperative trawl survey data from Bakkala (1984a) assuming 50% of the biomass is >60 cm.
4/ No daily ration information available for spring so spring ration is assumed to be 50% of autumn ration.

Table 9.—Estimates of population level consumption of commercially important prey items, walleye pollock and Tanner crab, during summer by key predators in the eastern Bering Sea using daily ration, diet population biomass estimates. (BRWD = percent body weight daily). (Where 1/100 x (2/100 x (3) x 91.25 = (4); and 91.25 is the number of days per season.)

<table>
<thead>
<tr>
<th>Predator</th>
<th>Daily ration (BRWD)</th>
<th>Pollock consumption (% total stomach content weight)</th>
<th>Crab consumption (% total stomach content weight)</th>
<th>Predator biomass (1000 t)</th>
<th>Population consumption of pollock (1000 t)</th>
<th>Population consumption of crab (1000 t)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1)</td>
<td>(2a)</td>
<td>(2b)</td>
<td>(3)</td>
<td>(4a)</td>
<td>(4b)</td>
</tr>
<tr>
<td>Flathead sole</td>
<td>&lt;25 cm</td>
<td>0.12</td>
<td>18.61</td>
<td>0.57</td>
<td>170.42/</td>
<td>3.47</td>
</tr>
<tr>
<td></td>
<td>&gt;25 cm</td>
<td>0.12</td>
<td>22.25</td>
<td>2.33</td>
<td>170.4</td>
<td>4.15</td>
</tr>
<tr>
<td>Yellowfin sole</td>
<td>&lt;25 cm</td>
<td>0.13</td>
<td>--</td>
<td>0.05</td>
<td>1580.0</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>&gt;25 cm</td>
<td>0.11</td>
<td>1.51</td>
<td>2.82</td>
<td>1720.0</td>
<td>2.61</td>
</tr>
<tr>
<td>Arrowtooth flounder</td>
<td>&lt;40 cm</td>
<td>0.61</td>
<td>61.93</td>
<td>0.03</td>
<td>44.5</td>
<td>15.83</td>
</tr>
<tr>
<td></td>
<td>&gt;40 cm</td>
<td>0.63</td>
<td>56.55</td>
<td>--</td>
<td>44.3</td>
<td>14.47</td>
</tr>
<tr>
<td>Greenland turbot</td>
<td>&lt;60 cm</td>
<td>0.58</td>
<td>25.53</td>
<td>--</td>
<td>62.4</td>
<td>8.43</td>
</tr>
<tr>
<td></td>
<td>&gt;60 cm</td>
<td>0.75</td>
<td>75.42</td>
<td>--</td>
<td>62.4</td>
<td>32.21</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>&lt;55 cm</td>
<td>0.62       /</td>
<td>1.64</td>
<td>45.41</td>
<td>243.0</td>
<td>2.25</td>
</tr>
<tr>
<td></td>
<td>&gt;55 cm</td>
<td>1.33</td>
<td>43.05</td>
<td>11.17</td>
<td>757.0</td>
<td>395.51</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>&lt;40 cm</td>
<td>0.42       /</td>
<td>--</td>
<td>0.06</td>
<td>6090.0</td>
<td>1.14</td>
</tr>
<tr>
<td></td>
<td>&gt;40 cm</td>
<td>0.46</td>
<td>50.25</td>
<td>--</td>
<td>4604.0</td>
<td>10.64</td>
</tr>
<tr>
<td><strong>Season total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>489.57</strong></td>
<td><strong>171.70</strong></td>
</tr>
</tbody>
</table>

1/ 1984 U.S. research trawl survey estimate from Bakkala (1984b) and assuming 50% of the biomass is <25 cm.
2/ Assuming daily ration of small cod in summer is twice the spring value, and daily ration of large cod is the same as in autumn.
Table 10.—Estimates of population level consumption of commercially important prey items, walleye pollock and Tanner crab, during autumn by key predators in the eastern Bering Sea using daily ration, diet population biomass estimates. (%BWD = percent body weight daily). (Where (1/100 x (2/100 x (3) x 91.25 x (4); and 91.25 is the number of days per season.)

<table>
<thead>
<tr>
<th>Predator</th>
<th>Daily ration (BWD)</th>
<th>Pollock consumption (% total stomach content weight)</th>
<th>Crab consumption (% total stomach content weight)</th>
<th>Predator biomass (1000 t)</th>
<th>Population consumption of pollock (1000 t)</th>
<th>Population consumption of crab (1000 t)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Autumn</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arrowtooth flounder</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;40 cm</td>
<td>0.12</td>
<td>65.95</td>
<td>--</td>
<td>44.5</td>
<td>2.21</td>
<td>--</td>
</tr>
<tr>
<td>Greenland turbot</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;60 cm</td>
<td>0.30</td>
<td>20.34</td>
<td>--</td>
<td>62.4</td>
<td>3.47</td>
<td>--</td>
</tr>
<tr>
<td>&gt;60 cm</td>
<td>0.71</td>
<td>46.57</td>
<td>--</td>
<td>62.4</td>
<td>18.83</td>
<td>--</td>
</tr>
<tr>
<td>Pacific cod</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;55 cm</td>
<td>0.62/</td>
<td>2.09</td>
<td>28.55</td>
<td>243.0</td>
<td>2.87</td>
<td>40.62</td>
</tr>
<tr>
<td>&gt;55 cm</td>
<td>1.33</td>
<td>27.10</td>
<td>6.00</td>
<td>757.0</td>
<td>248.97</td>
<td>55.12</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;40 cm</td>
<td>0.36/</td>
<td>41.51</td>
<td>0.05</td>
<td>6090.0</td>
<td>830.43</td>
<td>1.00</td>
</tr>
<tr>
<td>&gt;40 cm</td>
<td>0.29</td>
<td>57.17</td>
<td>0.13</td>
<td>4604.0</td>
<td>695.30</td>
<td>1.58</td>
</tr>
<tr>
<td><strong>Season total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>1803.08</strong></td>
<td><strong>98.32</strong></td>
</tr>
</tbody>
</table>

/ Assuming daily ration for <55 cm cod is the same as summer.


Table 11.—Estimates of population level consumption of commercially important prey items, walleye pollock and Tanner crab, during winter by key predators in the eastern Bering Sea using daily ration, diet population biomass estimates. (%BWD = percent body weight daily). (Where (1/100 x (2/100 x (3) x 91.25 x (4); and 91.25 is the number of days per season.)

<table>
<thead>
<tr>
<th>Predator</th>
<th>Daily ration (BWD)</th>
<th>Pollock consumption (% total stomach content weight)</th>
<th>Crab consumption (% total stomach content weight)</th>
<th>Predator biomass (1000 t)</th>
<th>Population consumption of pollock (1000 t)</th>
<th>Population consumption of crab (1000 t)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Winter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific cod</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;55 cm</td>
<td>0.31/</td>
<td>--</td>
<td>8.99</td>
<td>243.0</td>
<td>--</td>
<td>6.18</td>
</tr>
<tr>
<td>&gt;55 cm</td>
<td>0.86</td>
<td>52.49</td>
<td>5.62</td>
<td>757.0</td>
<td>239.30</td>
<td>25.62</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;40 cm</td>
<td>0.04/</td>
<td>--</td>
<td>0.10</td>
<td>6090.0</td>
<td>--</td>
<td>0.22</td>
</tr>
<tr>
<td>&gt;40 cm</td>
<td>0.26</td>
<td>64.37</td>
<td>0.12</td>
<td>4604.0</td>
<td><strong>703.11</strong></td>
<td><strong>1.21</strong></td>
</tr>
<tr>
<td><strong>Season total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>942.41</strong></td>
<td><strong>33.11</strong></td>
</tr>
<tr>
<td><strong>Annual total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>1390.81</strong></td>
<td><strong>338.52</strong></td>
</tr>
</tbody>
</table>

/ Assuming daily ration for cod in winter is 50% of cod daily ration in autumn.

pollock than crab was consumed during each season. The largest amount of crab consumed was during summer. Cod were the main source of crab predation throughout the year. During spring and summer, cod were also the main source of removal of walleye pollock. Pollock cannibalism during autumn accounted for most pollock predation mortality during that season. Although arrowtooth flounder and Greenland turbot diets contained large proportions of pollock, their low population biomass makes their pollock consumption seem small relative to the amounts consumed by pollock and cod.

Tables 12 and 13 summarize the population consumption of each key predator relative to the total population consumption by all key predators and relative to the total amount of available pollock and crab prey. About 69% by weight of the total annual amount of pollock consumed is consumed by pollock (Table 12). Large cod account for 28% by weight of pollock consumed. In total, all key predators consume about 56% by weight of the available population biomass of prey pollock (assuming most pollock consumed are <40 cm).

Cod account for almost 97% by weight of the total Tanner crab consumption during the year by key predator species (Table 13). Even though the diet of small cod is dominated by crustaceans and crab in particular, the larger biomass of cod >50 cm causes the estimate of their pollock consumption of crab to be higher than that for small cod. The total crab consumption estimate of 338.5 (1000 t) is almost three times as large as the estimate of available Tanner crab obtained from the eastern Bering Sea research surveys of 1984.

DISCUSSION

Feeding Behavior

Flathead sole appears to be a benthic and pelagic feeder because at times it consumed mostly benthic invertebrates such as brittle stars while some of its other prey are nektic species such as shrimp, euphausiids and fish. Similar feeding behavior was reported by Mito (1974) and Mineva (1964).

In some seasons, yellowfin sole depends almost totally on benthic fauna such as clams for its food. These fish may also rise in the water column to seek prey such as fish (Wakabayashi 1974) and crab larvae (Haflinger and Roy 1983).

Arrowtooth flounder seem to feed almost predominantly off the bottom. Its major prey item is fish, most of which is pollock. Squid and shrimp are also consumed. Mito (1974) found similar trends in arrowtooth flounder feeding behavior in the eastern Bering Sea.

Greenland turbot also feeds off the bottom, consuming mostly squid and pollock. Mito (1974) and Mikawa (1963) also noted fish and squid as major prey items.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Annual pollock consumption (1000 t)</th>
<th>Percent of total pollock consumed</th>
<th>Percent of available walleye pollock prey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>≤25 cm</td>
<td>2.61</td>
<td>≤0.1</td>
</tr>
<tr>
<td></td>
<td>≥25 cm</td>
<td></td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Flathead sole</td>
<td>≤25 cm</td>
<td>3.47</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>≥25 cm</td>
<td>4.15</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Arrowtooth flounder</td>
<td>≤40 cm</td>
<td>15.80</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>≥40 cm</td>
<td>31.82</td>
<td>0.5</td>
</tr>
<tr>
<td>Greenland turbot</td>
<td>≤60 cm</td>
<td>13.17</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>≥60 cm</td>
<td>76.79</td>
<td>2.3</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>≤55 cm</td>
<td>9.12</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>≥55 cm</td>
<td>963.33</td>
<td>28.4</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>≤40 cm</td>
<td>842.90</td>
<td>29.4</td>
</tr>
<tr>
<td></td>
<td>≥40 cm</td>
<td>1431.62</td>
<td>45.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>55.6</td>
</tr>
</tbody>
</table>

Assuming most pollock consumed were ≤40 cm (Livingston et al. 1985) and the 1982 biomass of pollock ≤40 cm was 6090 (1000 t) (Banks et al. 1984).

<table>
<thead>
<tr>
<th>Predator</th>
<th>Annual Tanner crab consumption (1000 t)</th>
<th>Percent of total Tanner crab consumed</th>
<th>Percent of available Tanner crab prey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowfin sole</td>
<td>≤25 cm</td>
<td>0.09</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td></td>
<td>≥25 cm</td>
<td>4.87</td>
<td>1.4</td>
</tr>
<tr>
<td>Flathead sole</td>
<td>≤25 cm</td>
<td>0.11</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td></td>
<td>≥25 cm</td>
<td>0.43</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Arrowtooth flounder</td>
<td>≤40 cm</td>
<td>0.02</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td></td>
<td>≥40 cm</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Greenland turbot</td>
<td>≤60 cm</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>≥60 cm</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>≤55 cm</td>
<td>116.36</td>
<td>34.4</td>
</tr>
<tr>
<td></td>
<td>≥55 cm</td>
<td>211.05</td>
<td>62.0</td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>≤40 cm</td>
<td>2.72</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>≥40 cm</td>
<td>2.89</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>338.52</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Assuming total available (recruits and pre-recruits) Tanner crab Chionocephalus spp. is assumed to be 129.5 (1000 t) (Otto et al. 1984).
Pacific cod feed on benthic prey such as crab and polychaetes when small (<55 cm) and switch to pollock prey with increasing cod size. Most other studies found identical changes in diet with cod size. Shimada and June (1982) report that the percentage of pollock in cod diets increased from about 15% in cod <45 cm to up to 60% in cod >65 cm in length. Mito (1974) found cod <50 cm long ate more shrimp and crab while cod >50 cm consumed mostly pollock.

Walleye pollock feeds pelagically in all seasons. Euphausiids and copepods dominate the diet in spring and summer and fish (mostly pollock) is consumed in autumn and winter. Takahashi and Yamauchi (1972), Mito (1974) and Bailey and Dunn (1979) also reported major prey items of pollock to be pollock and euphausiids.

**Diet Overlap**

Most dietary overlap observed during spring was very low. Intermediate dietary overlap was mostly intraspecific, or between two different size groups of the same species. In other seasons, intermediate diet overlap values were observed between several species which utilized juvenile pollock as prey.

Intermediate or high diet overlap values do not necessarily indicate high interspecific competition for prey. Predator populations may be segregated in time or space. This is partly true for the distributions of key predator species during summer in the eastern Bering Sea. The major areas of Greenland turbot abundance are at the slope while arrowtooth flounder are found at the slope and outer shelf areas. The center of abundance for yellowfin sole is in the shallower inshore regions while pollock and cod are more evenly distributed over shelf and slope regions.

Additionally, these predators may be opportunistically consuming a common prey item (pollock) that is very abundant. This also appears to be true as the walleye pollock resource constitutes about 50% of the groundfish biomass in the eastern Bering Sea and Aleutian Islands region. All of these predators exhibit evidence of prey switching in different seasons and thus are not extremely specialized feeders which must depend solely on one prey item as a food source.

**Daily Ration**

Daily ration values exhibited a trend by species: yellowfin sole and flathead sole had the lowest values, pollock had intermediate values and arrowtooth flounder, Greenland turbot and Pacific cod had the highest daily ration estimates. This trend seems reasonable as small, slow-growing fish should require less food than larger, faster-growing species.

In general, daily ration values for marine fish in warmer northwest and northeast Atlantic and North Pacific waters (6 to 12°C) range from about 0.6 to 4.6% BWD (Daan 1973; Durbin et al. 1983; Livingston 1983; Huebner and Langton 1982). The values presented here are lower partly due to the lower temperatures encountered in the eastern Bering Sea. Some of the values within a specific species (Table 7) however, seem somewhat inconsistent. For example, daily ration of arrowtooth flounder in autumn was 0.12% BWD while spring and summer rations were between 0.6 and 0.9% BWD. Insufficient sample sizes to partition rations calculations into 3-h intervals might cause error in ration estimates. An additional source of error which could cause low daily ration estimates would be the collection by inexperienced biologists of stomachs from fish which have regurgitated their stomach contents. This latter problem may be a real one as collections in spring, autumn, and winter are often made by less experienced persons. It may be necessary to provide independent estimates of the percentage of truly empty stomachs by 3-h interval for each season from samples collected by experienced biologists in order to verify or correct this type of bias.

This method of estimating daily ration from stomach content weights and gastric evacuation rates has also been used in the ICES North Sea predation study and has produced values there which seem low when compared to food intake estimates based on energetic requirements (Anonymous 1984). Table 14 compares the present daily ration results with daily ration estimates based on bioenergetic calculations which use observed growth increments of key fish species. Some of the values obtained from stomach content weights must be underestimates as they result in impossibly high conversion efficiencies. This at least provides some assurance that daily rations based on actual stomach content weights are conservative.

**Population Consumption**

In terms of biomass consumed, walleye pollock and Pacific cod are the major sources of predation mortality for walleye pollock. Previous studies have shown, however, that the size or age of pollock consumed can vary with the species and species size group of the predator (Mito 1974; Dwyer 1984; Livingston et al. 1985). For instance pollock, flathead sole, and small arrowtooth flounder consume mostly 0 to 1 yr old pollock. Large arrowtooth flounder, Greenland turbot, and Pacific cod consume prey pollock which range from 0-age to 4+ year olds. Sources of predation mortality, if expressed as numbers consumed by age of pollock, may be higher for predators which concentrate on 0 to 1 yr old pollock for prey.

Similarly for Tanner crab, Pacific cod was the major source of biomass removal through predation. Cod consumed Tanner crab which had an average carapace width of 18 mm (range 4 to 58 mm). The next major predator of Tanner crab was yellowfin sole which consumed crab 12 mm carapace width or
less. Haflinger and Roy (1983) reported yellowfin sole preying on crab larvae which, if it were expressed in age-specific mortality in numbers of crab, might be shown to have a larger impact on larval and pre-recruit Tanner crab than the crab predation by Pacific cod.

The estimate of total biomass of crab consumed by key predators was shown to be almost three times the estimated standing stock of recruit and pre-recruit Tanner crab in the eastern Bering Sea. Thus, the current results should be viewed with a high degree of skepticism until more detailed data analysis is performed. Several sources of error are present in these calculations. Relatively small numbers of cod stomachs were analyzed for estimating the proportions by weight of prey in the diet. Also these proportions were assumed to be representative over the whole eastern Bering Sea region which may not be true as crab consumption may only take place in certain subregions. When more samples are analyzed, breakdown of diet by various areas in the eastern Bering Sea may provide more accurate results. Finally, research trawl surveys designed primarily for estimating groundfish biomass may not provide the best survey design for estimating standing stocks of crab and thus the population biomass estimates for crab might not be very accurate.

CONCLUSIONS

Key predator species in the eastern Bering Sea utilize different feeding strategies for obtaining prey. Some are more benthic feeders, while others feed strictly pelagically, and some utilize a combination of benthic and pelagic prey.

Intermediate to high diet overlap occurs between most species during summer. Competition for scarce food resources seems doubtful as these key predators do not overlap spatially in some areas and may utilize different sizes of common prey. Since these predators are able to consume different prey in some other seasons, they are probably taking advantage of the large abundance of certain prey, such as juvenile pollock, during summer and autumn.

Some key predators such as walleye pollock and Pacific cod are considerable sources of biomass removal of young pollock and crab. Although seemingly small in terms of total biomass consumed, the predation impact of predators such as yellowfin sole and flathead sole which consume smaller sizes of prey may be a significant source of predation mortality in terms of numbers at younger stages of development of walleye pollock and Tanner crab.

Further improvements in the present work include; stomach analysis of more specimens, better seasonal and areal picture of food composition, further verification of daily ration estimates, and partitioning predation mortality by size or age of prey.

This latter analysis, the computation of predation mortality by age, is one of the major goals of the Trophic Interactions Program at NWFSC. These predation mortalities are not new, additional sources of natural mortality but are, for some age groups of fish, the main part of natural mortality which has been poorly estimated for younger age groups of fish in the past. Recent similar calculations by Daan (1985) show that predation mortality for 0 to 1 year old roundfish stocks in the North Sea is much higher than was previously assumed and varied considerably from year to year probably due to changes in the abundance of predator stocks. The ultimate goal is the improve management strategies by pinpointing major sources of commercial fish predation mortality and perhaps managing these species as a group using the knowledge of the strength of fish trophic interactions with economic considerations to make informed choices about catch limits of various species in the group. Although these predation mortalities represent only minimum estimates of natural mortality, as also cautioned by Daan (1985), since unknown sources of natural mortality occurring during very early life history stages are not included, they do provide us with knowledge about the degree of interaction through predation between commercial fish stocks. Although it may be important to identify physical factors which affect recruitment in order to improve our predictions, it is the interaction through predation that may allow us to control and manage predator stocks through changes in fishing pressure on trophically linked populations.

LITERATURE CITED


Bakkala, R. G. 1984b. Other flatfish. Ibid.


RELATIVE IMPACT OF PACIFIC HAKE, SABLEFISH AND PACIFIC COD ON WEST COAST OF VANCOUVER ISLAND HERRING STOCKS

by

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ABSTRACT

Stocks of Pacific herring off the west coast of Vancouver Island have experienced a 6 year run of below average recruitment and are currently near the historic low in abundance they reached in the late 1960s. A preliminary analysis of reconstructed time series of Pacific hake, sablefish and Pacific cod from 1960-81 showed that west coast of Vancouver Island herring year-class strength is correlated with the biomass and estimated annual food rations of these predators. Our results suggest that juvenile herring survival is most sensitive to variations in the biomass of adult Pacific hake. Juvenile sablefish may be important predators of juvenile herring at times, like the large 1977 year-class, but in the long run, like juvenile Pacific cod, they are probably less influential than hake. Our analysis indicates that west coast of Vancouver Island herring year-class strength has a strong negative correlation with oceanographic conditions, measured as annual sea surface temperatures. The biological interpretation of this correlation is not clear, but it may reflect a northward extension in the distribution of hake with rising temperatures, coupled with an increase in the incidence of herring in the diet. Alternatively, it could be caused by an increase in predation pressure by other piscivorous species like dogfish, lingcod and Pacific salmon, or a combination of these and other factors. A rough calculation suggested that the combined operations of adult Pacific hake, Pacific cod and sablefish can consume 22-42 thousand tonnes of adult herring, on average. This is equivalent to 29-54% of the adult herring biomass and is sufficient to account for the average annual mortality rate of 36%. A multi-disciplinary research project on the continental shelf off the lower west coast of Vancouver Island has been initiated to collect a time series of relevant oceanographic and fisheries data to test some of these hypotheses.

INTRODUCTION

Pacific herring off the west coast of Vancouver Island have declined steadily in abundance since the mid 1970s and are currently near the historical low they attained in the late 1960s. This recent decline has occurred following six consecutive years of poor recruitment. As a consequence, the herring fishery in this area was closed in 1985 and 1986. Between 1960-81 there have been major fluctuations in the abundance of three offshore herring predators: Pacific hake, Pacific cod, and sablefish. Concurrently the region has also experienced strong anomalies in oceanographic conditions (Thomson et al. 1984) that may have changed the abundance and distribution of the planktonic organisms herring normally feed on, and the distribution of their principal predators. During two previous episodes of above average sea surface temperatures in the early 1940s and 1960s west coast of Vancouver Island herring also experienced poor recruitment.

The primary objective of the work summarized in this paper, was to determine if year-class strength of the west coast herring stock is correlated with the estimated rations of known predator populations, and recent oceanographic conditions reflected in the annual sea surface temperatures. A secondary objective was to determine if Pacific hake, Pacific cod and sablefish have had a significant impact on adult herring over the last 25 years.

SPECIES DESCRIPTIONS AND DATA SOURCES

Pacific hake (Merluccius productus)

The main concentration of Pacific hake in the Canadian zone is found off the west coast of Vancouver Island (Fig. 1). These are mostly migratory fish which enter the Canadian zone, from the south, in late spring and leave in the fall (Francis 1983; Beamish and McFarlane 1985). In some years, like 1983, large numbers of hake were found off the northern tip of Vancouver Island. The timing of the hake migration into, and out of, the Canadian zone varies. Commercial concentrations have occurred in the area as early as February-March and as late as November-December. However, in most years large quantities are present from mid-June until late October (Beamish and McFarlane 1985).

Hake stratify along a north-south gradient according to size with older, larger, predominantly female fish in the Canadian zone. In most years the majority of the fish (85 to 97%) in this component of the stock range in age from 5 to 12 years. Recently, young hake (age 4) have appeared in the age structure due to the
recruitment of the strong 1980 year-class to the Canadian fishery. These strong year-classes are a dominant feature of hake population dynamics and have occurred about every 3 years since the early 1960s (Beamish and McFarlane 1985). Variations in abundance off the west coast of Vancouver Island reflect the size and time of recruitment of these strong year-classes, and changes in the northern extension of the summer feeding range, presumably due to oceanographic conditions.

Pacific hake consume large quantities of euphausiids and fish, particularly Pacific herring, off Vancouver Island. Outram and Haegeli (1972) found that euphausiids occurred in 94% and herring in 5% of hake stomachs examined in August 1970. These figures indicate the frequency of occurrence by numbers and not by weight, which was not measured. Herring were of greater importance (about 15%) in the diet of larger hake. Similarly, Jackowski (cited by Bailey et al. 1982) found that the two principal prey, euphausiids and Pacific herring, comprised 86% and 12% respectively of the diet of hake (by weight) in the summer of 1979. In a sample of 555 hake caught offshore in late August 1983, herring made up 59% of the diet (by weight) and euphausiids 37% (Shaw et al. 1985). These observations demonstrate that the proportion of herring in the hake diet varies significantly, probably due to inter-annual changes in relative availability of the two principal prey.

To estimate the annual food ration of Pacific hake we require information on stock biomass and mean fish weight. For the 1960-81 period, hake stock biomass data were obtained from Francis et al. (1984). Based on historical catch information, 25% of the total U.S./Canadian stock was assumed to spend the summer off the west coast of Vancouver Island below 49°N latitude. Mean body weights were obtained from age-frequency, and weight-at-age data for 1976, and 1978-82 (McFarlane et al. 1985a). A constant mean age (9 yr) and body weight (1183 g) was assumed for 1960-75 and 1977 because there were no sampling data.

Sablefish (Anoplopoma fimbria)

Adult sablefish are present along the entire west coast of British Columbia at depths exceeding 200 m, and are most abundant between 400-1800 m (McFarlane and Beamish 1983). Spawning occurs from January to March along the entire coast in deep water (>300 m). After hatching, the young move to the surface and are found in water <200 m by mid-summer. Juvenile sablefish remain in these shallower waters until approximately age 3 when they begin to recruit to the adult population. From approximately June to November juvenile sablefish are found on the major banks off the west coast of Vancouver Island. During the winter, they move seaward into deeper water (100-200 m).

Year-class success in sablefish is variable: average year-class abundance is roughly twice that of a poor year-class (McFarlane et al. 1985b). However, periodic very strong year-classes may be 5-10 times greater in abundance (McFarlane et al. 1985b). Juvenile sablefish grow very rapidly: the strong 1977 year-class averaged 28 cm in fork length in November (age 0+) and 40 cm by the end of their second year of growth (age 1+).

There is little information on the food habits of sablefish off the west coast of Vancouver Island, but the existing data indicate that euphausiids and Pacific herring are important, comprising about 94% and 5% respectively of the diet (by weight) in September 1977. More recent information suggests that the percentage of herring in the diets of juvenile and adult sablefish displays considerable seasonal and inter-annual variability (McFarlane, unpubl. data).

To estimate the annual food consumption of sablefish, we assumed that 20% of the stock resides off the lower west coast of Vancouver Island. Information on mean fish weight in the adult component of the stock (ages 3-35) was not available for 1960-78 and was therefore taken to be constant, and equal to the mean body weight (2236 g) during the 1979-82 period where annual sampling data are available. The biomass of juvenile sablefish (ages 1 and 2) was estimated by taking the ratio of McFarlane et al.'s (1985b) virtual population analysis estimates (VPA) of age-4 abundance, and McFarlane and Beamish's (1983) relative abundance estimates for the 1973, 1974 and 1975 year-classes. The resulting ratio was used to estimate the abundance of age-4 sablefish for the 1960-75 year-classes. Twenty percent of these fish were assumed to be off the lower west coast of Vancouver Island. The corresponding abundances at ages 1, 2 and 3 were obtained by back-calculation assuming an instantaneous annual mortality rate M = 1.0. We acknowledge that these estimates are crude, particularly since tagging studies of the strong 1977 year-class have shown considerable northward migration of age 2+ and 3+ juveniles out of the rearing area (Beamish and McFarlane 1983), however, they do allow us to examine trends in juvenile abundance and food consumption.

Pacific cod (Gadus macrocephalus)

Pacific cod is a fast growing, short-lived species which undergoes extreme fluctuations in abundance. Spawning occurs from January to March off Vancouver Island, where the main spawning ground is on Amphitrite Bank (Fig. 1). From April to September adult cod are found primarily on La Perouse and Swiftsure banks. The stock has undergone a steady decline in abundance in this area since 1972-73, and is currently at a very low level of abundance.

The feeding habits of Pacific cod in the area have been studied by Westheim...
and Harling (1983). Looking at average percent frequency of food in Pacific cod stomachs, they found that the principal prey were sand lance (in 59% of stomachs), herring (in 43%) and euphausiids (in 19%). Seasonally, the occurrence of herring in cod stomachs was maximal (75-100%) during the July-December period.

Since roughly half the male Pacific cod are mature by age-2, we considered age-2 fish to be part of both the adult, and juvenile components of the stock for our analysis. Biomass estimates for the adult stock off the west coast of Vancouver Island were obtained by multiplying VPA estimates of numbers-at-age and mean body weight-at-age (Westheim and Poucher 1985). Mean fish weight was calculated by dividing the annual stock biomass by the corresponding estimate of total abundance. The mean weight from 1960 to 1981 was 1994 g. The biomass of age-1 Pacific cod was obtained by dividing VPA estimates of abundance at age-2 by the assumed annual survival rate of 0.55, and then multiplying by the mean weight at age-2.

Pacific herring (Clupea harengus pallasi). Pacific herring spawn in protected, inshore waters along the west coast of Vancouver Island in February and March. After hatching the larvae and juveniles remain in these coastal embayments until late summer and fall of their first year of life, at which time they begin moving to offshore feeding grounds (Koolstra 1983). After remaining offshore for about 2 years until they recruit to the spawning stocks as mature adults in their third year. It is during this phase of their life cycle that pre-recruit (or juvenile) herring are vulnerable to offshore predators, and other vicissitudes associated with living on a dynamic continental shelf.

Adult herring tend to be present in greatest numbers near the southeast and southwest corners of La Perouse Bank at depths of 100-110 m. Juveniles (ages 1+ and 2+) usually are not found on the major fishing banks, but occasionally have been located at greater depths (140-200 m) seaward of La Perouse Bank (Miller 1979; Taylor 1984). In this context, Taylor and Kieser (1982) observed that although there was a tendency for fish north of Amphitrite Point in the fall to be mainly 2-yr-olds, the age groups were not segregated by area. In a later study, Taylor (1984) observed that there was considerable inner-annual variation in the seasonal movements and distribution of herring and other offshore pelagic species.

Estimates of year-class strength and adult (age 3+) biomass for the west coast of Vancouver Island herring stock were obtained from Haist et al. (1985).

RESULTS

PREDATOR BIOMASS AND RATIONS

The average biomass of juvenile and adult predator stocks between 1960 and 1981 is given in Table 1. In terms of absolute biomass, Pacific hake are 20 to 33 times more abundant than adult sablefish and Pacific cod, respectively, and therefore have the greatest potential to affect herring mortality. The annual rations of the stocks were estimated by using a production to biomass ratio approach, because the data were too fragmentary to support a more sophisticated calculation. The annual food ration \( R_i \) of predator stock \( i \) can be defined as follows:

\[
R_i = \frac{P_i}{K_i}
\]

(1)

where

- \( P_i \) = annual production of stock \( i \) (which includes somatic growth, reproductive output and survival).
- \( K_i \) = production efficiency (dimensionless).

\( P_i \) was estimated from a P/B ratio calculated from data given by McFarlane and Beamish (1983; Table 7) for sablefish:

\[
P_i / B_i = 3.45 W_i^{-0.36}
\]

(2)

where \( W_i \) = mean body weight (g) of fish in stock \( i \), \( B_i \) = mean biomass of stock \( i \) (tonnes). It is worth noting that, as a first approximation, eq. (2) also provides an acceptable P/B estimate for other commercial groundfish stocks. For example, Francis (1983) calculated a P/B ratio of 0.35 for Pacific hake with a mean fish weight of 594 g; eq. (2) yields the same result. Similarly, McKinnon (1973) obtained a P/B = 0.40 for 360 g plaice, the corresponding estimate from eq. (2) is 0.41.

The production, or growth, efficiency \( K \) was derived by averaging results given by Jones (1976) and Ware (1978). Average values for the parameters describing how \( K \) scales with body weight were chosen because in our opinion, Jones' (1976) figures, which are based on laboratory studies, may be too high for natural populations that presumably have greater metabolic expenses for food search, seasonal migrations, and other routine activities. In contrast, the values given by Ware (1978) were based on theoretical considerations of wild fish exposed to average feeding conditions, and therefore could be a bit low. Assuming reality lies somewhere between these two possibilities we obtained the following relationship:

\[
K_i = 0.42 W_i^{-0.1}
\]

(3)

Substituting eq. (2), and (3) into (1) yields
Eq. (4) was used to estimate the amount of food consumed, annually, by each stock. The results for the adult predators are shown in Figure 2. For comparison, Figure 3 shows the estimated total ration consumed by successive year-classes of juvenile sablefish and Pacific cod during their second and third growing seasons (ages 1+ and 2+). On average, the annual rations of the adult predator stocks are approximately equal to their respective biomasses (i.e., a 1:1 ratio), whereas for the juvenile component of the stocks the ratio is more like 1:7:1 for sablefish, and 1:3:1 for age-1 Pacific cod.

HERRING YEAR-CLASS STRENGTH

The variation in herring year-class strength between 1971 and 1981 is shown in Figure 2. To try to explain the observed pattern we tested the hypothesis that prerecruit herring mortality is determined largely by the juvenile component of the sablefish and Pacific cod stocks. Table 2 summarizes the results of the linear regression analysis where the annual sea surface temperature at Amphitrite Point was also included as an independent variable. The only biologically meaningful correlation was with the juvenile sablefish ration, which is negatively correlated with herring year-class strength, explaining 20% of the variation (P<0.05). Sea surface temperature accounted for an additional 18% of the variance, which is suggestive, but not sufficient to make the contribution of this variable statistically significant (P>0.05). The correlation between the annual ration of juvenile Pacific cod and herring year-class strength was positive which would seem to disprove the notion that Pacific cod has a significant negative impact on the survival of west coast of Vancouver Island juvenile herring. In fact, the correlations indicate that in this area both juvenile herring and cod survival tend to respond positively to the same environmental conditions, in the sense that both species produced large year-classes in the late 1960s and early 1970s, and have produced considerably smaller year-classes since.

The hypothesis that juvenile herring survival is more sensitive to predation from the adult components of the stocks was also tested by linear regression analysis (Table 3). Biologically, the most meaningful correlation was with the adult hake ration and sea surface temperature, which, respectively, explain 12% and 35% (for a total of 47%) of the variance in herring year-class strength (Fig. 4). The amount of variation explained by each variable is statistically significant at the 5% level. The highest multiple correlation coefficient was with a 2-year lag (R² = 0.46) in adult hake ration, whereas herring year-class strength in year T was regressed against the estimated hake ration in year T + 1. Because the multiple correlation coefficient was significantly smaller (R² = 0.37) with a two year lag in the ration, these results suggest that adult hake had the biggest impact on age 0+ and 1+ herring.

We also considered a three variable model using adult hake ration, sea surface temperature, and juvenile sablefish ration as independent variables. Stepwise regression analysis indicated that most of the variance was explained by the first two variables. The contribution of juvenile sablefish ration was nonsignificant (P = 0.2) and was therefore rejected. The resulting, best fitting regression equation is given in the caption to Figure 4.

ADULT HERRING MORTALITY

Existing information on the contribution of herring to the diet of offshore predators, while deficient, can be used to derive a rough estimate of the average biomass of herring eaten, annually, by Pacific hake, Pacific cod and sablefish. Specifically, the question is: Do the estimated rations of the adult groundfish stocks approximate a proportion of the adult herring stock which is nearly equal to the average, annual natural mortality rate of 1 - Exp(-0.45) = 0.36?

The diet of Pacific hake off Washington State and the west coast of Vancouver Island has been studied on a number of occasions (Table 4). A simple multivariate analysis of these data suggests: (1) that the proportion of herring in the diet (Q) increases when herring are more plentiful; and (2) that there seems to be a herring stock-temperature interaction which causes Q to rise sharply at higher temperatures, particularly when herring are abundant. The most extensive study by Polish scientists (cited by Bailey et al. 1982) indicates that juvenile and adult Pacific herring made up about 12% of the diet in the summer of 1979. Assuming that juvenile herring accounted for about half this amount, we suggest, that so far as adult herring are concerned in normal years, 6% < Q < 10%; in cold years 0 < Q < 5%; and in warm years 1% < Q < 20%. Although Table 4 indicates that Q may exceed 30% locally, or for a short time during the July to October feeding period, it must be less than this, on average, otherwise the hake stock theoretically could eat the entire west coast of Vancouver Island herring stock. Using the range of probable Q values for normal years we estimate that between 1970-81 the hake stock consumed, on average, about 16 to 26 thousand tonnes of adult herring, which represents about 21 to 34% of the stock -- with the impact being larger in warm years, and less in cool years.

Estimates of the loss of herring to sablefish and Pacific cod are even more problematical because less is known about
their feeding habits. However, some information for sablefish suggests that adult herring account for roughly 6 to 36% of the diet (McFarlane, unpubl. data). This figure seems to be higher for Pacific cod where it varies between 43 to 75% (Westrein and Harling 1981; these estimates, however, are based on incidence of occurrence). Using the average rations between 1960-81 and the foregoing estimates of Q, we calculate that adult sablefish remove on average between 1 to 7 thousand tonnes, and Pacific cod between 5 to 9 thousand tonnes of adult herring annually.

Thus, the combined action of these three predator stocks can consume an estimated 22-42 thousand tonnes. This is equivalent to 29% to 54% of the west coast of Vancouver Island adult herring stock, and is sufficient to account for most of the average, annual natural mortality rate.

**DISCUSSION**

Our analysis suggests that prerecruit herring survival is more sensitive to variations in adult hake than it is to either juvenile sablefish or juvenile cod (Tables 2, 3). The correlation between herring year-class strength and juvenile sablefish ration is negative as expected and suggests that at times, like the large 1977 year-class, sablefish can be important predators of juvenile herring, but in the long run they are probably less influential than hake. The correlation between herring year-class strength and the estimated food rations of both juvenile and adult Pacific cod had the wrong sign (positive instead of negative), and therefore, is inconsistent with the notion that they are key predators. Certainly, Pacific cod prey on juvenile herring but their impact on the west coast of Vancouver Island stock appears to be small compared to other sources of mortality.

Since little is known about the offshore distribution of juvenile herring it is difficult to say when and where they come into contact with adult hake. What information there is, suggests that late age 0+, age 1+ and 2+ herring are exposed to hake during their summer feeding period in the Canadian zone (July-October), primarily along the south and southeast edges of La Perouse Bank, and the seaward edge of Swiftsure Bank (Taylor and Kieser 1981; Taylor 1982). Juvenile herring would also be exposed to juvenile sablefish over most of the lower part of La Perouse Bank.

Sea surface temperature explained most of the variation in herring year-class strength. The biological significance of this negative correlation is unclear, but one interpretation of the finding is that it may reflect a geographical shift in the distribution of hake, or juvenile herring, on the continental shelf in response to changes in oceanographic conditions. During the 1982-1983 El Niño, for example, large numbers of hake migrated north of Cape Scott (50.5°N) - they are normally found south of 49°N. A northern extension of the feeding range at higher temperatures ought to expose more juvenile herring to hake predation, thus causing herring year-class strength to fall with a rise in temperature. This negative correlation probably has nothing to do with temperature per se (because the differences between years are so small), but rather is a measure of the contribution of other variables whose effects, in turn, may be positively correlated with ocean temperatures such as disease, or predation pressure by other piscivorous species like dogfish, lingcod, chinook salmon and coho salmon. Another possibility is that the relative availability of euphausiids and herring, the two principal prey of Pacific hake, may change in response to the same oceanographic conditions that affect temperature, resulting in both juvenile and adult herring constituting a higher proportion of the diet of hake in warm years. This may explain in part why herring had large stomach contents in the late summer of 1983 (the warmest year on record, +2.6 standard deviations above the mean), and only 5-12% in the summers of 1970 and 1979 (both relatively cooler years, 0 and +1 standard deviations above the mean, respectively).

To test some of these ideas a long-term, multi-disciplinary study was initiated on La Perouse Bank in 1985. The objectives are to measure inter-annual variations in: (1) ocean currents and conditions, (2) species composition and abundance of the planktonic organisms herring feed on, and (3) distribution of major herring predators, and the proportion of juvenile and adult herring in their diets. Specifically, the intent is to develop a clearer understanding of the recruitment process so we can more accurately forecast herring year-class success in advance, and enact appropriate management actions to optimally harvest the stock. In view of the circumstantial evidence presented here our working hypothesis is that the Pacific hake stock in the Canadian zone is large enough to force major changes in herring year-class strength and adult mortality. This process seems to be modulated by inter-annual variations in hake distribution and the relative availabilities of euphausiids and herring, so the latter species experiences a higher predation pressure in warm years.

**ACKNOWLEDGMENTS**

We thank W. Shaw for help in assembling the data, R. Hourston for assisting with the calculations, and D. Hay, V. Haist, A. Tyler and M. Stocker for constructive comments.

**REFERENCES**

Bailey, K. M., R. C. Francis, and P. R.


Table 1. Estimated stock biomass and mean weight of adult and juvenile Pacific hake, sablefish, and Pacific cod off the west coast of Vancouver Island between 1960-81.

<table>
<thead>
<tr>
<th>Stocks</th>
<th>Ages</th>
<th>Min.</th>
<th>Max.</th>
<th>Mean</th>
<th>Mean body wt. (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific hake</td>
<td>4-12</td>
<td>188</td>
<td>605</td>
<td>364</td>
<td>1166</td>
</tr>
<tr>
<td>Sablefish</td>
<td>3-35</td>
<td>18</td>
<td>23</td>
<td>18</td>
<td>2236</td>
</tr>
<tr>
<td>Pacific cod</td>
<td>2-7</td>
<td>4</td>
<td>21</td>
<td>11</td>
<td>1994</td>
</tr>
<tr>
<td>Sablefish</td>
<td>1</td>
<td>0.6</td>
<td>5.5</td>
<td>2.7</td>
<td>760</td>
</tr>
</tbody>
</table>

[a] The stock biomass trends are identical to the ration time series (Figs. 2, 3).
[b] Juvenile hake (ages 1-3 inclusive) from the coastal stock do not migrate into Canadian waters (Francis 1983).

Table 3. Results of correlation analysis relating west coast herring year-class strength (WCHYCS) to adult hake ration (HAKER), adult sablefish ration (SBLFR), adult cod ration (CODR) and SST at Amphitrite Point. The signs of the regression coefficients for each variable are shown in parentheses. $R^2$ signifies the total amount of variation explained by the regression.

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>$X_1$</th>
<th>$X_2$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>WCHYCS</td>
<td>HAKER (-)</td>
<td>*</td>
<td>0.12</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>HAKER (-)</td>
<td>SST (-)</td>
<td>0.47</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>SBLFR (-)</td>
<td>*</td>
<td>0.00</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>SBLFR (-)</td>
<td>SST (-)</td>
<td>0.35</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>CODR (+)</td>
<td>*</td>
<td>0.44</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>CODR (+)</td>
<td>SST (-)</td>
<td>0.50</td>
</tr>
</tbody>
</table>

Table 2. Results of correlation analysis relating west coast herring year-class strength (WCHYCS) to juvenile sablefish ration (JSFR), juvenile cod ration (JCODR) and sea surface temperature at Amphitrite Point (SST). The signs of the regression coefficients for each variable are shown in parentheses. $R^2$ is the total amount of variation explained by the regression.

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>$X_1$</th>
<th>$X_2$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>WCHYCS</td>
<td>JSFR (-)</td>
<td>*</td>
<td>0.20</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>JSFR (-)</td>
<td>SST (-)</td>
<td>0.18</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>JCODR (+)</td>
<td>*</td>
<td>0.28</td>
</tr>
<tr>
<td>WCHYCS</td>
<td>JCODR (+)</td>
<td>SST (-)</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Table 4. Percentage by weight of herring ($Q$) in the diet of Pacific hake off the west coast of Vancouver Island (WVI) and Washington State, in relation to the abundance of adult herring and average, annual sea surface temperature at Amphitrite Point (SST).

<table>
<thead>
<tr>
<th>Period</th>
<th>Location</th>
<th>$Q$ (%)</th>
<th>SST (°C)</th>
<th>Biomass (10^3 tonnes)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1970</td>
<td>WVI</td>
<td>54</td>
<td>26</td>
<td>Outram &amp; Hine (1972)</td>
<td></td>
</tr>
<tr>
<td>Summer 1979</td>
<td>WVI</td>
<td>12.5</td>
<td>67</td>
<td>Bailey et al. (1982)</td>
<td></td>
</tr>
<tr>
<td>Aug-Sept 1983</td>
<td>WVI</td>
<td>11.5</td>
<td>23</td>
<td>Shaw et al. (1983)</td>
<td></td>
</tr>
</tbody>
</table>

*Percent occurrence; percent by weight was not measured.
Fig. 1. Major banks and canyons off the west coast of Vancouver Island. Amphitrite Point is located at the northwestern tip of Barkley Sound (roughly midway along, and just above the upper margin of the map).
Fig. 2. Annual food rations (thousands of tonnes) of adult Pacific hake, adult Pacific cod, and adult sablefish, 1960-81. The estimates for hake shown here are 2/3 of the annual ration because the stock only spends 2/3 of the growing season in Canadian waters (i.e. July-October, inclusive).
Fig. 3. Food ration (thousands of tonnes) consumed by successive year classes of sablefish and Pacific cod during their 2nd and 3rd growing seasons (ages 1+ and 2+).
Fig. 4. Relative year-class strength of west coast of Vancouver Island herring (WCHYCS). The solid line indicates the estimated values, the dashed line indicates the values predicted from the regression equation: WCHYCS = 13885 - 2.37 HAKER - 1156 SST, where HAKER is the estimated hake ration (thousands of tonnes) and SST is the annual sea surface temperature at Amphitrite Point.
A THEORETICAL ENERGY BUDGET FOR JUVENILE WALLEYE POLLOCK IN ALASKAN WATERS

by

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and

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ABSTRACT

Eight separate estimates are provided of various components of the annual energy budget for one year old walleye pollock. All eight utilize data collected in the field on monthly increase in length and on monthly condition factor values. These include estimates for energy storage, energy for growth, energy for change in condition, energy of active metabolism and four of total energy requirement.

The first estimate is derived from laboratory measurements of the energy content in pollock exhibiting a range of condition factors, and on the conversion efficiency exhibited by pollock. The amount of energy stored in one year, 170 Kcal/yr, allows calculation of total energy requirement of 510 Kcal/yr. The second estimate, derived from laboratory studies, is 347 Kcal/yr for growth. The third estimate is based on laboratory studies that relate energy (food) intake to change in condition. This estimate is 376 Kcal/yr for change in condition. A fourth estimate, the energy required for active metabolism, amounts to 315 Kcal, but does not include the energy of growth. The last four estimates are of the total energy required based on balanced energy equations. Using $I = G + M + E$, energy intake is 630 Kcal/yr and 662 Kcal/yr, depending on the metabolism estimate used; using Winberg's balanced energy equation, the total energy required is 606 Kcal/yr and 638 Kcal/yr.

Both the derivation and the utility of these eight estimates are discussed. In addition, the annual energy requirement is expressed in terms of biomass of euphausiids prey.

INTRODUCTION

Walleye pollock, *Theragra chalcogramma* (Pallas), is an important north Pacific Ocean fishery resource. Exploitable populations exist in British Columbia, northern Gulf of Alaska, southeast Bering Sea, Aleutian Basin, northwest Bering Sea, Japanese waters and Korea. Alaska's annual catch is about one million metric tons of which about 90% is caught in the southeastern Bering Sea (Piagggi and Thompson 1980). The annual Bering Sea harvest quota for pollock is derived from two equilibrium yield models: a cohort analysis and a computer simulation of pollock population dynamics, PROBUB (Laevastu and Larkin 1981).

The PROBUB model requires information about the relationships between food intake, fish weight and ambient temperature. Heretofore, pollock bioenergetic requirements were poorly known, necessitating the use of values for food intake, food elimination and caloric requirements derived from species of north Atlantic gadids (Jones 1978; Jones and Hislop 1978).

Recently two studies have provided some of the information on pollock energetics needed for PROBUB. Smith et al. (1986) reported on the effects of food (caloric) intake and temperature on the growth and conversion efficiency of juvenile, Alaskan pollock. Yoshida and Sakurai (1984) described growth relative to food consumption as a percent of body weight per day in captive Japanese pollock.

The present paper is a first attempt at estimating the energy requirement of juvenile pollock in Alaskan waters. In this exercise we bring together data on monthly progressions of temperature, length, weight, condition and caloric values. These data plus the feeding and growth relationships of Smith et al. (1986) allowed us to make eight different estimates of the energy requirements of juvenile walleye pollock.

MATERIALS AND METHODS

Estimates of energy requirements of juvenile walleye pollock require information on progressive increase in length, weight and condition factor. For this purpose, the monthly length measurements of 0- and 1 year old pollock from the Strait of Georgia, British Columbia (Shaw and McFarlane 1983) (Figure 1) and monthly values for condition factor in southeast Bering Sea juvenile pollock (Chen 1983) (Figure 2) were used. Weights to correspond with the lengths and condition factors were calculated using the formula $K = 100(W/L)$), where $K$ is condition factor, $W$ is weight in grams and $L$ is length in cm. Three of our estimates require monthly temperature data. For this information we used the 100 m isobath of an annual vertical temperature profile from Prince William Sound, Alaska (Station
PWS-16, Muench and Schmidt 1975) (Figures 3 and 4). The temperatures presented are representative of the temperatures to be expected on the southeast Bering Sea shelf, where the major Alaskan stock of pollock exists. However, we have no precise information on the actual depth or temperature distribution of juvenile pollock for the entire year.

One energy estimate was based on the amount of energy actually stored in the body throughout a year. This estimate uses the progressive increase in weight, changes in condition factor and measurements from Harris et al. (1985) of the caloric content of juvenile pollock exhibiting a range of condition factors.

A second estimate of annual energy requirement was based on the energy required for growth at different temperatures suggested by the laboratory study of juvenile pollock by Smith et al. (1986). For this exercise, the annual temperature profile was used to provide the monthly temperatures necessary to calculate energy required for growth. Each month's energy estimate was scaled to the appropriate temperature and to the calculated fish weight.

A third estimate was based on the energy required to change condition factor in juvenile pollock held in captivity (Smith et al. 1986). Again, each month's energy estimate was scaled to the appropriate temperature and appropriate fish weight using the equations in Smith et al. (1986).

A fourth estimate was derived from information on maintenance ration of juvenile pollock at different temperatures (Smith et al. 1986) and on the assumption that cold-water fishes have active metabolic rates about three times their resting metabolic rates (Brett and Groves 1979).
A fifth and a sixth estimate of the annual energy requirement for juvenile pollock are based on the food intake equation:

\[ I = G + M + E, \text{ where:} \]

\[ I = \text{food (energy) intake; } G = \text{growth; } M = \text{metabolism; and } E = \text{excretion}. \]

A seventh and eighth estimate of annual energy requirement used Winberg's (1956) balanced energy equation:

\[ Q_0 = 1.25 (Q_r + Q_g), \text{ where:} \]

\[ Q_0 = \text{energy of food consumed; } Q_r = \text{energy of metabolism; and } Q_g = \text{energy of weight increase}. \]

RESULTS AND DISCUSSION

Stored Energy Estimate

The relationship between condition and energy content in juvenile pollock (Figure 5) allows a calculation of the energy stored during one year. Table 1 presents the monthly data on water temperature, pollock length, wet weight, condition and total body energy in Kcal. The Kcal value is calculated by converting the wet weight to dry weight (dry wt = 25% wet wt) and then multiplying the dry weight by the Kcal/g dry weight for that particular condition (Kcal/g dry weight = 4.39K + 1.72, Figure 5). The final column is the amount of energy gained or lost since the initial month, September. The energy gain from September to September was 170 Kcal. However, the total energy required to store 170 Kcal is far greater. We calculated a mean conversion efficiency of 33% for juvenile pollock based on data in Smith et al. (1986). Thus, the total energy requirement, estimated by this method, is 170x3 = 510 Kcal.

The estimate of energy actually stored in pollock tissue during a year (Table 1) is certainly far below the total energy required. It does not include any energy requirement for feeding, digestion, or for active swimming. Dividing the stored energy estimate by the conversion efficiency yields an estimate that takes some of these other requirements into account. However, pollock maintained in captivity may not exhibit

Table 1. Energy gain and loss associated with monthly change in weight and condition (K) of juvenile pollock. The column marked "change, Kcal" is cumulative from September. Conversion of wet weight to Kcal uses the results of Harris et al. 1985.

<table>
<thead>
<tr>
<th>Month</th>
<th>( Q_0 )</th>
<th>Fork length</th>
<th>Wet weight(^a)</th>
<th>K</th>
<th>Total Kcal(^*)</th>
<th>Change (Kcal)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>4</td>
<td>11</td>
<td>14</td>
<td>1.02</td>
<td>21.7</td>
<td>0</td>
</tr>
<tr>
<td>O</td>
<td>4</td>
<td>12</td>
<td>18</td>
<td>1.02</td>
<td>27.9</td>
<td>6.2</td>
</tr>
<tr>
<td>N</td>
<td>4</td>
<td>12</td>
<td>18</td>
<td>1.02</td>
<td>27.9</td>
<td>6.2</td>
</tr>
<tr>
<td>D</td>
<td>5</td>
<td>12.5</td>
<td>18</td>
<td>0.9</td>
<td>25.5</td>
<td>3.8</td>
</tr>
<tr>
<td>J</td>
<td>6.5</td>
<td>12.6</td>
<td>16</td>
<td>0.8</td>
<td>20.1</td>
<td>-1.6</td>
</tr>
<tr>
<td>F</td>
<td>6.2</td>
<td>14</td>
<td>19</td>
<td>0.7</td>
<td>22.8</td>
<td>1.1</td>
</tr>
<tr>
<td>M</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>A</td>
<td>3.5</td>
<td>16.5</td>
<td>31</td>
<td>0.6</td>
<td>33.7</td>
<td>12.0</td>
</tr>
<tr>
<td>M</td>
<td>3.5</td>
<td>17</td>
<td>34</td>
<td>0.7</td>
<td>40.8</td>
<td>19.1</td>
</tr>
<tr>
<td>J</td>
<td>3</td>
<td>20</td>
<td>82</td>
<td>1.03</td>
<td>127.9</td>
<td>106.2</td>
</tr>
<tr>
<td>J</td>
<td>3.5</td>
<td>22.5</td>
<td>115</td>
<td>1.01</td>
<td>176.9</td>
<td>155.2</td>
</tr>
<tr>
<td>A</td>
<td>4</td>
<td>22.5</td>
<td>115</td>
<td>1.01</td>
<td>176.9</td>
<td>155.2</td>
</tr>
<tr>
<td>S</td>
<td>4</td>
<td>23</td>
<td>124</td>
<td>1.02</td>
<td>192.1</td>
<td>170.4</td>
</tr>
</tbody>
</table>

\(^a\) dry wt = 25% wet weight
\(^*\) Kcal/g dry wt = 4.39K + 1.72 (Harris et al. 1985)

Total Energy Gain (September to September) = 170 Kcal
Conversion Efficiency = 33%
Total Energy Requirement = 510 Kcal
their full range of activities, tending to make the efficiency estimate higher than it would be in nature.

Estimate of Energy for Growth

The equations for growth in juvenile pollock (Figure 6) allow calculation of the caloric requirement for growth during each month of the year. Since these equations were derived for a pollock of mean weight 45 g, each month's energy requirement had to be scaled to the actual fish weight. We also applied a temperature correction factor to account for the temperatures in the annual profile we selected. In Table 2, monthly growth is tabulated (column 5) as is the number of Kcal needed to achieve that growth (column 6). The sum of the values in column 6, 347 Kcal, is the annual (October to September) energy requirement for growth.

Figure 6. Growth of juvenile walleye pollock, held in the laboratory, as a function of food consumption in calories per day (from Smith et al. 1986).

Estimate Based on Change in Condition

The relationship between caloric intake and change in condition in laboratory-reared juvenile pollock (Figure 7) allow a third estimate of annual energy requirement. Table 3 tabulates the monthly change in condition (column 6) and the energy needed to achieve those changes in condition (column 7). The sum of the values in column 7, 376 Kcal, is the annual energy required to accomplish the changes in condition.

Energy Required for Active Metabolism

A fourth energy estimate can be obtained by using the maintenance ration values reported for 45 g pollock by Smith et al. (1986): 225 cal/day at 3°C, 322 cal/day at 7.5°C. Maintenance ration was scaled to fish weight and to temperature and was calculated for each month of the year (Table 4, column 5). The sum of these monthly values, from October to September, is 105 Kcal. The rough estimate of energy required for active metabolism is based on the generalization of Brett and Groves (1979) that cold-adapted northern fishes can increase their active metabolism to about three times their resting metabolism. For the purpose of this estimate, we assume that their generalization is true for juvenile pollock and that our maintenance ration value is a rough estimate of resting metabolic requirement. Using this method, the active metabolic requirement is 315 Kcal for the year.

Table 2. Energy, in Kcal, needed for growth of juvenile pollock based on laboratory growth studies of Smith et al. 1986.

<table>
<thead>
<tr>
<th>Month</th>
<th>°C</th>
<th>Fork length</th>
<th>Wet weight (g)</th>
<th>Growth (%b.w./day)</th>
<th>Kcal needed per 30 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>4</td>
<td>11</td>
<td>14</td>
<td>0.9</td>
<td>11.8</td>
</tr>
<tr>
<td>O</td>
<td>4</td>
<td>12</td>
<td>18</td>
<td>0</td>
<td>3.1</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>12</td>
<td>18</td>
<td>0</td>
<td>3.5</td>
</tr>
<tr>
<td>D</td>
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<td>12.5</td>
<td>18</td>
<td>-0.4</td>
<td>4.2</td>
</tr>
<tr>
<td>J</td>
<td>6.2</td>
<td>12.6</td>
<td>16</td>
<td>0.6</td>
<td>11.4</td>
</tr>
<tr>
<td>F</td>
<td>4</td>
<td>14</td>
<td>19</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>M</td>
<td>3.5</td>
<td>16.5</td>
<td>31</td>
<td>1.0</td>
<td>33.8 (60 days)</td>
</tr>
<tr>
<td>A</td>
<td>3</td>
<td>17</td>
<td>34</td>
<td>0.3</td>
<td>12.9</td>
</tr>
<tr>
<td>M</td>
<td>3.5</td>
<td>20</td>
<td>82</td>
<td>4.7</td>
<td>118.7</td>
</tr>
<tr>
<td>J</td>
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<td>22.5</td>
<td>115</td>
<td>1.3</td>
<td>90.7</td>
</tr>
<tr>
<td>A</td>
<td>4</td>
<td>22.5</td>
<td>115</td>
<td>0</td>
<td>19.9</td>
</tr>
<tr>
<td>S</td>
<td>4</td>
<td>23</td>
<td>124</td>
<td>0.2</td>
<td>37.0</td>
</tr>
</tbody>
</table>

Total Energy Required For Growth (Oct. to Sept.) = 347 Kcal
Balanced Energy Equations

A fifth estimate of the energy needs of juvenile pollock is based on the balanced energy equation:

\[ I = G + M + E, \]

in which energy intake (I) can be calculated if growth (G), metabolism (M), and excretory loss (E) can be assessed. In the above discussion we provide estimates of the energy required for growth of new body tissue (170 Kcal, Table 1), and for active metabolism, (315 Kcal, Table 4). No laboratory studies of excretory energy loss

Table 3. Energy, in Kcal, needed to achieve change in condition (\(^K\)) observed in the field. The relationship of energy intake to change in K is from Smith et al. 1986.

<table>
<thead>
<tr>
<th>Month</th>
<th>(^\circ C)</th>
<th>Fork length</th>
<th>Wet weight (g)</th>
<th>K</th>
<th>(^K)</th>
<th>Energy required Kcal per 30 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>4</td>
<td>11</td>
<td>14</td>
<td>1.02</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>O</td>
<td>4</td>
<td>12</td>
<td>18</td>
<td>1.02</td>
<td>0</td>
<td>9.1</td>
</tr>
<tr>
<td>N</td>
<td>4</td>
<td>12</td>
<td>18</td>
<td>1.02</td>
<td>0</td>
<td>9.1</td>
</tr>
<tr>
<td>D</td>
<td>5</td>
<td>12.5</td>
<td>18</td>
<td>0.9</td>
<td>-0.12</td>
<td>0</td>
</tr>
<tr>
<td>J</td>
<td>6.5</td>
<td>12.6</td>
<td>16</td>
<td>0.8</td>
<td>-0.1</td>
<td>0</td>
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<td>124</td>
<td>1.02</td>
<td>0.01</td>
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</table>

Total Energy Required for Observed Changes in K (Oct. to Sept.): 176 Kcal

Table 4. Energy requirement of juvenile pollock at maintenance ration and active metabolism based on maintenance rations in Smith et al. (1986), and on assumption that active metabolism is about three times the resting metabolism (maintenance ration) (Brett and Groves 1979).

<table>
<thead>
<tr>
<th>Month</th>
<th>(^\circ C)</th>
<th>Fork length</th>
<th>Wet weight (g)</th>
<th>Maint. ration Kcal/30days</th>
<th>Active metabolism Kcal/30days</th>
</tr>
</thead>
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<tr>
<td>O</td>
<td>4</td>
<td>12</td>
<td>18</td>
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<td>9.4</td>
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<td>21.5</td>
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</tbody>
</table>

Energy for Maintenance Ration (Oct. to Sept.): 105 Kcal
Energy for Active Metabolism (Oct. to Sept.): 315 Kcal
in pollock have been published to date. However, Holdway and Beamish (1984) found that in western Atlantic cod (Gadus morhua) excretory energy loss amounted to 23% of the total energy intake. Substituting these values in the equation above gives:

\[ I = 170 + 315 \times 0.237, \text{ or:} \]
\[ I = 485/0.77 = 630 \text{ Kcal,} \]
\[ E = (0.23)(630) = 145 \text{ Kcal.} \]

Using the same equation but substituting the 510 Kcal (energy stored/conversion efficiency, Table 1) for growth plus metabolism yields a total energy requirement of 662 Kcal.

Similar values for the total energy requirement is obtained if we use Winberg's (1956) balanced energy equation:

\[ Q_c = 1.25 (Q_F + Q_g), \]

where \( Q_c \) is the energy of the food consumed, \( Q_F \) is the energy of metabolism and \( Q_g \) is the energy of weight increase. Using our estimates for the energies of metabolism (315 Kcal) and weight increase (170 Kcal), the \( Q_c \) value is 606 Kcal. Using 510 Kcal for both growth and metabolism, Winberg's equation yields 638 Kcal.

**Euphausiids as Food**

Juvenile walleye pollock of the size range used in this exercise consume euphausiids as the major prey taxon (Takahashi and Yamiguchi 1972, Smith et al. 1978). One might wish to know what weight of euphausiids is required to meet the energy demands of pollock. A mean caloric value of 5615 cal per g dry weight for five species of euphausiids found in Alaskan waters (Euphausia pacifica, Thysanoessa inermis, T. longipes, T. raschii, and T. spinifera) was calculated from the results of Harris (1985). With a dry weight of 20% of wet weight, each gram of euphausiid yields about 1123 cal. Thus, using the 630 Kcal energy requirement, juvenile pollock would have to ingest about 562 g of euphausiids, an amount equivalent to about 30 times their October weight of 18 g.

**Utility of the Estimates**

In terms of accounting for the entire range of behavioral and physiological activities performed by juvenile walleye pollock, the energy estimates based on the balanced energy equations are the most meaningful. One might argue about the real magnitude of active metabolism but until it is measured at different temperatures and seasons we will have no more reasonable estimate. Similarly, we need a measurement of the excretory energy loss in pollock to refine these estimates.

**LITERATURE CITED**


INTERACTIONS BETWEEN PACIFIC COD (Gadus macrocephalus) AND HERRING (Clupea harengus pallasi) IN THE HECATE STRAIT, BRITISH COLUMBIA

by

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ABSTRACT

Pacific cod and herring in the Hecate Strait have shown fluctuations consistent with the hypothesis that herring recruitment rates are strongly influenced by cod predation. Regression analyses of herring juvenile survival, as measured by log recruits per herring spawner, on Pacific cod abundance indicate that the cod may cause a total instantaneous mortality rate averaging around 0.75 yr⁻¹ with each cod consuming several hundred herring. Somewhat lower estimates of herring consumption per cod were expected on the basis of stomach contents data, but the discrepancy may well be due to systematic underestimates of cod abundance, but it is impossible to determine from historical data whether this correlation reflects predator-prey interdependence or the impacts of older cod on their own offspring, since cod and herring abundances are inversely correlated. Peak cod abundances in northern B.C. during the late 1950's may be partly responsible for the collapse of the herring reduction fishery of the 1960's, and management of the two species should be coordinated to reflect the possibility of similar events in the future.

INTRODUCTION

Species interactions involving predation are a major topic of discussion in fisheries, but it has been difficult to demonstrate the importance of such interactions as causes of variation in recruitment and survival rates. The presence of individuals of one species in the guts of another does not imply that the predation will cause changes in aggregate recruitment/mortality rates in the prey population, since the predator may select individuals that would soon die anyway; likewise, aggregate rates in the predator population may not respond to changes in the abundance of one prey species, since the predators may still have no difficulty in capturing enough of the same or alternative prey. Therefore, it is necessary to demonstrate empirically that aggregate recruitment/mortality rates in the interacting species do change as their abundances change, and to demonstrate that the rate changes are not due to some external factor that has an opposite influence on the species (e.g., enhance predator survival while reducing prey survival). The role of external factors cannot be determined unambiguously unless controlled experiments are carried out to deliberately establish contrasting prey/predator abundance combinations. Such large scale experiments have not been conducted in marine systems, so at present we can only determine whether the recruitment/survival correlations predicted by predation theory are present in historical time series. The purpose of this paper is to show that recruitment rates for Pacific cod and herring in the Hecate Strait have fluctuated in a pattern consistent with simple predation models.

The analyses presented here were conducted as part of a 1984 workshop aimed at developing ecosystem models of the Hecate Strait (Tyler et al. 1985). During that workshop, participants assembled a microcomputer database of time series data for 1955-1975 on catches and abundance estimates for a variety of fish species and several physical variables such as sea surface temperatures and Ekman transport rates. Based on spatial distribution and stomach contents data, a number of potentially important predator-prey linkages were identified, including that of cod and herring. It was further noted that cod and herring are among the most abundant species in the Strait. Other abundant piscivores besides cod are Pacific salmon (Oncorhynchus spp.), spiny dogfish (Squalus acanthias), rock sole (Lepidopsetta bilineata), and sabelfish (Anoplopoma fimbria). The most abundant alternative prey fish besides herring is the sand lance (Ammodys hexapterus). Cod and herring stocks fluctuated greatly over the 1955-75 period, and cod stomach samples indicate that sand lance abundance may also have fluctuated markedly (Westrheim and Harling 1982). Crude, preliminary estimates of abundance and feeding rates were made for the various piscivores and these estimates led us to look more closely at the cod-herring interaction; most other predator-prey linkages appear to be

This paper was originally prepared for publication in the Canadian Journal of Fisheries and Aquatic Sciences. Prior to its publication it was presented at the 1985 INPFC Symposium because the organizing committee felt that the subject matter was of keen interest to all participants. Duplication in publication is not intended, and thus the source for citation for this paper is: Can. J. Fish. Aquat. Sci. 43: 830-837.
quantitatively much less important, and time series data involving contrasting abundances were not available for most of them.

DATA SOURCES AND ESTIMATION PROCEDURE

For statistical purposes, we defined Hecate Strait as comprising international Statistical Areas SC and SD (Fig. 1). The trawl fishery there for Pacific cod (age > 2) varies temporally and spatially (Westrheim and Tagart 1984; Westrheim and Foucher 1985). During April–September most of the cod are caught in relatively shallow water (18–108 m), principally in northern SD and central SC; landings during October–December are minimal. During January–March, cod congregate for spawning at 50–69 fathoms (92–126 m) in southeast SD, and to a lesser extent in west central SC. The reproductive distributions of juvenile and adult cod are not known, but juveniles (age 0–2) are often found in catches of adult cod.

The temporal and spatial distribution of herring in Hecate Strait is not fully known. Adult herring concentrate during January–March in the same areas as cod, but spawn in the nearby inlets. However, the herring stocks spawning in inlets adjacent to Hecate Strait do not necessarily reside in Hecate Strait for the rest of the year. The major migratory herring populations that spawn in inlets surrounding the Strait, and that are thought to reside in the Strait are: (1) the Queen Charlotte Islands stock grouping, (2) the North Coast stock grouping, and (3) the Central Coast stock grouping (Haist and Stocker, 1984). The latter stock grouping spawns along the mainland coast but may stray into Hecate Strait. Because the Central Coast stock grouping is in phase with the combined stocks to the north, these three populations were combined to form a major north coast stock-complex. It was at this level of aggregation that stock reconstruction was carried out for the analysis presented below.

Stomach contents samples for cod were collected routinely over the 1955–75 study period (Westrheim 1977; Westrheim and Harling 1983). These samples indicate that cod feed on herring mainly in the winter months, January to March, when there is an average of 6–8 herring per cod stomach representing about 30% of the cod diet by weight. Herring of all sizes are taken. Stomach samples taken from cod landed commercially indicate that age-2 fish and older are eaten, though very large herring are not found (D. Hay, Pacific Biological Station, unpublished data). Where herring are found in the guts of smaller cod, the main predation appears to be by mature, spawning cod (age-1), though every other year during January–March, the above information implies that mature cod each eat around 420 herring per year. These cod grow around 1 kg/year; assuming that they have a growth efficiency of around 20% and that (0.25)x(0.3) of this growth is due to feeding on herring in winter, and that the herring consumed average around 12 g each, a lower estimate would be around 75 herring per mature cod per year. We present these estimates only to indicate that stomach contents data imply that the annual herring consumption per cod is in the neighborhood of one to a few hundred, if Pacific cod are anything like Atlantic cod (Gadus morhua) in feeding and digestion rates (Jones 1979; Durbin et al. 1983).

Extensive age composition data have been gathered from landings of cod and herring stocks as defined above. Cod have been aged mainly by length frequency analysis, and the data are summarized in Foucher and Westrheim (1984) and Westrheim and Foucher (1985). Herring age compositions have been determined mainly by scale analysis, and the estimates used here are from corrected summaries prepared by V. Haist (Pacific Biological Station, Nanaimo, B.C. pers. comm.) using data extracted from Hourston and Nash (1972) and Hourston (1981).

Recruitment rates and stock sizes at age for 1955–75 have been estimated from the age composition data using cohort analysis for cod (Walters et al. 1982) and the more sophisticated maximum likelihood procedure of Fournier and Archibald (1982) as modified for herring by Stocker et al. (1983). The VPA and Fournier procedures give qualitatively similar recruitment patterns over time. Our analysis for herring was based on the Fournier procedure; assuming a constant natural mortality rate of 0.45 for older fish, and using spawn survey as well as catch at age data (Haist and Stocker 1984). We decided to base our analyses for cod on VPA estimates following the procedures of Walters et al. (1982) rather than Fournier (1983); the VPA estimates used above for age composition data not available when Fournier did his analysis, are more conservative (lower) than his estimates, and indicate more variable recruitment rates over time. For our analyses, the major difficulties with these estimates is that the variation in cohort strengths over time has probably been underestimated, due to “smearing” of sampled fish across cohorts by ageing errors. This difficulty may be particularly severe for the cod data (Westrheim and Foucher 1985, p. 180).

The numbers of adult (≥ age-3) cod and adult (≥ age-3) herring were taken as indices of spawning stock each year, and were multiplied by an average effective fecundity (2000 and 1000 for herring and cod respectively) to give an annual larval production estimate, Eq. The effective fecundity of 2000 for herring represents approximately 20% of the average total fecundity, and here it allows for substantial prehatching and early larval mortality (the precise levels of these losses are not critical to our analyses); annual average fecundities were not estimated from age-size composition data since the average sizes at age and percentage age-comp-
...positions did not vary significantly over the time period studied here (W. 1985; Hourston 1981; Hourston and Nash 1972). We then took $Z_t = \log (\text{recruits/eggs})$ as indices of the recruitment success of each stock in each stock in year $t$. According to standard Rickert's stock-recruitment theory, intraspecific competition and cannibalism should result approximately in the linear relationship

$$Z_t = a - bE_t + W_t$$

Where $a$ is a background, density-independent mortality rate $bE_t$ represents additional density dependent mortality due to intraspecific competition or possibly cannibalism and $W_t$ is a random mortality component due to abiotic factors and biotic factors not closely correlated with stock size as measured by $E_t$. We employed a simple extension of equation (1) to account for species interactions, with the linear relationship

$$Z_t = a - bE_t + qZ_t + W_t$$

Where $P_t$ is the number of predators (for herring $E_t$ predictions) or prey (for cod $Z_t$ predictions). The parameter $q$ should be negative if $P_t$ is the number of predators, and is interpreted as the fraction of the prey stock taken by each predator prior to prey recruitment. The value of $q$ should be positive if $P_t$ is the prey stock, and represents the effect of increasing prey abundance on predator fecundity and/or juvenile survival; enhanced survival might occur for example if the predator cannibalizes fewer of its young when the prey species is more abundant. Equation (2) is the functional form used to represent species interactions in the Anderson-Ursin (1977) and Shepard (1984) models, and has been recommended (Doyle, p. 47 in R. M. May (ed.) 1984) as a framework for exploratory data analysis of possible species interactions using multiple regression techniques. Obviously equation (2) can be generalized to include a whole series of terms for different predators and alternative prey species.

Equation (2) makes two key assumptions when applied to the $Z_t$ time series for a prey species such as herring. First, it proposes that predation loss (as represented by $P_t$) is independent of loss due to intraspecific interactions (represented by $bE_t$) such as food competition. If, for example, increased juvenile density results in more juveniles with poor growth and these individuals are subject to higher predation losses, such losses will be reflected in the $b$ coefficient rather than the predation coefficient $q$. Second, it proposes that the predator's individual functional response to prey density is linear, i.e. captures per predator $= q$ (prey available), thus ignoring effects of predator handling time and satiation when prey density is high. If the predator attacks a variety of prey species $j = 1, \ldots, n$ at random, where the prey densities are $N_i$, rates of effective search are $a_j$, and handling times per prey are $h_i$, then the attack rate per predator $C_t$ on any prey species $i$ would be more realistically represented by the multispecies disc equation (Murdoch 1973, Walters 1985a):

$$C_t = \frac{a_i N_i}{1 + \sum_j a_j h_j N_j}$$

$$= \frac{a_i N_i}{1 + a_i h_i N_i + B}$$

where $B = \sum_j a_j h_j N_j$ represented the effect of alternative prey on the rate of species $i$. The total instantaneous mortality rate on species $i$ would be given by

$$C_t P_t / N_t = a_i P_t / (1 + a_i h_i N_i + B)$$

In pretending that this mortality rate is adequately represented by $qP_t$, equation (2) assumes that $h_i$ is negligible (satiation on prey $i$ rare) and that the densities of alternative prey are relatively constant (so that $a_i / (1+B)$ is a constant). In principle we could substitute equation (4) into equation (2) to give a nonlinear regression model for predation effects, but Monte Carlo simulation tests of that approach (using fake data with known parameters) indicated that poor convergence and estimates could be expected from nonlinear estimations for data sets such as the Bcette Strait herring and cod.

A few further words of caution are needed about using equation (2) as a regression model to estimate the importance of species interactions. First, the regression independent variables $E_t$, $P_t$ are estimated with both random error and systematic (autocorrelated) error due to massaging of fish. Such errors will tend to cause $b$ to be overestimated (Walters and Ludwig 1981), and may cause $q$ to be underestimated (make $q$ appear to be independent of $P_t$). Second, the $E_t$ and $P_t$ are not designed independent variables, but are instead random variables that are correlated with past values of the random effects $W_t$. Such correlations may exaggerate the biases due to measurement errors (Goodyear and Christiansen 1984; Walters 1985b). Third, there may be a correlation between environmental factors (whose effects are supposedly measured by $W_t$) and the space-time pattern of contact between prey and predators, so that $q$ is in fact time varying and correlated with $W_t$; such correlations may either exaggerate or mask the apparent predation effects as measured by $qP_t$ where $q$ is the (constant) estimate from regression analysis. Fourth, there is hidden ambiguity in equation (2) about when the prey are actually eaten. $Z_t$ is assumed to be a mortality prior to recruitment, but is calculated from estimated recruitment which in turn is estimated from catches 3-10 years later; thus...
predation mortality occurring anywhere in the prey life cycle (years $t+1$, $t+2$, etc.) and influencing the cohort catches will also influence the recruitment estimate, provided the recruitment estimate was obtained with a model assuming constant natural mortality. Finally, and perhaps most important, we examined many time series before noticing the correlations presented here; such examinations are likely to uncover correlations that are due to chance alone, and we were unable to quantify this risk since no record was kept of the number of time series examined.

RESULTS

A general indication of the possible importance of the cod-herring interaction on the B.C. coast is provided by Figure 2, where we compare Haist and Stocker (1984) estimates for herring adult ($\geq$ age-3) stock size to the cod landings per unit effort (CPUE) reported in Westheim and Poucher (1985), for four major regions. The pattern for Hecate Strait is reminiscent of a predator-prey cycle, where years of high herring abundance are followed by strong cod catches and strong cod catches are followed by low herring abundance.

Egg deposition and recruitment estimates for Hecate Strait cod and herring as defined above are presented in Table 1. Linear regression of $E_t$ calculated from Table 1 on $E_{t-1}$ and $E_{t-2}$, as defined in equation (1) and (2), gave reasonable estimates for the $b$ and $q$ parameters (Table 2). The sign of the $q$ parameters was as predicted by predation theory: increases in cod abundance apparently have a negative effect on herring juvenile survival, while increases in herring abundance have a positive effect on cod recruitment. Standard measures of statistical significance for the parameter estimates are not presented; such measures would be misleading in view of the correlation patterns that are likely present in the data, and in view of the unknown risk that we stumbled upon a spurious correlation after examining many data series.

Figures 3 and 4 compare fits to the recruitment time series for equation (1) versus equation (2). It is obvious that the standard Ricker stock-recruitment relationships (equation 1) cannot account for much of the observed fluctuations in recruitment rates, especially for herring. By including the effects of cod predation, we can account for much of the decline and recovery in herring recruitment rates that followed the peak herring recruitment years of 1958-60. These peak years are not fully accounted for by the model, nor is the peak in cod recruitment that followed in 1961-62 (age-2 recruits in 63-64). It is a trivial matter to simulate the dynamics implied by equations (2.3) and (2.4) in Table 2; using reasonable estimates of recruitment rates (0.5-0.6 for both species), such simulations indicate damping oscillations to a predator-prey equilibrium. However, oscillation of the period (8-10 yrs) and amplitude observed (Fig. 1) are obtained when the $a$ parameters are increased by about 2 (to -3.47 and -3.91), especially if herring recruitment is modelled with random normal environmental effects ($W_t$) added to $\lambda_t$.

A variety of other regression models were fit to the recruitment time series, using various combinations and components of the prey and predator stock sizes as predictors along with environmental indices such as sea surface levels and temperatures. None of these models gave substantially better fits to the data, though they helped us identify one basic confounding of factors. Cod and herring stock sizes are inversely correlated (Fig. 2), so that it is impossible to distinguish whether low survivals from high herring egg depositions are due to competition-cannibalism within the herring stock ($b$ parameter), or heavy predation later in life by cod ($q$ parameter). To emphasize this point, Figure 5 shows the fit to the herring time series of the model

$$R_{t+1} = E_t \exp{-6.135 - 0.1758P_t}$$

where $P_t = \text{age 2+ cod abundance (i.e., including juvenile cod as predators).}$ This model assumes no density dependence at all in the herring recruitment dynamics ($b=0$), and instead generates a "dose-shaped" relationship due to the apparent numerical response of the cod. Interestingly, a good fit to the cod recruitment cannot be obtained by a similar model change: density independence plus herring abundance leads to a cod recruitment model that predicts peak recruitments out of phase with the estimated time series.

Comparing Figures 3 and 4, it appears that the production of strong cod year classes may require a series of good recruitment years for herring, through some effect such as cumulative increase in cod fecundity or survival over several years of good food conditions. To test this possibility, we fit the cod recruitment data to an extended version of equation (2.5 see Table 2) with herring age 1 recruits the previous two years included as $P_{t-1}$, $P_{t-2}$, along with the current herring recruitment $E_t$. The resulting equation was

$$R_{t+1} = E_t \exp{-6.29 - 3.16 \times 10^{-4}E_t - 1.44 \times 10^{-5}P_{t-1} - 6.00 \times 10^{-5}P_{t-2} - 6.51 \times 10^{-5}P_t}$$

The predictions of this equation (Fig. 6) are a bit better than equation (2.4), but it is still unable to explain the sharpness of the 1961-62 peak in cod recruitment. Perhaps it is worth noting at this point that Fournier (1983) did not estimate the 1961-62 recruitment peak to be so large (compared to other years) as we have assumed terms of the log recruits per spawner $\lambda_t$. 
in using VPA estimates.

Table 2 presents estimates of average total mortality rates in the first year of life due to density dependent mortality (qP) and predation (qP). For example, the estimate qP = 0.75 for equation (2.3) implies that the baseline instantaneous mortality rate of 5.47 for the herring first year of life is increased by 0.75 when the cod stock is at its average level of 3.6 million fish. Not that as shown in Figure 3, equation (2.3) predicts the herring 2 remarkably well, and ascribes a total range of variation of around 1.5 (from 6.5 to 8.0) in this rate to cod predation. This surprisingly high contribution to apparent mortality can be understood by examining the estimate of q (0.249) more closely. In equation (2.3), q is interpreted crudely as the probability of juvenile herring mortality per million cod present in the system, i.e., qP (number of juvenile herring eaten)/(number at risk to cod). According to this interpretation, we can estimate the annual herring consumption per million cod as q x (number at risk). If juvenile herring are mainly eaten in the winter months as they approach their first birthday, then the number at risk is best estimated by the age 1 recruitment R1 rather than the massively larger larval production P0-l. Using the average age 1 herring abundance (3870 million) as the mean number at risk, we obtain the estimate q = 0.249 (3870 - 3870) and juvenile herring consumed per cod per year. This estimate is substantially higher than expected on the basis of stomach contents or growth energetics arguments (see above). Obvious explanations for the discrepancy include: (1) we may have underestimated cod abundance P0 using a conservative VPA procedure; (2) herring abundance may be overestimated by the Fournier procedure; and (3) we may in fact be estimating a total mortality rate that is spread across several years of the herring's life, rather than concentrated around the first birthday. In view of these possibilities, the qP estimates in Table 2 are not unreasonable.

**DISCUSSION**

Most previous research on Pacific cod and herring has sought explanations for recruitment variation in terms of abiotic environmental factors and overfishing during the peak herring reduction fishery of the early 1960s (Houde 1980; Fournier 1983; Stocker et al. 1985). Recently Ward and Stocker (MS in prep.) have questioned such explanations for herring on the northern coast of Vancouver Island, and have suggested that predation, especially by Pacific hake (Merluccius productus) may be an important cause of recruitment variation. We examined saffron fish predation as well in the Hecate Strait workshop, and concluded that this is unlikely to be a major factor in the Hecate Strait. By examining recruitment relationships statistically in we have presumably accounted for basic variations in recruitment due to recruitment overfishing: equations (1) and (2) propose that recruitment is proportional to spawning stock when the stock is very low, with the proportionality constant determined by fecundity and the herring parameter "a".

Several lines of evidence support the possibility that predator-prey interactions have been a major determinant of recruitment variation in the Hecate Strait. First, there is a broad cline in herring recruitment variability along the B.C. coast (Fig. 2), with recruitments being less variable and not apparently cyclic where cod are less abundant. Associated with this cline is an increase in the herring "a" parameter for herring stock-recruitment: Walters et al. (1982) estimated that the Georgia Strait herring have a Rickert 2 parameter around 0.2-1.0 larger (i.e., 2.0-2.1) smaller than the other stocks shown in Figure 2. This cline may reflect a better statistical fits to the recruitment time series are obtained by using predator and prey abundances as predictors than are obtained with any individual environmental indices identified to date. The simple recruitment equations that we have tested do not fully explain the recruitment variations, especially over the 1957-62 period, but there are indications (Fig. 6) that we may simply have failed to identify the correct timing and delay structure for when herring are eaten and how this consumption is translated into cod recruitment and survival. Finally, the estimates of herring consumption per cod based on recruitment regression analysis are not wildly divergent from expectations based on diet composition and energetics, though these estimates suggest that we have overestimated the impact of adult cod. Information on numbers and size of herring in cod stomachs will be available soon (D. Hay, pers. comm.). Such information will allow the development of more precise expectations, and will give clues about the best regression model structures to use instead of equation (2).

Assuming that cod predation rates are an additive component of the herring natural mortality rate, there is still considerable ambiguity about what mechanisms drive the "cycle" evident for the Hecate Strait in Figure 2. At least three alternative biotic explanations are partly consistent with the data. First, there may be a basic predator-prey instability in the classical sense, with increases in herring stimulating increases in cod which then drive the herring down which then results in a stock collapse. Second, the equations (2.3)- (2.4) are capable of producing such cycles after some adjustment in parameter estimates. Second, the herring stock-recruitment relationship may be strongly dome shaped (due to competition, cannibalism) even though the recruitment cycles even in the absence of cod predation; cod may just track these cycles without significantly reinforcing them.
Such a model could not explain the geographic pattern in Figure 2, since it would predict stronger cycling in the more productive Georgia Strait herring stock. Third, the cod may cycle due to a dome shaped recruitment relationship, without being significantly affected by herring, and the herring may simply track the cod cycle. Equation (5) reflects this possibility, and it is supported by stomach contents data which indicate that the cod are not dependent on herring except perhaps in winter just prior to spawning.

Simulation trials of equations (2.3)-(2.4), but with randomly varying environmental effects on herring recruitment, indicate that occasional production of strong herring year classes can maintain or exaggerate an otherwise weak predator-prey cycle. Such an "environmental forcing" hypothesis is consistent with the regression results in Figures 3 and 4, especially if the herring and cod have opposite survival responses to the environmental factor(s) involved. For example, high transport northward through the Strait during late winter may be unfavorable for larval cod survival, but favorable to larval herring survival by holding the larvae in more productive inshore waters (Tyler and Westheim, unpublished data). It is noteworthy that the relatively enclosed, inshore environment of the Georgia Strait provides good survival conditions for herring but apparently poor conditions for cod.

The relatively poor fit of the model to the 1961 herring year-class is likely due to the influence of a physical oceanographic factor. Apparently some coast-wide phenomenon enhanced recruitment of a number of species in various locations: for example, Pacific halibut (Hippoglossus stenolepis) in the Gulf of Alaska (Deriso 1985), English sole (Parophrys vetulus) off Oregon (Hayman et al. 1980), and Pacific hake (Merluccius productus) off southern California (Bailey 1981). Consequently we would not expect the predation model to "predict" abundance this year.

The major herring reduction fishery off B.C. collapsed in 1966-68, and this collapse has been attributed to overfishing causing weak year classes in 1963-65 (Hourston 1980). The predator-prey hypotheses outlined above suggest an alternative scenario for events leading to the collapse. According to these hypotheses, the trouble really began in the late 1950s, when either historical cod-herring "imbalance" or some environmental forcing factor led to the production of exceptionally strong herring year classes. The strong herring year classes led to very strong cod year classes in the early 1960s. Considering that similar herring declines occurred both before after (late 1970s, early 1980s) the reduction fishery collapse, we must consider whether the fishery and its management have had much impact at all on changes in herring abundance. This argument is reminiscent of the Thompson-Burkenroad debate (Skud 1975) and other more recent examples (Skud 1983) of controversy about the relative importance of environmental factors (including predation) versus management in the declines and recoveries of stocks.

Fishing efforts and exploitation rates for cod have been relatively high in the 1970s and 1980s (Westheim and Poucherie 1985; Fournier 1983), and this appears to be resulting in stabilization of the cod stock at a population structure involving high recruitment rates and low abundance of older individuals. Our predator-prey models (Table 2) suggest two possible scenarios for the next decade. If the herring recruitment relationship is not dome shaped, then low recruitment rates will gradually increase as will the stock size, due to the present relative scarcity of cod. Alternatively, if the herring recruitment relationship is dome shaped, then there may be a resurgence of the herring stock followed by more violent, longer period oscillations (due to larger Ricker "a" value for herring if cod are held down by fishing). Neither of these scenarios is particularly helpful for herring management, and they suggest the need to re-examine "co-management" strategies that may prevent the two fisheries from destabilizing each other's fishing opportunities. The search for such strategies is an exciting area for further research.

CONCLUSION

Much evidence points to the existence of a cod-herring interaction in the Hecate Strait, and if it is strong this interaction has important management implications. Obviously, biological studies are necessary now to establish the distribution, behaviour, and diet of both cod and herring at ages 0, 1 and 2. Is this the only likely time during which substantial cod-herring interactions could take place in Hecate Strait?

However, it remains possible that the appearance of "cycles" in abundances has resulted from a mere coincidence of factors in the short time series now available, or from environmental forcing that affects the species in opposite directions. The environmental forcing hypothesis cannot be tested merely by patiently gathering longer time series in conjunction with more detailed studies on recruitment biology. Both it and the predator-prey hypotheses predict continued, fairly regular fluctuations into the future if historical fishing patterns are maintained. A bold step now would be to seek an experimental fishing policy that would manipulate cod and herring stock sizes to levels where the various hypotheses make distinctive predictions. Without such a deliberate experiment, we may remain forever uncertain about the importance of the predator-prey inter-
REFERENCES


Westrheim, J. 1977. Length-weight and length-girth relationship, maturity,

Table 1. Stock and recruitment data assumed for cod and herring. Herring effective egg deposition \( E_t \) was taken as column (1) \( \times 2000 \). Cod effective egg deposition \( E_t \) was taken as column (3) \( \times 1000 \). All numbers are millions of fish.

<table>
<thead>
<tr>
<th>Year</th>
<th>Herring Stock Size (( &gt; \text{age-3} ))</th>
<th>Herring Age 1 Recruits</th>
<th>Cod Stock Size (( &gt; \text{age-3} ))</th>
<th>Cod Age 1 Recruits</th>
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<tr>
<td></td>
<td>Adult</td>
<td>Year+t-1</td>
<td>Adult</td>
<td>Year+t-1</td>
</tr>
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<td>3590</td>
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</tr>
<tr>
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<td>1975</td>
<td>3670</td>
<td>2100</td>
<td>3</td>
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Table 2. Stock recruitment models for cod and herring. Estimated by multiple regression from data in Table 1. \( R_t = \text{age 1 recruits} \), \( E_t = \text{effective egg deposition} \), \( P_t = \text{as defined} \). The \( bE \) and \( qP \) are measures of average total mortality rate attributable to density and interaction dependence, respectively.

**Ricker Models (Equation 1)**

(2.1) Herring:

\[
R_{t+1} = E_t \exp(-6.14 - 2.133x10^{-7}E_t) \quad bE=1.31
\]

(2.2) Cod:

\[
R_{t+1} = E_t \exp(-5.45 - 3.949x10^{-4}E_t) \quad bE=1.20
\]

**Interaction Models (Equation 2)**

(2.3) Herring:

\[
R_{t+1} = E_t \exp(-5.47 + 2.002x10^{-7}E_t - 0.249P_t) \quad bE=1.23 \quad qP=0.75
\]

(2.4) Cod:

\[
R_{t+1} = E_t \exp(-5.91 + 4.072x10^{-4}E_t + 1.475x10^{-4}P_t) \quad bE=1.23 \quad qP=0.45
\]

(2.5) Cod:

\[
R_{t+1} = E_t \exp(-5.68 - 3.719x10^{-4}E_t + 3.074x10^{-4}P_t) \quad bE=1.13 \quad qP=0.12
\]
Fig. 1. Location of the Hecate Strait and other statistical areas off the B.C. Coast.
Fig. 2. Estimates of adult herring stock size compared to adult cod stock size (landings per unit effort) for various regions of the B.C. Coast, from data in Haist and Stocker (1984) and Westheim and Poucher (1985). Cod catch regions are as named. Hecate Strait (Areas 5C-D) herring include Queen Charlottes and North Coast stocks, Queen Charlotte Sound (Areas 5A-B) herring are central coast stock, West Coast Vancouver Island (Areas 3C-D) and Georgia Strait plus Johnstone Strait (Area 4B) stocks are as reported in Haist and Stocker (1983).
Fig. 3. Herring year class strength estimated by Fournier method, compared to stock recruitment predictions from Table 2.
Fig. 4. Cod year class strength estimated from VPA, compared to stock recruitment regression predictions from Table 2.
Fig. 5. Fit to the herring recruitment time series of a model assuming no density dependence in herring juvenile survival but predation by juvenile and adult cod. Predictions are from equation (5).
Fig. 6. Prediction of cod recruitment using Ricker stock-recruit relation plus herring recruitments of past years (equation 6).
A LESLIE MATRIX - DIFERENTIAL EQUATION MODEL
FOR YIELD ANALYSIS OF GROUNDFISH RESOURCES

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ABSTRACT

The tropical Sunda Shelf of the South China Sea has a complex groundfish community that is typified by a great number of species. As such it was impractical to determine the dynamics of the community on a traditional species-by-species basis. Instead, a Leslie-matrix population dynamics model is developed where productivity of a species group is related to the biomass dynamics for the remainder of the demersal fish community combined. The model generates equilibrium yield curves for the two species groups, thereby, allowing the equilibrium catch from any combination of fishing mortality upon the two groups to be examined. The model indicated that when fishing is nonselective for species, as is the case, the maximum sustainable yield (MSY) for the community is 17% lower than the maximum possible if fishing is selective. In addition, the non-selective fishery achieves a sustainable yield that is 20% lower than the MSY estimated by the traditional pooled-species surplus production model.

INTRODUCTION

The Sunda Shelf (Fig. 1) is considered a very productive continental shelf for groundfish resources. Its history of trawl fishing activities, however, is comparatively young—dating back only to the mid-1930s. The majority of the fishing is now conducted by Thailand and Japan, although Taiwan and bordering countries occasionally fish the shelf. Taiwan first fished the Sunda Shelf in the late 1960s, following exploratory surveys conducted by the Taiwan Fisheries Research Institute in 1954 and 1960-62. By 1971 and 1972, Taiwanese fishing activities covered almost all of the Sunda Shelf, except for the Gulf of Thailand. In 1973, a sudden doubling of fuel oil prices due to the first worldwide oil shortage resulted in a significant reduction of Taiwanese trawl activities there. Since fuel prices have remained high and neighboring countries of the Sunda Shelf have started charging for fishing privileges inside their exclusive economic zones, Taiwan no longer has an extensive fishery there.

The demersal fauna and catch of the tropical Sunda shelf are characterized by the presence of a large number of species, none of which is really dominant (Liu et al. 1978). A single commercial haul on the Sunda Shelf, for instance, usually brings up 50 or more species (Yeh 1981). Since the fish community is made up of many species which are likely to have very complex ecosystem interactions, it was practically difficult to determine the dynamics of the resources on a species-by-species basis. Therefore, we analysed the dynamics of the resources by reducing them into a smaller number of related species groups. A detailed catch-per-unit effort analysis of the resources suggested that there are at least two major biological groups whose abundances are inversely related (Yeh et al. 1982). As a result, a two species group model using a Leslie matrix analytical procedure is used to determine the interactive mechanisms and population dynamics of the two groups.

Fig. 1. Map of the study area on the Sunda Shelf.
SOURCES OF DATA

The data used were derived from logbook records of Taiwanese trawlers that operated on the Sunda Shelf, especially those during 1970-77 (Anon. 1970-1977). The data were compiled by the Demersal Fish Research Center (DFRC) that was established by Taiwan in 1969, the year when major expansion of Taiwanese trawling activities on the Sunda Shelf took place. Since the primary purpose for the logbooks was scientific, it was generally believed that the reliability of the data records was high. Moreover, the recovery rates of the logbooks were also high. For example, recovery rates were 80% in 1970, 75% in 1971, and 70% in 1972. The manner in which the data were collected were as follows.

Every trawler above 50 gross registered tons was required to communicate daily with the Kaohsiung Fisheries Radio Station and report its daily trawling position, haul number, and total catch. After each trip, captains were also requested to mail in their logbooks to the Statistical Division of the Taiwan Fisheries Bureau. Such information as: date, trawling position, daily hauls, and daily catch in cases (one case weighs about 30 kg) by species or species groups were recorded in the logbooks. The catch of lizard fish (Saurida spp.) was reported by 3 size categories, i.e., (1) large (fork length greater than 32 cm); (2) medium (fork length between 22 cm and 32 cm); and (3) small (fork length less than 22 cm).

The fishing grounds were subdivided into half-degree square blocks (HSB). The captains were required to report their trawling position by HSB number. Catch statistics were compiled in number of cases, by month, by species, by tonnage class, and by HSB location. Effort data were compiled along with catch statistics. Effort was expressed in number of hauls.

FORMULATION OF TWO SPECIES COUPLING MODEL

Characteristics of the species groups

Catch per unit effort (CPUE) trends for individual species groups have been analysed by Yeh and Liu (1983). The trends show that relative abundance declined with increasing fishing effort for most species. Among the species that had the reverse trend, the lizard fish in region R8A of the Sunda Shelf (Fig. 1) is the most prominent example. Despite increasing exploitation, its density index increased about two and a half times in the late 1970s from the early 1970s. Since lizard fish was an important catch and had been studied extensively by Yeh and Liu (1973), Liu and Yeh (1974), Yeh et al. (1977), an attempt was made to determine the interactive relationship between lizard fish and the remainder of the demersal fish community in region R8A.

The lizard fish is known to be a major predator in the sandy bottom regions.

A preliminary study of the stomach contents of lizard fish indicated that considerable amounts of smaller lizard fish were consumed by the larger ones. Since lizard fish are elongated with a huge mouth, the smaller lizard fish consumed may reach half the fork length of the predator. To the best of our knowledge, lizard fish appears to be the only cannibalistic species in the Sunda Shelf. Cannibalism may also be the most crucial factor limiting its population size. Otherwise such a successful predator could easily consume most of the other species and dominate the entire niche. The biomass of adult lizard fish, therefore, could be the key factor determining the strength of future year classes. If this postulate is true, then there should be a maximum threshold biomass of adult lizard fish beyond which the successful settlement for future recruits is diminished.

The fork length of small sized lizard fish range from 16 cm to 22 cm (with the mode at about 19 cm). According to age-length keys, the vast majority of this size range are from newly recruited one year olds. First maturation is achieved at about 25 cm for males and 28 cm for females. Therefore, medium and large sized categories of lizard fish could be viewed as parental stock.

![Fig. 2. Scatter diagrams of age 1 lizard fish recruitment versus parental stock (top panel) and versus the remainder of the species (middle panel), and lizard fish parental stock versus the remainder of the groundfish species (bottom panel).](image-url)
Mathematical formulation of the model

Based on the postulations on the biology of the species, an attempt was made to determine a parent-recruit relationship for the lizard fish population. Three scatter diagrams are shown in Figure 2 to depict these relationships: (1) newly recruited age 1 lizard fish biomass \( r(1,t+1) \) in year \( t+1 \) versus parental stock biomass of the fish \( p(t) \) in year \( t \); (2) \( r(1,t+1) \) versus the biomass for the remainder of the groundfish species \( Q(t) \) in year \( t \); and (3) \( p(t) \) versus \( Q(t) \). Since the food web system among species is largely unknown, the impacts by different species on the \( r(1,t+1) \) are impossible to consider separately. A lumped biomass \( Q(t) \) was used here. Based on the eight years of observation, there was a clear relationship between the biomass of small sized lizard fish in year \( t+1 \) and the biomass of medium and large sized lizard fish in year \( t \). Furthermore, the linearity between the pair of biomass variables appeared highly significant. An empirical relationship between parental stock biomass and their recruit size may, therefore, be formulated as

\[
r(1,t+1) = a_0 + a_1 p(t) + a_2 Q(t) \tag{1}
\]

By applying multiple linear regression, the three parameters \((a_0, a_1, a_2)\) in equation (1) can be estimated, as shown in Table 1. Since \( r(1,t+1) \) could not be negative, we set its minimum value to equal 0.5 when \( p(t) \) moves towards higher biomass (Fig. 2). At the lower biomass range of \( p(t) \), there was no data for \( r(1,t+1) \) in this domain in region R8A. Instead, data from the neighboring region R6A were used. The data showed that

\[
r(1,t+1) = (12.5/50) p(t) \quad \text{when} \quad p(t) < 50
\]

The empirical equation (1) with two modifications at the higher and lower biomass segments resulted in a dome-shaped parent-recruit relationship for lizard fish. This relationship was then incorporated into the first row vector of the matrix \( S(t) \) in equation (3).

Most of the species in group \( Q(t) \) are intermediate predators. For example, the adults of one species usually prey on juveniles of many other species, thus creating a very complex food web. This web is still unknown at the present time. Under such a circumstance, the surplus-production model with an additional competitive term is the simplest applicable technique to investigate how the group as a whole is likely to react under the pressures from fishing and biological competitors.

Based on the discussions above, the two biological entities, i.e., the lizard fish population and the remainder of the groundfish species, may be viewed as two interactive groups in a demersal community. A two species system model is therefore applied to study the long term effects of fishing upon a community with interactive groups. The formulation of the system is shown as follows:

\[
\frac{dQ}{dt} = [a-b Q(t)] + tFq Q(t) \tag{2}
\]

\[
P(t+1) = S(t) P(t) \tag{3}
\]

\[
Y(t) = tFq Q(t) + H(t) P(t) \tag{4}
\]

where \( t \) = time in calendar year

\( Q(t) \) = total biomass of the demersal community, not including lizard fish

\( P(t), P(t+1) = (8x1) \) column vectors of mean biomass distribution of lizard fish by age in year \( t \) and \( t+1 \) respectively

\( tFq \) = annual fishing mortality for the \( O \) group fish in year \( t \)

\( H(t) = (1x8) \) row vector of annual harvest rate coefficients for lizard fish

\( S(t) = (8x8) \) regulatory matrix projecting \( P(t) \) into \( P(t+1) \)

\( Y(t) = \) total demersal yield in year \( t \)

\( C = \{0, c, c, c, c, c, c, c\} \)

\( a, b, c \) are constants.

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<td>9.2</td>
<td>6.9</td>
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Table 1.--Multiple linear regression analysis of \( r(1,t+1) \) vs. \( p(t) \) and \( Q(t) \) where \( r(1,t+1) \) is age 1 lizard fish recruitment, \( p(t) \) is lizard fish parental stock, and \( Q(t) \) is remainder of the groundfish species in thousands of metric tons.

Model: \( r(1,t+1) = a_0 + a_1 p(t) + a_2 Q(t) \)

| Results of parameter estimation | \( a_0 = 10.3408 \) | \( a_1 = -0.1109 \) | \( a_2 = 0.0321 \) | \( R^2 = 0.7349 \) |
The model consists of a differential equation for biomass of the mixed species \( Q \) and a 8x8 Leslie matrix projection of age structured biomass of lizard fish. Mathematical expression of the matrix and vectors of equations (3) and (4) are as follows:

\[
P(t) = [r(1,t), \ldots, r(n,t), 1]^T, \quad n = 7
\]

\[
P(t+1) = [r(1,t+1), \ldots, r(n,t+1), 1]^T
\]

where \( r(i,t) \) = biomass of age \( i \) lizard fish in year \( t \):

\[
S(t) = \begin{bmatrix}
0 & a_1 & a_1 & a_1 & a_1 & a_1 & a_{1} + a_2 Q(t) \\
0 & s(1,t) & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & s(2,t) & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & s(3,t) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & s(4,t) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & s(5,t) & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & s(6,t)
\end{bmatrix} \quad (1)
\]

where \( s(i,t) = \frac{W_i}{W_1} \exp[-(M_i + tF)] \)

\( W_i \) = mean body weight of lizard fish at age \( i \)

\( M_i \) = natural mortality of lizard fish at age \( i/1 + 1 \)

\( tF \) = annual fishing mortality rate for lizard fish in year \( t \)

\( H(t) = [h_1, h_2, h_3, h_4, h_5, h_6, 0, 0] \)

where \( h_i = \frac{(W_i + W_{i+1})}{2} \) \[1 - \exp(Z(i,t))\] \[
\begin{array}{c}
\frac{tF}{Z(i,t)}
\end{array}
\]

\( Z(i,t) = -(M_i + tF) \).

Estimation of model parameters

Before running the model, some parameters had to be estimated—first, the parameters of \( a, b, \) and \( c \) in equation (2). Here we adopted Schaefer's theoretical equilibrium yield (YE) technique, where

\[
YE = Y(i) + \frac{B(i+1) - B(i-1)}{2}. \quad \text{At a steady state, equation (2) becomes}
\]

\[
YE = F(t) Q(t) = [a - b(t) - c p(t)] Q(t)
\]

or

\[
YE/Q(t) = a - b Q(t) - c p(t)
\]

Scatter diagrams of plotting \( YE/Q(t) \) versus \( Q(t) \): \( YE/Q(t) \) versus \( p(t) \); and \( Q(t) \) versus \( p(t) \) are shown in Figure 3. The linear multiple regression technique was applied to estimate these parameters. The results are shown in Table 2.

Next, the age specific natural mortality rates \( M \) were estimated. Since the species is cannibalistic, it seemed reasonable to set up a functional relationship between natural mortality rate of an age class and the biomass of older fish. In order to estimate the most representative \( M \) for each age group, a search algorithm was used to determine an optimum set of \( M \) by minimizing the sum of squares between the observed \( p(t) \) and calculated values. In so doing, the initial biomass distribution by age must be known. Fortunately, in 1970 and 1971, the DFRC carried out two years of intensive length frequency sampling of commercial sized fish. Based on the length frequency samples and age-length keys, the biomass distribution by age of lizard fish in 1970 was calculated as shown in Table 3. Employing the biomass distribution by age in 1970 as an initial condition, the optimized set of \( M \) values were obtained by the searching algorithm (Table 3).

Now all parameters in the system are derived. To run the model, a series of annual effort data is needed. The annual estimated total effort from 1970 to 1977 in RPA (Yeh et al. 1981) was consequently applied.

Table 2.--Multiple linear regression analysis of \( YE/Q(t) \) vs. \( p(t) \) and \( Q(t) \) where \( YE \) is equilibrium yield, \( B(t) \) is parental stock of lizard fish and \( Q(t) \) is the remainder of the groundfish species in thousands of metric tons.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( p(t) )</td>
<td>57.3</td>
<td>47.1</td>
<td>67.1</td>
<td>114.0</td>
<td>103.2</td>
<td>126.2</td>
<td>110.0</td>
</tr>
<tr>
<td>( Q(t) )</td>
<td>391.0</td>
<td>345.0</td>
<td>366.7</td>
<td>267.5</td>
<td>220.0</td>
<td>264.8</td>
<td>266.0</td>
</tr>
<tr>
<td>( YE/Q(t) )</td>
<td>0.175</td>
<td>0.146</td>
<td>0.108</td>
<td>-0.044</td>
<td>0.302</td>
<td>0.314</td>
<td>0.230</td>
</tr>
</tbody>
</table>

Model: \( YE/Q(t) = a + b Q(t) + c p(t) \)

| Results of parameter estimation | 0.5194 | -0.000927 | 0.0007007 |
| \( R^2 \) | 0.200 |
Fig. 3. Scatter diagrams of YE/Q(t) versus Q(t) at top panel, YE/Q(t) versus p(t) at middle panel, and p(t) versus Q(t) at bottom panel where YE is equilibrium yield, p(t) is parental stock of lizard fish, and Q(t) is the remainder of the groundfish species.

RESULTS OF TWO SPECIES COUPLING MODEL

The results of annual yield and mean CPUE from simulations and the observed data are shown in Figure 4. The results revealed a good correspondence between the two. After 1977, various levels of constant fishing effort were used in the model. The results are also shown in Figure 4. Since the fisheries were virtually nonselective, the results of the two groups should be compared at the same level of fishing effort. At a low constant level of fishing mortality, the abundance of lizard fish tend to fluctuate with a period of about nine years. As simulation time increased, the periodic fluctuations dampened off to a steady state. At a higher constant fishing mortality, however, the periodic phenomenon was less pronounced and a steady state was reached faster. At the constant fishing mortality greater than F = 0.4, which is equivalent to 1.0 million hours of standard hauls per year, the remaining species (group Q) decreases in biomass significantly; whereas the lizard fish seems more tolerant to this level of fishing pressure. Evidently, a reduction in group Q fish in the community results in a significant increase in lizard fish.

Fig. 4. Comparison of yield and catch per unit effort (CPUE) levels between observed data and simulated outcomes for lizard fish (p species) and the remainder of the groundfish species (Q group fish).

Fig. 5. Equilibrium yields for lizard fish (P species), the remainder of the groundfish species (Q group), and for the combined species.
Under a nonselective fishing situation, equilibrium yields of lizard fish, the group Q fish, and the groups combined at the same fishing mortality rates are shown in Figure 5. The equilibrium yield curve of the group Q fish is basically dome-shaped, that of the lizard fish is quite a long flat plateau. Therefore the pooled species curve is also dome-shaped but slightly skewed to the right. The maximum yield occurs at $F = 0.34$ for both groups combined. At that level, lizard fish is exploited at about 90% of its potential. An increase of fishing rate will unfortunately greatly reduce the group Q fish and result in a sharp decrease in pooled yield. The maximum pooled equilibrium yield is about 200,000 t (50,000 t from lizard fish and the rest from the group Q fish). The optimum fishing effort is about 0.85 million hours of standard hauls per year.

If we assume that it is possible to target on a species, we could then allocate different amounts of fishing effort to the two groups. In so doing, an isopleth diagram of equilibrium catch for any combination of fishing mortalities can be obtained. The resulting isopleth diagrams for lizard fish, the group Q fish, and the groups combined are shown in Figs. 6, 7, and 8, respectively. The highest equilibrium yield for lizard fish occurs at $F = 0.6$ and almost zero for lizard fish and the group Q fish, respectively. That of group Q fish occurs at $F = 1.2$ and 0.3 for lizard fish and group Q fish, respectively. Finally, the highest equilibrium yield for the pooled

Table 3.--Age structure of lizard fish in subregion R8A in 1970 and computed age-specific mortality rates.

<table>
<thead>
<tr>
<th>Lizard fish caught in 1970</th>
<th>Size Category</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
</tr>
<tr>
<td>Catch rate (kg/hr)</td>
<td>6.0</td>
</tr>
<tr>
<td>Biomass (x1000 t)</td>
<td>8.1</td>
</tr>
<tr>
<td>Mean Fork Length (cm)</td>
<td>18.00</td>
</tr>
<tr>
<td>Standard Error</td>
<td>2.70</td>
</tr>
</tbody>
</table>

Age-Length Key

<table>
<thead>
<tr>
<th>Fork Length (cm) Intervals</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>II</td>
</tr>
<tr>
<td>22-24</td>
<td>0.714</td>
</tr>
<tr>
<td>24-26</td>
<td>0.382</td>
</tr>
<tr>
<td>26-28</td>
<td>0.031</td>
</tr>
<tr>
<td>28-30</td>
<td>0.522</td>
</tr>
<tr>
<td>30-32</td>
<td>0.268</td>
</tr>
<tr>
<td>32-34</td>
<td>0.109</td>
</tr>
<tr>
<td>34-36</td>
<td>0.003</td>
</tr>
<tr>
<td>36-38</td>
<td>0.066</td>
</tr>
<tr>
<td>38-40</td>
<td>0.004</td>
</tr>
<tr>
<td>40-42</td>
<td>0.192</td>
</tr>
</tbody>
</table>

Length-weight key

<table>
<thead>
<tr>
<th>Age</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average Length (cm)</td>
<td>18.0</td>
<td>23.5</td>
<td>30.5</td>
<td>35.0</td>
<td>39.0</td>
</tr>
<tr>
<td></td>
<td>Average Weight (gm)</td>
<td>35</td>
<td>110</td>
<td>250</td>
<td>400</td>
<td>530</td>
</tr>
</tbody>
</table>

Age Structure in 1970

<table>
<thead>
<tr>
<th>Age</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Catch rate (kg/hr)</td>
<td>6.0</td>
<td>3.2</td>
<td>11.5</td>
<td>12.5</td>
<td>6.6</td>
</tr>
<tr>
<td></td>
<td>Biomass (x1000 t)</td>
<td>8.1</td>
<td>4.3</td>
<td>15.6</td>
<td>17.0</td>
<td>9.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Age</th>
<th>I/II</th>
<th>II/III</th>
<th>III/IV</th>
<th>IV/V</th>
<th>V/VI</th>
<th>VI/VI+</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mortality rate ($M_t$)</td>
<td>0.75</td>
<td>0.10</td>
<td>0.20</td>
<td>0.25</td>
<td>0.80</td>
</tr>
</tbody>
</table>

groups occurs at F = 0.8 and 0.3 for lizard fish and group Q fish, respectively. The highest pooled equilibrium yield for the system is about 240,000 t. If all the species in the demersal community have the same rates of availability and vulnerability to the trawl gear, then the current nonselective fishing practice cannot achieve the highest potential yield, but only 83% of the maximum equilibrium yield of the system.

The average wholesale prices of lizard fish and the group Q fish in the Taiwanese fish market in 1979 were $0.15 and $0.37 per kg, respectively. If this price ratio between the two groups holds, then the fishing practice would gain 12% less total revenue in the long run (Fig. 9). If lizard fish becomes more expensive, say, to $0.38 per kg and group Q fish drop to $0.08 per kg, then the revenue would be 42% less than maximum (Fig. 10). This type of analyses should provide the fishermen some ideas on whether or not to employ special targeting technology on one species or another.

Fig. 7. Isopleth diagram of equilibrium yield (in thousands of metric tons) for the remainder of the groundfish species (group Q fish).

Fig. 6. Isopleth diagram of equilibrium yield (in thousands of metric tons) for lizard fish.

Fig. 8. Isopleth diagram of equilibrium yield (in thousands of metric tons) for combined groundfish species.
DISCUSSION

Figure 4 shows the results of simulation under 3 levels of fishing intensity: F = 0, F = 0.2, and F = 0.3. It shows that if fishing was terminated (F = 0), population recovery for both species groups in the model could be very rapid. This probably reflects the short production cycle of the species due to their short life history.

If the two species groups are exploited at the same non-selective fishing intensity (Fig. 5), such as at F = 0.34, the maximum combined potential yield in region R8A is about 200,000 t. This is about 17% lower than the maximum yield of 240,000 t that could be obtained as a result of selective optimal fishing for each species (Fig. 8). Yeh et al. (1981) estimated the maximum sustainable yield in region R8A to be 250,000 t from a total biomass surplus production model. By comparison, the maximum potential yield estimated by the two species model when fishing is non-selective is 20% lower than that estimated by the surplus production model. The implication of lower yield by the two species model is due to species interactions which may not be explicitly incorporated in the surplus production models.

Studies have indicated that the pooled-species surplus production model generally fits the data better than the fits from component stocks (FAO 1978). However, as Pauly (1979) pointed out, if the relationship between overall biomass and effort is an artifact of the pattern in time series of species exploitation (such as the exploitation starting on lower density high value species with low mortality moving on to the high density low value high mortality species), then the MSY estimated by the pooled-species surplus production model could be artificially high.

This study demonstrates that the MSY estimated from the two species coupled model (which takes into consideration possible species interactions) is about 20% lower than that estimated by using the pooled-species surplus production model. Therefore, we suggest that when the total groundfish catch reaches 80% of the surplus production model MSY, caution should be taken to prevent potential damage to the resources.

![Fig. 9. Isopleth diagram of total revenue (in millions of dollars) when the price of lizard fish and the remainder of the groundfish species (Q) were 15 cents and 37 cents per kg, respectively.](image)

![Fig. 10. Isopleth diagram of total revenue (in millions of dollars) when the price of lizard fish and the remainder of the groundfish species (Q) were 38 cents and 8 cents per kg, respectively.](image)
LITERATURE CITED

Anon. 1970-1977. Annual report of effort and catch statistics by area on Taiwanese demersal fish fisheries. Demersal Fish Research Center, National Taiwan Univ., Taipei, Taiwan, ROC.


ON THE MECHANISM OF DRASTIC CHANGES IN SPECIES COMPOSITION OF
JAPANESE NERITIC PELAGIC FISH RESOURCES

by

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ABSTRACT

The interesting phenomena on drastic changes in species composition in Japanese neritic seas are characterized as follows. First, the dominant species which play a leading role may be limited to few in number and second, the alternation of dominant species occurs from smaller sized species to larger ones in a time series. Further, each species spawns at almost same season in spring in Japan, are plankton feeders, and migrate over a relatively wide range. Those features may be similar to those in other seas of the world.

The question is how to investigate and explain, without contradiction, the above-mentioned phenomena. The authors believe that mortality of larval fish is an essential element in such phenomena. It is therefore important to clarify the causes of larval mortality as one approach to understanding the mechanism of drastic changes.

The authors' premise is that the occurrence of larval mortality must be in predation, that is, divided into two elemental items. One pattern is the cannibalistic mortality on fish eater's larvae (Kawai and Isibasi 1979) and the other is the predation by carnivorous plankton on planktivore's larvae (Kawai and Isibasi 1981). This premise has been proved by quantitative examination. The authors analyzed the drastic changes in species composition in relation to larval mortality by carnivorous plankton and obtained a working hypothesis as follows.

Assuming that a huge number of carnivorous plankton has been generated in some spring season at a coastal area by a certain cause, the majority of eggs and larvae of the dominant fish species at that period must be taken and the area should temporarily become empty. The new fish species may enter the empty but nutritious ground from just outside of it. The new entrant may become the new dominant species until the next big generation of carnivorous plankton occurs. This repetition brings about the big alternation in fish species composition.

Considered thus, it is possible to explain reasonably various phenomena. Namely, the individual spawning season of all fishes which can become the dominant species must be in the same period, the highly migratory species are better able to search for fine spawning grounds, and the change in species composition should occur from a coastal species to an offshore one.

Comparing the quantitative fluctuations of Chaetognatha, one of the typical carnivorous plankton, with the periods of drastic changes in species composition, the relation between the two conditions appears certain. Through analysis on the periodicity of the quantity of carnivorous plankton, the authors estimated that the next change in species composition may occur in a few years.

The management of fish stocks which have a big fluctuation such as the dominant species in the drastic changes in species composition cannot be solved absolutely by using the equilibrium theory. It should be necessary to explore a new management scheme based on ecological characteristics of a certain fish species or species group. The authors introduce a concept of "Index of Fish Stock Health," as indicated by the position of the age at maximum biomass of a cohort. The method is effective not only for assessment of stocks of fishes that show drastic changes, but also for stable resources.

INTRODUCTION

The catch of Japanese sardines fluctuates on a large scale which is no less acute than that of Peruvian anchovy. In the 1930s, the catch of sardine reached 1,600 thousand tonnes which was 41% of all fisheries production in Japan. However, the catch decreased steadily to a minor production of less than 10 thousand tonnes and it was said that the sardine was the phantom fish. Since the 1970s, the condition of the sardine resources has been gradually recovering. In recent years, the catch has increased year by year some hundreds of thousand of tonnes and reached over 4 million tonnes in 1984.

Were there no fishes in the sea when the sardine were in low abundance? There were mackerel during one period, jack mackerel or saury in other periods, in place of the sardine. It is true that the leading role in the sea is alternatively changing from one species to another, a phenomenon called "Gyoshu Koutai (Species Alternation)" in Japan. Although this alternation has been reported recently by many countries, it is not a new occurrence. There are some records of the
large fluctuations in Japanese sardine since the 19th century and it seems appropriate that we think such situations have been occurring over a long period. Moreover, the authors conclude through their evolitional analysis on marine teleosts that the fishes should have been performing the play of the species alternation through some millions of years. It seems that species alternation is a reasonable phenomenon for fishes though it would be considered troublesome for men.

Considering species alternation based on the above-mentioned opinion, the initial power to produce it must lie with the basic character of fish and saury can be dynamic energy as much as power to effect the big changes. The authors pay attention to the prolificity of fish and estimate that the dynamism in larval mortality of fish should be just the initial power which they looked for. The authors, further analyze the method of diagnosing and assessing the big changeable resources condition. The main problem in that respect is how to diagnose the fish resources under conditions of disequilibrium.

SOME FEATURES OF THE PHENOMENA OF SPECIES ALTERNATION

Figure 1 shows the species composition of pelagic fishes caught in Japanese neritic seas. Although the statistics are shown since 1901, those prior to 1955 do not accurately reflect the condition of fish resources because the fisheries were not yet fully developed. The total catch was still unstable in the 1930s and decreased in the 1940s during the Second World War. Thus, the statistics for only the last thirty years can be analyzed. The statistics are illustrated for three typical sea regions and are noteworthy in two features (Kawai 1979).

First, the species that can come to a leading role in species alternation are rather limited in number. The common species in the three areas are sardine and mackerel, but jack mackerel, saury, or other fishes relative to sardine cannot attain the leading role in the species alternation. These phenomena are almost the same in all seas of the world: additional species are only anchovy or herring. What type of species can reach the leading role in species alternation? Three common characteristics of that particular species are as follows:

1. They are planktivores.
2. They are rather highly migratory pelagic fishes.
3. They have a spawning season in the same period, during March and May, in Japanese waters.

The second point is the sequence of the species alternation, which is a change of the leading role from a small species to a large one. In Fig. 1, we see the change of the leading role from smaller species to larger ones. For instance, the alternation in the Japan Sea region starts at sardine, changes to jack mackerel and mackerel, and returns to sardine. In the North Pacific region, the sequence of alternation is sardine, saury, mackerel, and sardine. Clearly, the uppermost species is mackerel which should be the largest planktivore and the leading role again returns to smaller species. This phenomenon must be concerned with the mechanism of the species alternation. This relationship can also be seen in other countries' waters, e.g., the species alternation in the northeast Atlantic Ocean is from herring to mackerel, in the east Indian Ocean from mackerel to sardine through anchovy, in the southern east Pacific Ocean from anchovy to sardine (FAO fisheries statistics since 1965 when the presentation of statistics with species classification was begun) (Isibasi 1981).

As mentioned above, the features of Japanese species alternation are common in other seas and it is imaginable that the mechanism of species alternation may be common in the world.

TWO TYPES OF LARVAL MORTALITY IN MARINE TELEOSTS

Using the information of various fish species (Matsubara and Ochiai 1965; Suehiro 1941), Kawai (1978a and b) analyzed physiological, ecological, and morphological features of teleosts and found that the feeding habits of fishes have influenced conditions of the reproduction process and that feeding habits can be divided into two extremes, i.e. piscivore and planktivore.

Piscivores generally have small eggs, feature faster growth with slower maturity, and can become large in size and a prolific fish. In contrast, although planktivores have almost same size eggs as piscivores, they have a slower growth with faster maturity so that they cannot become as large and have smaller numbers of eggs (Okada 1965) (Fig. 2). As typical examples, we can look at two species, the big-eye tuna and anchovy. Big-eye tuna have an egg of 0.6 mm in diameter, hatched larva of 1.5 mm, and age one year fish are 55 cm in body length. However, the age at first maturity is three years and the biological minimum size is 100 cm so that the fecundity is a marvelous 4.5 million eggs. On the other hand, anchovy have an egg of 1.1 mm, hatched larva of 2.8 mm, and age one year fish of 11 cm in body length. Age at first maturity is one year and anchovy fecundity is about two thousand eggs. The big-eye tuna has a high growth velocity, five times that of anchovy, and
slow maturity, one-third of anchovy, so that their fecundity becomes 2,250 times that of anchovy.

The spawning ground of piscivores is located somewhat off shore where waters are not rich in nutrition and that of planktivores is located in nutritious coastal waters. This phenomenon, high fecundity in unproductive water and low fecundity in nutritious, must be thought an unreasonable thing. Considering the main cause of larval mortality as predatory loss, and combining this with the above-mentioned features, the following hypothesis is advanced.

The main cause of larval mortality of fishes having feeding habits of the piscivore should be cannibalism and that of planktivores should be the predatory loss by carnivorous plankton.

1. Biological basis of cannibalism

Generally, a large spawning in unproductive water means survival rate will be very low. However, if it is effective for development of the species, those produced may have become nutrition for themselves. The mouth size (jaw length) of larval piscivores is usually large and it is not rare to have a mouth large enough to catch fish the same length as themselves even just after hatching (Uchida 1958). Moreover, the jaw length relative to body length reaches a maximum at post-larval stage when larval mortality rate becomes highest (Fig. 3) (Shirota 1978). Those phenomena support the ideas of cannibalism theory. Though it is clear from various observations that cannibalism exists in the larval stage of fishes (Asami 1967), the quantitative influence is still unknown. A mathematical model was developed to calculate this influence.

The initial stock biomass \( W_0 \) is given by:

\[
W_0 = N_0 \cdot W_0 \quad \text{..............................(1)}
\]

where \( N_0 \): initial stock number

and \( W_0 \): body weight of a fish

Assuming that all the brood hatch simultaneously and the stock weight changes due to cannibalism to the biomass \( W_1 \) (assumed to take place simultaneously),

\[
W_1 = \frac{N_0}{2} \cdot W_0 \cdot \left(1 + r\right) \cdot \frac{1 + r}{2} \cdot W_0 \quad \text{..............................(2)}
\]

where \( r \): food efficiency

After the second cannibalism the stock biomass would be

\[
W_2 = \frac{N_0}{2^2} \cdot W_0 \cdot (1 + r)^2 \cdot \frac{1 + r}{2} \cdot W_0 \quad \text{..............................(3)}
\]

due to the stock biomass after \( n \)-th cannibalism is given by:

\[
W_n = \left(\frac{1 + r}{2}\right)^n W_0 = Q^n W_0 \quad (Q = 1) \quad \text{.................(4)}
\]

The change in \( W_n/W_0 \) against \( n \) for various \( r \) is shown in Fig. 4.

A trial application of the above function was made using data for yellowtail around Japan. Adopting an \( r \) for yellowtail in rearing conditions of about 0.25 (Ichimura 1978) and assuming that the growth in length during the post-larval stage is about double, the increase in weight would be about eight times. Therefore

\[
\frac{W_n}{W_0} = (1 + r)^n = 8 \quad \text{and} \quad n = 9.3 \quad \text{.................(5)}
\]

This indicates that about 9-10 cycles of cannibalism would take place for larvae which survived to the post-larval stage. The survival rate during the same period is accordingly estimated to be:

\[
S = \left(\frac{1}{2}\right)^{9.3} = 0.00159 \quad \text{....................(6)}
\]

which accords well with the global estimate of larval survival rate of about 1/1,000.

2. Biological ground of predatory loss by carnivorous plankton

It can sometimes be observed in plankton surveys that large plankton such as medusae or chaetognatha eat fish larvae (Fraser 1969; Hamada 1965; Hattori 1962; Lebour 1923). Laboratory experiments on plankton have been reported that show predation on fish larvae by carnivorous plankton. For instance, Lillevold and Larsen (1971) found a certain copepod eating anchovy larvae and it killed an average of 15 larvae in 24 hours.

The authors estimate the reality of their hypothesis, that larval of planktivores should be lost by predation of carnivorous plankton, through analysis of the quantitative relation between the two: the number of carnivorous plankton and of larvae of fish that are planktivores. The first method is a comparative analysis between the two, under the assumptions that the biomass of zooplankton should total ten times the fish biomass and that carnivorous planktons are medusae, polychaeta, chaetognatha and amphipoda. According to this analysis, the fish larvae exist at about eight times the level of carnivorous plankton so that each plankton must take eight larvae in order to remove all fish larvae. This may be possible according to the results of above-mentioned laboratory experiments.
Second, an attempt was made to calculate the ratio of the two, i.e. the number of carnivorous plankton and planktivore fish larvae, using the data from CSK surveys (Yamazi 1971). The results show that carnivorous planktons exist at 15 times the level of fish larvae.

Quantitative analysis by a mathematical model was also attempted as follows:

\[ N_t = N_0 e^{-Mt} \]  \hspace{1cm} (7)

\[ W_t = W_0 + ct \]  \hspace{1cm} (8)

where: \( N_0 \) and \( W_0 \) are initial stock number and body weight.

\( M \): the natural mortality coefficient which may be proportional to the abundance of carnivorous plankton

\( c \): coefficient of growth which may be proportional to the abundance of food

The stock numbers \( (N_t) \) and individual body weight \( (W_t) \) change during the critical period as

\[ N_t = N_0 e^{-Mt} \]  \hspace{1cm} (7)

\[ W_t = W_0 + ct \]  \hspace{1cm} (8)

where \( M \) denotes the rate of weight increments against the initial body weight \( (c/W_0) \) where an approximation with linear growth function is applied for the rather short time interval during the critical stage. To identify the change in stock biomass in connection with the changes in \( M \), the following are derived from equation (9):

\[ \frac{dW}{dt} = W_0 (G - M - MGt) e^{-Mt} = 0 \]  \hspace{1cm} (10)

the maximum stock biomass \( W_s \) and the time when \( W_s \) is realized are given by

\[ t_s = \frac{1}{M} - \frac{1}{G} \]  \hspace{1cm} (11)

\[ W_s = \frac{G}{M} W_0 e^{-(1 - \frac{M}{G})} \]  \hspace{1cm} (12)

The coordinates of the turning point \((t_h, W_h)\) are given by

\[ t_h = \frac{2}{M} - \frac{1}{G} \]  \hspace{1cm} (13)

\[ W_h = \frac{2G}{M} W_0 e^{-(2 - \frac{M}{G})} \]  \hspace{1cm} (14)

The curves of \( W_t/W_0 \) against \( t \) are shown in Fig. 5 for various values of \( M \).

Equation (11) or Fig. 5 shows that \( W_t > W_0 \) under conditions of \( M < G \) and vice versa. It is generally accepted in natural conditions that the probability of encountering feed is greater than encountering a predator. The stock biomass might therefore be increased slightly to \( W_t > W_0 \), in contrast with the case in cannibalism where \( W_t \) never increased, and \( M < G \) would be realized which gives conditions for the upper limit of \( M \). It is likely, on the other hand, that stock biomass would decrease from initial size \( (W_0) \) at the end of the critical period even though \( W_t \) increased somewhat at intermediate stages. The stock biomass at the end of the critical period (for the entire time interval of \( T \)) is given as

\[ W_T = W_0 (1 + GT) e^{-MT} \]  \hspace{1cm} (15)

\[ W_T > W_0 \]

hence

\[ M > \frac{1}{T} \log (1 + GT) \]  \hspace{1cm} (16)

The above notation gives the condition of the lower limit of \( M \).

The body length of larvae grows generally about double during the post-larva period and the body weight grows accordingly eight times during the same period as

\[ W_0 + ct = 8 W_0 \]  \hspace{1cm} (17)

hence

\[ c = \frac{7}{T} W_0 \]  \hspace{1cm} (18)

the possible range of \( M \) is therefore given by

\[ \frac{\log 8}{T} < M < \frac{7}{T} \]  \hspace{1cm} (19)

or in survival rate \((S)\), as

\[ 0.0009 < S < 0.125 \]

since

\[ S = \frac{N_t}{N_0} = e^{-MT} \]  \hspace{1cm} (20)

The range of the survival rate obtained here for planktivores appears to be well balanced with that of piscivores (about 1/10,000) and also with general information on the larval mortality of this type of fish.

What is the biological meaning of the predatory loss by carnivorous plankton in larval mortality of fish? More than 90\% of fish larvae die every year which means the existence of a large number of predatory animals preying on fish larvae in the sea. There is some discussion that
adult planktivores may eat their larvae together with many plankton. Even if true, adult planktivores have to filter more than 90% sea water. Thus, because of more than 90% larval mortality, this should be impossible. An animal that preys upon fish larvae of a few millimeters length must be small, at most some millimeters or so.

Though the view of fish larval mortality through predation by plankton is a reversal of usual ideas, the point that under certain conditions fishes become nutrition for planktons can show the biological coexistence between fishes and planktons and can be supported by natural theory.

A HYPOTHESIS ON THE MECHANISM OF SPECIES ALTERNATION

1. Proposed hypothesis

The hypothesis on species alternation is now clear from the discussions mentioned above. First, the turning point in species alternation depends on a change in fish larval mortality rate. As the leading role in the alternation is played by planktivores, we must throw light on the predatory loss by carnivorous plankton. Second, it is noted that in the alternation, species switch from a small size to a larger one and mackerel is the largest fish. The authors believe that in this order there should be a switch from a coastal species to an offshore one. Third, the hypothesis considers that each of those species have features of higher migratory fish and have the same spawning season.

The hypothesis on the mechanism of the species alternation, considering those three conditions, is as follows:

If a certain fish species has existed as the dominant stock at present, they would use coastal waters as their spawning ground, as this locale should be nutritionally rich and advantageous as a nursery. In a future period, it can be assumed that a great abundance of carnivorous plankton appear and eat the majority of fish eggs and larvae of the dominant stock species. The nutritious area should become temporarily empty and another species which may be a future dominant species arrives from the offshore side and increases its stock size. The newly entered species must occupy the nutritious area and exist for awhile as a new dominant species until the great abundance of carnivorous plankton next appears.

While Fig. 6 shows a model of the hypothesis, the facts are not so simple and various cases can be considered, e.g. in cases where large generations of carnivorous plankton are continuous or temporary, the effects must be different. But considering this, the solution of some puzzles may be possible. The species alternation always begins with the appearance of a dominant year class and can be explained by the outbreak in a year of carnivorous plankton. The species of leading role is limited to a few migratory species and we can explain the advantage of arrival to the empty coastal water. The most interesting thing is that the outbreak of carnivorous plankton must be a strong enemy for fish larvae, while the plankton should be an available food for adult fish. The coexistence between the carnivorous plankton and fish may be more adroit than we imagine. We note that in the comparative distribution of fish larvae and plankton shown in Fig. 7 (summarized from CSK data), the fish larvae appear more numerous in areas where there are many carnivorous plankton in comparison with total plankton.

2. Examination of the hypothesis

The sampled abundance of carnivorous plankton in oceanographic surveys and the changes of species composition of pelagic fishes in Japanese south coastal waters are compared in Fig. 8. The abundance of carnivorous plankton is represented by chaetognatha sampled during February and March and separated into two areas, inside and outside of the Kuroshio current. As the indicator of species composition the authors use the diversity index of caught fishes which may show the changing period of the species alternation (Kawai, Isibasi, and Takahashi 1983).

Looking at the changes in diversity index, it is at a high level and shows the alternation period from 1960 to 1965 but decreases from 1965 to a lower level during 1970 and 1972 which indicates the increase of the dominant species (mackerel in this case). The diversity index increases then again changes its trend after 1973. It decreases rapidly and shows the rise of a new dominant species (sardeine in this case) and in 1981 finally reaches the lowest value after 1960.

In contrast, the abundance of chaetognatha, especially on the outside the Kuroshio, always shows a big peak just before the decreasing period in the diversity index. In particular, the outbreaks of chaetognatha in 1966 and 1972 correspond well with the changes of diversity indices which change with a time lag of one or two years after the outbreaks. However, the outbreaks of chaetognatha do not always correspond with the species alternation. It seems that the outbreaks in the alternating period accelerate somewhat the alternation. Thus, it is unreasonable to consider that the relation can be seen in all peaks of the two lines showing plankton abundance and diversity index in Fig. 8.

We can also examine the clear relations between the sampled abundance of chaetognatha and catch of specified dominant fish. For instance, mackerel...
resources came to the leading role by the
dominancy of year classes in 1960, 1961, and 1963-68, which correspond with the
periods of maximum biomass of carnivorous
plankton. Further, sardine resources have
increased by appearance of the dominant
year class in 1972 which also corresponded
with a carnivorous plankton outbreak
(Yamazi 1971; Kidachi 1962).

As the above-mentioned shows, the
sampled abundance of chaetognatha may be
useful information for this analysis.
Nevertheless, as carnivorous plankton
should be not only chaetognatha but
medusae, amphipoda, or polychaeta also, it
is important to conduct further studies
that include those species.

3. Forecast on sardine stock

Can we forecast by applying this
hypothesis on species alternation,
particularly for the present sardine
stock? Since the main cause of alternation
depends on outside conditions such as
predatory loss by carnivorous plankton, the
possibility of forecasting outside conditions
is decisive for forecasting changes in the
sardine stock.

The abundance of chaetognatha
shown in Fig. 8 appears to have a certain
cycle. The biological basis of the cycle
is unknown but the cycle is estimated to be
six or seven years. Hence, if the last
peak in chaetognatha abundance was in 1979,
the next peak may appear in 1985 or 1986.
As mentioned above, although the peak of
chaetognatha abundance appears just prior
to the period of species alternation, it is
not always a sign of species alternation.
Thus, the forecast of the next alternation
in 1985 or 1986 is only a possibility and
even if it comes about we must look a few
years later for the alternation in catch
statistics.

A NEW METHOD TO ASSESS THE STATE OF
STOCKS ACCOMPANIED BY LARGE FLUCTUATIONS

It seems to be very difficult to
assess stocks which fluctuate on a large
scale such as those in the leading role of
species alternation. Even in natural
conditions, it may fluctuate so violently
that it would be unreasonable to use
methods dependant on equilibrium conditions
for stock assessment. Hence, we must find
a new index which can represent the
biological state of fish stocks and
consider new methods of stock management.
In various fishes, Kawai (1980) noted that
the age at maximum biomass of a cohort is a
little later than age at first maturity, and
averages at one-third of the distance
from first maturity to the end of the life
span. It is biologically reasonable that a
period of the maximum biomass should be
that most active in the reproduction
process. Moreover, if the mortality rate
of the cohort increases and the peak point
shifts position towards the young and
finally reaches and goes beyond the point
of age at first maturity, this should be
biologically disadvantageous. The authors
use this relation to establish a
mathematical model of the new index of fish
stock health.

In the estimation of age at
maximum biomass of a cohort (t_s), the
biomass of the cohort after the critical
period (W_t) is given by

\[ W_t = w_0 N_t = w_\infty (1 - e^{-kt})^3 N_0 e^{-M_t} \]  \hspace{0.5cm} (21)

where \( w_\infty \) denotes the maximum body weight
and \( k \) the growth coefficient. The age
(\( t_s \)) at the maximum \( W_t \) is given under
the condition of \( d W / d t = 0 \) as,

\[ \frac{3ke^{-kt_s}}{1 - e^{-kt_s}} - M = 0 \] \hspace{0.5cm} (22)

hence

\[ t_s = \frac{1}{k} \log \left( \frac{1 + \frac{3k}{M}}{2} \right) \] \hspace{0.5cm} (23)

The age (\( t_s \)) therefore can be determined
by \( k \) and \( M \). However, some modification of
the function will be better by reason that
\( k \) and \( M \) are usually unstable. Kawai (1970)
reported that the growth coefficient (\( k \))
can be approximated from the age at first
maturity (\( t_m \)) by

\[ k = \frac{0.826}{t_m} + \frac{5}{6} \cdot \frac{1}{t_m} \] \hspace{0.5cm} (24)

Tanaka (1960) proposed the approximation of
the relationship between \( M \) and lifespan
(\( t_1 \)) to be

\[ M = \frac{2.5}{t_1} + \frac{5}{2} \cdot \frac{1}{t_1} \] \hspace{0.5cm} (25)

Substituting these relations into equation
(23), \( t_s \) is now given as

\[ t_s = \frac{6}{5} t_m \log \left( 1 + \frac{t_1}{t_m} \right) \] \hspace{0.5cm} (26)

The age at maximum biomass can, therefore,
be estimated from the age at first maturity
(\( t_m \)) and lifespan (\( t_1 \)).

It was ascertained, after the
investigation of about 30 marine fish
species, that there is a general rule that
\( t_s > t_m \)
which may be rational in reproductive
potential maintenance.

More importantly, the distribution
of \( t_s \) is concentrated in a zone around
1/3 of the interval between \( t_m \) and \( t_i \) as is shown in Fig. 9. On average, the relationship is given as

\[
t_s = t_m - \frac{1}{3} (t_i - t_m)
\]  

(27)

It is surprising to find that the relationship is commonly observed, irrespective of fish species (variation of \( t_i \) and \( t_m \)), which may be derived from the close relationship among the three ages and their potential effects throughout fish species.

When the mortality coefficient is increased/decreased by a difference, \( \bar{\alpha} \), the age at maximum biomass changes to \( t_s' \) as

\[
t_s' = \frac{1}{k} \log \left( 1 + \frac{3k}{M + \alpha} \right)
\]  

(28)

The difference between \( t_s \) and \( t_s' \) is

\[
t_s - t_s' = \frac{1}{k} \log \left( 1 + \frac{3a}{M(N + a + 3k)} \right)
\]  

(29)

that is \( \alpha > 0 \), \( t_s' < t_s \)

and \( \alpha < 0 \), \( t_s > t_s' \)

In other words, the age at maximum biomass decreases in accordance with the increase in mortality. If mortality is seriously increased, \( t_s' \) approaches rapidly to \( t_m \) and would even surpass it in an extreme case which is considered to be a badly deteriorative condition for the cohort for future reproduction.

The condition under which \( t_s = t_m \) is given from

\[
\frac{1}{k} \log \left( 1 + \frac{3k}{M + \alpha} \right) = t_m
\]  

(30)

hence

\[
\frac{\alpha}{M} = 0.769 \left( \frac{t_i}{t_m} \right) - 1
\]  

(31)

the average value of \( t_i/t_m \) for the 30 species which were examined was 2.626, putting this into equation (31).

\[ \alpha = 1.018 \ M \]

which indicates that the age at maximum biomass decreases equivalent to the age at first maturity when the mortality coefficient is increased to about double, for any reasons, of the usual value which is stable in natural conditions.

The authors, therefore, identify the index of fish stock health \( (H) \) as follows:

\[
H = \frac{(t_s' - t_m)}{t_s - t_m}
\]  

(32)

namely, when \( t_s' = t_s \) or \( H = 1 \) the state of fish resources must be most comfortable. So that, \( H \) should be classified into three grades as follows:

- Healthy \( 0 < H < 1 \)
- Borderline \( H = 0 \)
- Unhealthy \( H < 0 \)

The authors are studying the application of this theory, a few actual examples of which are shown in Fig. 10.

**DISCUSSION**

The above-mentioned ideas are the authors' conclusions on the mechanism of species alternation. The authors wish finally to discuss the rationality or the inevitability of species alternation. In animal ecology, it is generally said that species diversity should be connected with the stability of total resources (diversity stability rule). The authors (1983) showed that this rule can be seen in fish ecology also and they estimate that the species alternation is the very phenomenon of this rule.

Pelagic fishes are generally lacking in diversity compared with demersal fishes but each species has the ability to become a large stock. That must be the basic cause of instability of pelagic fish stocks. That is to say, species alternation should be the control process in pelagic fishes in order to extricate themselves from the extreme uniformity (opposite of diversity) of resources by the appearance of dominant cohorts and to stabilize their stock condition. Hence, we should never destroy or avoid the species alternation which must be accordant with the evolution of pelagic fishes. And, if we think about the effective utilization of those fishes, it is important to extricate ourselves from looking at species alternation as a black sheep. The view must be that effective utilization of total production of those fishes is necessary.

Scientific names of fish species shown in this paper:

<table>
<thead>
<tr>
<th>English name</th>
<th>Scientific name</th>
</tr>
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<tr>
<td>Sardine</td>
<td>Sardinops melanosticta</td>
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<td>Engraulis japonica</td>
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<tr>
<td>Mackerel</td>
<td>Scomber japonicus</td>
</tr>
<tr>
<td>Jack mackerel</td>
<td>Trachurus japonicus</td>
</tr>
<tr>
<td>Saury pike</td>
<td>Cololabis saira</td>
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<tr>
<td>Herring</td>
<td>Clupea palisii</td>
</tr>
<tr>
<td>Flying fish</td>
<td>Prionichthys ago</td>
</tr>
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<td>Seriola quingeraida</td>
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<tr>
<td>Mullet</td>
<td>Mugil cephalus</td>
</tr>
<tr>
<td>Big-eye tuna</td>
<td>Thunnus obesus</td>
</tr>
</tbody>
</table>
REFERENCES


Fig. 1. Historical change in the total catch and species composition of neritic pelagic fish around Japan by major sea region.
Fig. 2. Relations between food habits and some ecological features.
Fig. 3. Relative growth of upper jaw against body length during larval and post-larval stages by the type of fish (Shirota 1975).

Group I. T: **Thunnus thynnus**  
Ta: **T. alalunga**  
Tb: **T. albacares**  
K: **Katsuwonus pelamis**

Group II. Se: **Seriola quinqueradiata**  
Tr: **Trachurus japonicus**  
Sc: **Scomber japonicus**  
L: **Lateolabrax japonicus**  
P: **Pagrus major**

Group III. B: **Engraulis japonica**

Group IV. C: **Cololabis saira**
Fig. 4. Change in the relative stock biomass ($W_n/W_0$) against the number of cannibalism ($n$) for various values of feeding efficiency ($r$).
Fig. 5. Change in the relative stock biomass ($W_t/W_0$) with time (t) for various natural mortality coefficients ($M$).
Fig. 6. A model of the mechanism of species alternation.
Fig. 7. Comparison of the abundances among fish larvae, total zooplankton and carnivorous plankton in waters around Japan by 10° square area.

n: number of observation
L: fish larvae
TP: total zooplankton
CP: carnivorous plankton
Fig. 8. Annual changes of the abundance of chaetognatha in number per ten cubic meters and the diversity index on species composition in Shannon's equation. The solid line shows the number of chaetognatha in coastal side water of the Kuroshio current and the dotted line shows that in the offshore side. The line with black circles shows the diversity index.
Fig. 9. Frequency distribution of the number of species against the relative position of the age at maximum biomass.
Fig. 10. Change in the age composition in weight of the selected year classes of Japanese sardine and branquillos in comparison with the age at first maturity ($t_m$) and at maximum biomass ($t_s$).
SPECIES INTERRELATIONSHIPS ON FOOD AND HABITAT UTILIZATION IN FISHES OF SHIJIKI BAY

by

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ABSTRACT

The red sea bream Pagrus major is one of the most important demersal fishes for coastal fishing in Japan. A series of investigations on the ecology of 0-age red sea bream has been carried out since 1975 in Shijiki Bay (Hirado Island, Nagasaki Pref.) to clarify their recruitment process. The present paper deals with the interspecific relationships among fishes especially with the relationships of red sea bream to other species in the nursery ground.

In Shijiki Bay, a greater part of the bottom is covered with well sorted fine sand (Mdₚ = 2-3) forming a healthy and fertile nursery ground for red sea bream. Demersal juveniles of red sea bream begin to occur in this bay in early May. They gradually concentrate in the innermost part of the bay where food is abundant, and reach the young stage in June. In September the majority emigrate to the outside of the bay for wintering.

The seasonal occurrence, minor habitat and food habits of red sea bream were compared with those of other abundant fishes caught in the innermost part of the bay. The latter occupied different niches from the red sea bream. The difference in seasonal occurrence peak was detected for crimson sea bream and stripedfin goatfish; the difference in minor habitat for streaked goby, tiny stinger and net-work filefish; the difference in main food for hairycbin gobty; the difference in feeding time for barface cardinalfish. "Interactive segregation" occurred between red sea bream and hairycbin gobty, i.e., red sea bream always fed mainly on gammaridean amphipods independently of the coexistence with hairycbin gobty; hairycbin gobty shifted their main food from gammaridean amphipods to myisids in the presence of red sea bream.

INTRODUCTION

The red sea bream Pagrus major is one of the most delicious and valuable demersal fishes in Japan. Its landings totaled 15,000 metric tons in 1983. Since the 200-mile fishing jurisdiction was established, it became all the more imperative to exploit the potential of the seas around Japan to meet the increasing demand for fish and shellfish of high quality.

The technology to increase living resources like red sea bream and other species such as chum salmon, scallop, etc., through releasing operation and fisheries management is in progress in our country. To develop this technology, it is essential to estimate the carrying capacity and develop releasing techniques. Information on species interrelationships surrounding target species such as predator-prey interaction, habitat segregation and food segregation is urgently needed.

A series of investigations on the ecology of 0-age red sea bream has been carried out since 1975 in Shijiki Bay (Hirado Island, Nagasaki Pref.) to clarify their recruitment process. The present paper deals with the relationships between red sea bream and other fish species on the nursery ground, by comparing their niches. The niche has three main dimensions: time, habitat and food (e.g., Pianka 1974; Christiansen and Fenichel 1977). The minor habitats are compared first, and the fish species coexistent with red sea bream are identified. Then seasonal occurrences, feeding time, and food habits are compared.

ENVIRONMENTAL FEATURES OF SHIJIKI BAY

Shijiki Bay, about 10 km² in area, is located at the southern end of Hirado Island, Nagasaki Prefecture. Few rivers run into the bay, and almost all the bottom consists of well-sorted, fine sand (Mdₚ = 2-3). Sargassum spp. and Eisenia bicylis grow in the rocky-bottom area; Zostera marina grows densely in the sandy-bottom area, shallower than 7 m, in the innermost part of the bay (Fig. 1).

The flow pattern in Shijiki Bay indicates that the bay can be further subdivided. Two imaginary lines, one between Megasaki and Nagatenohana and the other between Shiomibana and Iidabana, divide the bay into three parts. The outer part has an offshore water mass; the innermost part has a proper bay water mass; and the central part has mixed water of the two adjacent water masses (Tamai 1980). These divisions
are also distinguished by the distribution of nutrients, transparency, sediment, chlorophyll-a and particulate organic matter (Hamada 1980; Kiso 1980a; Sudo et al. 1983), as well as zooplankton fauna (Ueda 1980), macrobenthic fauna (Azuma and Jinno 1980) and demersal fish fauna (Nakabo 1980).

Shijiki Bay, as a whole, is an open bay, because of the strong influence of the Tsushima Current and the absence of rivers. However, in the innermost, relatively enclosed area, detritus from phytoplankton, seaweed, and seagrass are accumulated on the bottom and decomposed by bacteria under aerobic conditions (Sudo et al. 1983). This abundant detritus seems to support the high productivity of benthic crustaceans including gammaridean amphipods. Thus a healthy and fertile nursery ground for fishes is formed in the innermost part of the bay.

GROWTH AND MIGRATION OF 0-AGE RED SEA BREAM IN SHIJKI BAY

The migration pattern of 0-age red sebream in Shijiki Bay closely correlates with the environmental structure of this bay (Fig. 2).

Red sea bream larvae hatched in the adjacent waters of Hirado Island are transported with the current, and are concentrated at the center of the outer part of the bay from early April to late May. Some of them are transported into the central part of the bay, close to the exchange of seawater. The majority of them, however, cannot immigrate into the central part, because of the boundary between the offshore water mass and the inner-bay water mass. Thus these larvae continue to grow in the middle and bottom water of the outer part. When a little larger than 10 mm in total length, red sea bream larvae metamorphose into pelagic juveniles and actively immigrate into the central part across the boundary. They then settle on the bottom at 13-15 mm in total length (Tanaka 1980).

Demersal juveniles feed on calanoid copepods swarming near the bottom, and gradually immigrate and concentrate in the sandy-bottom area of the innermost part where food is abundant. They feed heavily on gammaridean amphipods and grow at the rate of 0.7 mm per day. In June they reach the young stage. In August they reach 70-90 mm in fork length and begin to extend their habitat toward the sandy-bottom area in the central part, the Žostera and the Sargassum zone. By extending their habitat, mysids and others are added to their diet. The majority of them emigrate in September to the outside of the bay for wintering, although some of them remain in the bay even in winter (Azeta et al. 1980a).

INTERSPECIFIC RELATIONSHIPS BETWEEN RED SEA BREAM AND OTHER FISHES

Over 200 species of demersal fishes have been caught by the beam trawl and the Gochi trawl in Shijiki Bay. Here, the relationships of red sea bream to other fish species are examined by comparing niches.

Habitat Analysis

For habitat analysis, demersal fishes were caught at 14 sampling sites in the inner part of the bay, the nursery ground of young red sea bream, on June 12 and July 12, 1977 by beam trawl and the Gochi trawl, respectively. The former caught 1,479 individuals (53 species) and the latter, 4,619 individuals (53 species). 0-age red sea bream (Pagrus major) and hairychin goby (Sagamia geneionema) held first or second rank in number of individuals caught (beam trawl): hairychin goby, 28.1%; red sea bream 27.1% and Gochi trawl: red sea bream 49.3%; hairychin goby, 18.1%.

Figure 3 shows the matrices of C₄ (index of interspecific overlapping, Morisita 1959) on major fish species in the inner part of the bay. These matrices suggest that three distinct fish groups can be discerned: the sandy-bottom group, including Pagrus major, Upenes bensasi, Acentrogobius pflaumii, Hypodytes rubripinnis, Sagamia geneionema and Eynnis japonica; the rocky-bottom group, including Pteragogus flagellifer, Pseudolabrus japonicus, Halichoeres tenuispinna and Sebastiscus marmoratus; and the Žostera zone group, including Rudarius erodes, Dictyopteres viridis, Pseudobleniunus cottoides, Plootosus lineatus, Aulichthys japonicus, Takifugu pardalis and Chaenogobius heptacanthus.

Imabayashi et al. (1975) discussed the interspecific competition for food between red sea bream and net-work filefish (Rudarius erodes) or tiny-stinger (Hypodytes rubripinnis). In Shijiki Bay, net-work filefish and tiny-stinger are year-round residents in the Žostera zone (Fig. 4). Thus the minor habitat of these two species is different from that of the red sea bream.

Seasonal Occurrence Pattern

The habitat analysis of demersal fishes in the inner part of the bay showed that streaked goby (Acentrogobius pflaumii), crimson sea bream (Eynnis japonica), hairychin goby (Sagamia geneionema) and striped-fin goatfish (Upenes bensasi) as well as red sea bream belonged to the sandy-bottom group. Seasonal occurrence patterns of these four species in the sandy-bottom area of the inner part are compared with that of red sea bream, on the basis of monthly data from May 1975 to April 1976 (Fig. 5). The summary of seasonal occurrence patterns of the five species, including red sebream, is as follows:
Red sea bream (*Pseudomugil major*): The density of red sea bream concentrated in the sandy-bottom area of the inner part is highest from mid-June through early July. They begin to extend their habitat toward the sandy-bottom area in the central part, the *Zostera* and the *Sargassum* zones, in August. In September the majority of them emigrate outside of the Bay for wintering (Fig. 2).

Streaked goby (*Acentrogobius plicam*): Newly-born streaked goby begin to appear in the *Zostera* zone of the inner part in September, and extend their habitat to include the sandy-bottom area in December. In late April their density in the sandy-bottom area becomes higher than that in the *Zostera* zone. In May, however, they are distributed only within the *Zostera* zone.

Crimson sea bream (*Evynnis japonica*): Crimson sea bream hatched in the adjacent waters off Hirado Island first occur as demersal juveniles in the sandy-bottom area of the inner part in December. Here, they reach the young stage. Their density is highest in mid-May. In July, the majority of them emigrate outside of the bay.

Stripedfin goatfish (*Upeneus bensasi*): Stripedfin goatfish begin to occur in the sandy-bottom area of the inner part in late June, and their density is highest in mid-August. Unlike the other four species, however, they are distributed throughout almost all the sandy-bottom areas of the bay. In October, the majority of them emigrate outside the bay.

Hairchin goby (*Sagamia geneionema*): Newly-hatched hairchin goby begin to appear in the sandy-bottom area and the *Zostera* zone of the inner part in May. Their density is highest from mid-June through early July in the sandy-bottom area. They are distributed only in the *Zostera* zone in August.

The differences in niche between red sea bream and the other four species are as follows: Streaked goby are different from red sea bream in the minor habitat, because they are distributed only in the *Zostera* zone of the inner part in May, when red sea bream begin to appear in the sandy-bottom area of the inner part. Crimson sea bream and stripedfin goatfish differ from red sea bream in the peak month of occurrence (crimson sea bream: mid-May; red sea bream: mid-June–early July; stripedfin goatfish: mid-August). On the other hand, hairchin goby just overlap with red sea bream in the minor habitat and the seasonal occurrence pattern. Moreover, each species holds a very high rank in number among demersal fishes every year. Thus the food habits of hairchin goby are compared with those of red sea bream.

**Food Habits of Red Sea Bream and Hairchin Goby**

0-age red sea bream in Shijiki Bay change their main food with growth in the following order: Copepoda - Gammaridea - Mysidacea (*Kiso 1980b*). Demersal juveniles of red seabream occurring in the sandy-bottom area of the inner part in late May feed mainly on calanoid copepods swarming near the bottom (*Acartia clausi* and *Acartia steueri*). They feed mainly on gammaridean amphipods from June through August, and then begin to emigrate from the sandy-bottom area of the inner part. In late May hairchin goby occurring in the same area feed mainly on calanoid copepods swarming near the bottom. They feed mainly on mysids from June through July, and then emigrate to the *Zostera* zone of the inner part (*Matsumiya et al. 1980*). Thus these two species feed on the same copepods swarming near the bottom in late May when both of them are few in number. In June when both of them increase in number, however, diet overlapping between the two species become insignificant and the diet overlap index (*a*, Schoener 1970) is lowest at their peaks of abundance. This is because red sea bream feed heavily on gammarids whereas hairchin goby feed heavily on mysids (Fig. 6).

Figure 7 shows Ivlev's electivity indices (*Ivlev 1961*) of three major food items consumed by red sea bream & hairchin goby plotted against each prey supply (prey supply index: biomass of prey/the total number of these two fish species). As is evident from Figure 7, red sea bream prefer gammarids whereas hairchin goby prefer mysids, at the sites where the two species coexist. In the sites where the two species do not coexist, hairchin goby also come to feed on gammarids.

The relation between the electivity index and the prey supply index shows that red sea bream come to select gammarids more strongly with the increase of the gammarid supply; there is no correlation between the mysid selection by hairchin goby and the mysid supply. However, hairchin goby also come to select gammarids with the increase of the gammarid supply independently of the coexistence with red sea bream.

These results suggest that red sea bream always feed mainly on gammarids independently of the coexistence with hairchin goby; hairchin goby shift their main food from gammarids to mysids in the presence of red sea bream. However, the degree of this food segregation varies with the gammarid supply. It is pronounced when the gammarid supply is limited, but less pronounced or nonexistent when the gammarid supply is superabundant.

The term "interactive segregation" was defined by Brian (1956) to mean that ecological differences between species are magnified by interaction. In practice, it is often difficult to prove that the segregation is a direct result of interaction or of ecological divergence (*Nilsson 1977*). However, the process of food segregation between red sea bream and hairchin goby indicates that interactive segregation occurs between the two species in Shijiki Bay, as a result of the dietary shift only by hairchin goby.
Feeding Time of Red Sea Bream and Barface Cardinalfish

The barface cardinalfish Apogon semilineatus is a year-round resident species in Shijiki Bay. Many barface cardinalfish were caught at night in the sandy-bottom area of the inner part. Here, their mode of life is described briefly and compared to that of red seabream with emphasis on feeding habits.

Juvenile barface cardinalfish about 20 mm in fork length first appear in the rocky- and sandy-bottom areas in August. They are active during the day in August, but turn the diurnal activity pattern into the nocturnal one in September (about 30 mm in fork length). They grow to 50-60 mm in December and then their growth stagnates during January-March. Their growth rate increases again in April, and they reach about 70 mm in May and 80 mm in July.

They feed mainly on calanoid copepods during the day in August when they are diurnal. After establishing the nocturnal habits in September, they aggregate quietly beneath rocks or in the shadow of the overhanging ledge without feeding during the day. During the evening twilight, however, they come out into the sandy-bottom area near the rocky habitat and feed mainly on gammarids or mysids. After spending the twilight time on the sandy-bottom habitat, they return to the diurnal shelter during the morning twilight (Azeta et al. 1983).

Figure 8 shows the diel feeding pattern of barface cardinalfish in the sandy-bottom area of the inner part of the bay from July 16 to July 17, 1977. Feeding begins about one hour after sunset and they continue to feed on small crustaceans, mainly gammarids or mysids, until one hour before sunrise. Red sea bream keep still on the bottom without feeding during the night (Azeta et al. 1980b), when many crustaceans including gammarids come up to the bottom surface and the water column. Thus the feeding time of barface cardinalfish is different from that of red sea bream, although the two fish species share gammarids as food.

REFERENCES


Fig. 1. Map of Shijiki Bay. Depth contours are shown in meters.
Fig. 2. Growth and migration of 0-age red sea bream in Shijiki Bay.
Fig. 3. Matrices of C\(\text{\textcopyright}}\) (index of inter specific overlapping) on major fish species in the inner part of Shijiki Bay. Top: the beam trawl catch on 12 June; bottom: the Gochi trawl catch on 12 July, 1977. Pm: Pagrus major; Ub: Openeus bensasi; Ap: Acentrogobius pflaumii; Hr: Hypodytes rubripinnis; Sg: Sagamia geneionema; Pf: Pteragogus flagellifer; Pj: Pseudolabrus japonicus; Ht: Halichoeres tenuipinnis; Sm: Sebastiscus marmoratus; Re: Rudarius erodes; Dv: Ditrema viridis; Pc: Pseudoblennius cottoides; Pl: Plotosus lineatus; Aj: Aulichthys japonicus; Tp: Takifugu pardalis; Ej: Evinus japonica; Rh: Reppomucenus huquenini; Lr: Leiognathus rivulatus; Ch: Chaenogobius heptacanthus.
Fig. 4. Monthly changes in the number of tiny-stinger (*Hypodytes rubripinnis*) and net-work filefish (*Rudarius ercodes*) in the *Zostera* zone and the sandy-bottom area of the inner part of Shijiki Bay from May 1975 to May 1976.
Fig. 5. Seasonal-occurrence patterns of fishes in the sandy-bottom area of the inner part of Shijiki Bay. Top: the growth and emigration; bottom: the changes in relative abundance. Ap: Acentrogobius pflaumi (streaked goby); Ej: Evynis japonica (crimson sea bream); Sg: Sagamia geneionema (hairychin goby); Pm: Pagrus major (red sea bream); Ub: Upeneus bensasi (stripedfin goatfish).
Fig. 6. Changes in diet overlap index (α) between red sea bream and hairychin goby in the sandy-bottom area of the inner part of Shijiki Bay in 1976.
Fig. 7. Ivlev's electivity indices of gammarids (top), mysids (middle), and copepods (bottom) consumed by red sea bream (closed circle) and hairychin goby (open circle) plotted against prey supply indices in the inner part of Shijiki Bay on 12 June, 1977 (modified from Azuma et al. 1983). The left part: sites where the two fish species coexist; the right part: sites where the two fish species do not coexist. The prey supply index: biomass of prey (mg wet wt./15 m²) / the total number of the two fish species (no./haul).
Fig. 8. Diel changes in the feeding rate and food composition (weight %) of barface cardinalfish in the sandy-bottom area of the inner part of Shijiki Bay from July 16-17, 1977 (modified from Azeta et al. 1983). Black bar indicates the dark period. The feeding rate (%): \[
\frac{\text{stomach content weight}}{\text{fish body weight-stomach content weight}} \times 100.
\]
Ga: Gammaridea; My: Mysidacea; Pi: Pisces; Os: Ostracoda.
ABSTRACT

A model of the pelagic ecosystem is used to investigate temporal fluctuations in the density of biomass in the Japan Sea. The model is based on biomass flows between five trophic 'components': 'phytoplankton' (P₀), zooplankton (P₁), non-plankton planktivores (P₂), and small (P₃) and large (P₄) piscivores; and between these components and the outside. Both the body size of individuals, and the trophic levels associated with a component, increase from (P₀) to (P₄). Within a component, biomass increases with growth and immigration, and decreases with emigration, predation, and fishing mortality. Predation rates are calculated using Ivlev's equation and other parameters are estimated from catch statistics. Pelagic fishes act as important agents of biomass flow between components because of their role as predators and because of ontogenetic changes in diet which allow the growth stages of a single species to overlap different trophic components. The importance of the size, or developmental stage, of a pelagic fish in determining its feeding niche contrasts with the predominance of interspecific niche differences characteristic of most groundfish and terrestrial vertebrates.

1. INTRODUCTION

The Japan Sea ecosystem model was originally developed by Menchutkin et al. (1974), and work on the model has continued as part of a cooperative project ('Research on the relationship between the productivity of marine biological resources and their environment') among the Japan Sea Fisheries Research Laboratory, the Meteorological Agency, the Maritime Safety Agency, Hokkaido University, Kyoto University, and several prefectural Fisheries Experimental Stations. Presently the low-level, planktonic high-level, and the benthic high-level production submodels, developed between 1981 and 1985, are being combined to form a whole ecosystem model. In this paper, we describe the planktonic high-level production submodel.

2. THE STRUCTURE OF PELAGIC ECOSYSTEMS

Feeding interactions within pelagic ecosystems are characterized by predator-prey size ratios which vary little with absolute size. This tendency for larger species and larger individuals within a species to consume larger prey is particularly evident in pelagic fishes. Small larvae feed on comparatively small planktonic organisms, and, as these larvae grow, they retain the planktivorous habit while exploiting increasingly larger prey. Some pelagic forms with small adults, such as sardine, anchovy, saury, sand eel, and flying fish, remain planktivorous throughout development, while the members of other species, such as mackerel, horse mackerel, squid, and skipjack, shift to piscivory when they become sufficiently large to prey upon smaller planktivores. These piscivores are, in turn, preyed upon by the large piscivorous adults of species such as yellowtail, tuna, and swordfish.

As a result of the considerable size range spanned by the growth stages of a single pelagic species, cannibalism between these stages can often have important consequences for intraspecific patterns of growth and mortality. This can be a factor even within the juvenile stages as high growth rates may allow early hatching young to cannibalize conspecifics hatching later in the same season.

The importance of a predator's size in determining its diet is a significant characteristic of pelagic ecosystems which sets them apart from terrestrial ones. In terrestrial environments species differences in feeding niche tend to predominate, possibly because the greater spatial complexity found there affords more opportunities for feeding specialization. Marine benthic species seem intermediate between pelagic and terrestrial ones in this regard. While predation is still strongly size-dependent, particularly for species with pelagic juvenile stages, distinct species differences in diet become evident in the demersal adult stages. For example, the bastard halibut, Paralichthys olivaceus, and Magarei, Limanda herzensteini, have very similar body form as adults, but feed on fish and infauna, respectively.

3. COMPONENTS OF THE PELAGIC ECOSYSTEM

The key role of body size in pelagic trophic ecology is reflected in the five trophic components forming the basis of the pelagic ecosystem model (Fig. 1): 'phytoplankton' (P₀), zooplankton (P₁), non-plankton planktivores (P₂), and small...
and (3) are shown in Figure 3. Letting $G(P_{n-1})$ denote the feeding rate \( \text{per unit of predator biomass density} \: \text{mg/m}^2 \) of predators in component \( n \) on prey in component \( n-1 \). In general, when the biomass of component \( n-1 \) is \( P_{n-1} \), then the total predation rate \( \text{mg/m}^2 \text{/time} \) of component \( n \) on \( n-1 \) is

\[
G(P_{n-1})P_n = R_{\text{max}}(1-\exp(k(P_{n-1}-P_{n-1})))P_n
\]

If predators in component \( n \) feed on prey in \( n-1 \) and \( n-2 \) with selectivities on \( a_{n,n-1} \) and \( a_{n,n-2} \), respectively, then the total feeding rate of \( n \) on \( n-1 \) can be written as

\[
C_1 G(a_{n,n-1}P_{n-1}+a_{n,n-2}P_{n-2})P_n
\]

and of \( n \) on \( n-2 \) as

\[
C_2 G(a_{n,n-1}P_{n-1}+a_{n,n-2}P_{n-2})P_n
\]

where

\[
C_1 = (a_{n,n-1}P_{n-1})/(a_{n,n-1}P_{n-1}+a_{n,n-2}P_{n-2})
\]

and

\[
C_2 = (a_{n,n-2}P_{n-2})/(a_{n,n-1}P_{n-1}+a_{n,n-2}P_{n-2})
\]

The selectivity coefficients \( a \) can range from 1 for the most preferable prey to zero for prey that are not consumed. Because field data are presently inadequate to estimate \( R_{\text{max}} \) and \( k \) (eqn. 3), these were estimated according to Ishiwata (1969a, b) and others as follows:

\[
R_{\text{max}} \quad \text{(Maximum feeding rate)}
\]

\[
k = 0.001 \quad 0.000962 \quad 0.00962 \quad 0.0962 \quad (Ivlev's \: constant)
\]

Ivlev's constant \( k \) was obtained by assuming that feeding occurred at half the maximum rate under the initial prey density, thus

\[
R_{\text{max}} \cdot (1-\exp(k(P_{\text{min}}-P))) = R_{\text{max}}/2
\]

and

\[
k = \ln 2/(P-P_{\text{min}}) = 0.693/(P-P_{\text{min}})
\]
6. NATURAL MORTALITY

Natural mortality is death other than that by predation and we assumed the following values:

\[
P_1 = 0.0011, \quad P_2 = 0.00082, \quad P_3 = 0.00055, \quad P_4 = 0.00027
\]

Natural mortality represents biomass that is lost from the system.

7. ASSIMILATION EFFICIENCY AND LOSS BY MAINTENANCE

Only a portion of the food ingested is assimilated by the organism. Hackney and Minns (1974) used an assimilation efficiency \( K \) of 0.8 and Hughes (1970, 1971) obtained a value of 0.39 to 0.41 for a mollusc species. We used \( K = 0.7 \) for all components and estimated the biomass assimilation rate \( (A) \) as

\[
As = \frac{K}{1 - \frac{1}{p_n}} \sum_{i=1}^{n} P_i
\]

The portion of the biomass assimilated by a component subsequently used for its maintenance was estimated as 0.015/day for all components. This is the mean of a number of values given by Ishiwata (1970a, b). The biomass remaining after losses to non-assimilation and maintenance have been deducted represents the increase in the biomass of the component due to predation.

8. FISHING MORTALITY

Daily fishing mortality coefficients, which were assumed to be constant throughout the year, were set at 0.002 \((P_1 \text{ and } P_2)\), 0.005 \((P_3)\), and 0.01 \((P_4)\). Because these values are applied to all the species within a component, they are somewhat lower than those for target species in the fishery.

9. IMMIGRATION AND EMIGRATION

The processes of immigration and emigration are assumed to occur only between the components and the outside and shifts of organisms between components due to growth are not considered in the model. Estimation of the importance of these processes is very difficult and has necessitated an expansion of our research from coastal waters to include biomass movements within the entire Japan Sea. We base our estimates of immigration and emigration on catch data for Moyama Bay. These data were broken down into categories corresponding to the components in our model and immigration was then assumed to be a constant multiple of this catch. These coefficients are 5, 10, 3, and 3 for \( P_1 \) through \( P_4 \), respectively. Emigration was estimated as follows. Letting

\[
P_{i-1} = \text{biomass at the beginning of time interval } i;
\]

\[
P_i = \text{biomass at the end of time interval } i;
\]

\[
C_i = \text{catch in time interval } i;
\]

\[
C_{i-1} = \text{catch in time interval } i-1;
\]

\[
L_i = \text{emigration coefficient in time interval } i;
\]

the biomass lost from a component due to emigration and fishing in time interval \( i \) is

\[
P_{i-1} = P_i - C_i + P_i L_i
\]

Rearranging gives

\[
L_i = 1 - \frac{C_i}{P_i} - \frac{P_i}{P_{i-1}} \quad (8).
\]

Denoting the proportion of biomass removed by the fishery as \( E \) (constant), then

\[
P_{i-1} = \frac{C_{i-1}}{E} \quad \text{and} \quad P_i = \frac{C_i}{E}
\]

Substituting these into (8) gives

\[
L_i = 1 - \frac{C_i}{P_{i-1}} \left(1 + \frac{E}{(C_i/E)/(C_{i-1}/E)}\right)
\]

or

\[
L_i = 1 - \frac{C_i}{C_{i-1}}(E+1) \quad (9)
\]

subject to the constraint that \( 1 > L_i > 0 \).

10. EXPRESSIONS

Defining the following parameters:

\[
P_1 = \text{biomass of component } i;
\]

\[
K_i = \text{assimilation efficiency of component } i;
\]

\[
a_{i,j} = \text{selectivity component of predator } j \text{ for prey } i;
\]

\[
G_i(P) = \text{feeding rate per unit of predator biomass density in component } i \text{ when biomass of prey is } P;
\]

\[
M_i = \text{natural mortality of component } i;
\]

\[
P_i = \text{fishing mortality of component } i;
\]
Change in $P_1 = (\text{predation on } P_0) - (\text{predation by } P_2) - (\text{predation by } P_3) - (\text{natural mortality}) - (\text{maintenance cost}) + (\text{immigration}) - (\text{fishing mortality})$

\[
\frac{dP_1}{dt} = x_{1,2}P_0 - x_{2,3}P_1 - x_{3,4}P_2 + s_2 s_3 P_2 P_3 + s_2 s_3 s_4 P_2 P_3 P_4
\]

Change in $P_2 = (\text{predation on } P_0) + (\text{predation on } P_1) - (\text{predation by } P_3) - (\text{predation by } P_4) - (\text{natural mortality}) - (\text{maintenance cost}) - (\text{emigration}) - (\text{fishing mortality})$

\[
\frac{dP_2}{dt} = x_{2,1}P_0 + x_{1,2}P_1 - x_{3,4}P_2 + s_2 s_3 P_2 P_3 + s_2 s_3 s_4 P_2 P_3 P_4
\]

Change in $P_3 = (\text{predation on } P_1) + (\text{predation on } P_2) - (\text{predation by } P_4) - (\text{natural mortality}) - (\text{maintenance cost}) - (\text{emigration}) + (\text{immigration}) - (\text{fishing mortality})$

\[
\frac{dP_3}{dt} = x_{3,1}P_1 + x_{2,3}P_2 - x_{3,4}P_3 + s_2 s_3 P_2 P_3 + s_2 s_3 s_4 P_2 P_3 P_4
\]

Input values of $P_0$, equations (10) to (13) and initial values of $P_1$ through $P_4$, are necessary conditions to simulate the seasonal biomass changes of the seasonal biomass changes of the components.

11. AN EXAMPLE OF OUTPUT

An example of the model output for Toyama Bay is shown in Figures 4 and 5. These results are for an arbitrary set of initial values and parameters. Figure 4 shows the seasonal changes in biomass density in each component. Densities for $P_0$ are input, other densities are simulated by the model. Figure 5 shows the biomass density of each component and movements of biomass for a single day. Productivity in any component over some time interval is obtained by summing daily values.

12. REFERENCES


Fig. 1. Schematic diagram of the Japan Sea pelagic ecosystem.
Fig. 2. Biological processes of the pelagic ecosystem. L: Emigration; R: Immigration; F: Fishing mortality; M: Natural mortality; Double lines indicate predation.
Fig. 3. Relationship between feeding rate ($R$) and density of prey ($P$), according to Ivlev (1945).
Fig. 4. Seasonal changes of estimated biomass in each component.
Fig. 5. Estimated biomass of each component and daily biomass movements for August 3.
TOPIC NO. 2

ENVIRONMENTAL AND BIOLOGICAL FACTORS AFFECTING RECRUITMENT,
DISTRIBUTION, AND ABUNDANCE OF NON-ANADROMOUS SPECIES

SESSION CO-CHAIRMEN
R.J. Beamish
K. Wakabayashi
RECENT INFORMATION ON THE CAUSES OF VARIABILITY
IN RECRUITMENT OF ALASKA POLLOCK IN THE EASTERN BERING SEA:
PHYSICAL CONDITIONS AND BIOLOGICAL INTERACTIONS

by

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INTRODUCTION

A difficult problem confronting fisheries biologists is to determine the factors responsible for variations in recruitment. For some fish stocks we have a reasonable idea of the major processes that are involved. Starvation, predation, and transport into unfavorable nursery areas appear to be the most important influences upon larval survival. Predation on juveniles may also be important.

Since the collapse of the Peruvian anchovetta, pollock has been the world's largest single species fishery. Pollock comprises 75-80% of the total fish catch in the eastern Bering Sea, and about 1.3% of the world's fish catch. Considering the commercial and ecological importance of pollock, and that recruitment, along with growth and natural mortality, drives stock production, the study of factors that influence recruitment is critical. The relative importance of the various factors and their effect upon the abundance of Alaska pollock in the eastern Bering Sea remains controversial, and trends between environmental indices and recruitment strength are not clearly evident (Bakkala et al. 1985).

The purpose of this paper is to critically review information on the potential causes of fluctuations in year class strength of pollock in the eastern Bering Sea, including work on spawning, larval growth and feeding, predation on eggs and larvae, predation on juveniles, and transport. We will then use this information to deduce the interaction of biotic and abiotic conditions that gave rise to the strong 1978 year class, and compare these conditions to those in several contrasting years.

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SPAWNING ECOLOGY

Where and when spawning occurs can be critical to the survival of young fish. The location of spawning can influence whether larvae are distributed in suitable nursery areas. The time of spawning determines the overlap of larval presence in the water column with the occurrence of environmental conditions that are suitable for survival. Three recent studies have advanced our knowledge of stock structure and spawning. These are the studies of Lynde et al. (1985), Hinckley (1985) and Sakurai (1982). Prior to this work, several models for spawning in the Bering Sea were proposed. These include the familiar one stock (Takahashi and Yamaguchi 1972) and two stock (Hida 1972) models (Fig. 1). For both of these schemes, spawning begins over the outer shelf and spreads inshore. The major spawning season was considered to be from February until July with the peak of spawning from the middle of March until the middle of May. Spawning was successfully related to bottom temperature, probably being restricted to the seaward side of the 2.5°C isotherm (Nishiyama and Haryu 1981). Intense spawning was recently detected in the Aleutian basin (Okada 1983). Nishiyama and Haryu (1981) proposed this to be the first spawning of fish which would later spawn again over the continental shelf.

A new picture of stock structure has emerged with the work of Lynde et al. (1985). Based on length at age characteristics, the fish over the Basin appear to be a separate "production unit" from fish over the southern shelf. Furthermore, fish over the northern slope have growth characteristics which closely resemble those of the Basin fish.

Hinckley's (1985) findings support the concept of at least two "production
determine the annual potential production of eggs, although some fraction of eggs may remain unspawned.

Hinckley (1985) found that the relative fecundity (eggs/unit weight) of fish spawning over the Basin is much lower than that of fish spawning over the shelf. The low fecundity combined with the low growth rates of fish over the Basin indicates a low production potential compared with fish spawned over the shelf.

**LARVAL FEEDING AND GROWTH**

The role of starvation as an important source of larval pollock mortality was considered minimal by a number of investigators (Walline 1983, 1985; Clarke 1984; Nishiyama et al. 1983; Paul 1983).

Walline concluded from his study of larval otoliths that since 1) growth rates were relatively uniform, 2) hatching dates of survivors were spread out over a long period, and 3) dominant year classes don't appear in the population, that annual variations in food supplies may have little effect on the survival of larvae and on eventual recruitment. He postulated that the strength of a year class is determined after the larval period, and may be more heavily influenced by predation than starvation. We advise caution about the general acceptance of these conclusions. First, Walline used analyses by Chang (1974) and Smith (1981) to conclude that no dominant year classes were present in the population. More recent analyses indicate that these earlier studies may not accurately represent year class structure of the pollock population. Dominant year classes do appear and persist in the population (Francis and Bailey 1983; Bakkala et al. 1985). Second, Walline's samples were all collected well after the main spawning season. Therefore, massive starvation may have occurred, but was not detected by his sampling. Third, hatching dates of survivors alone are not indicative of survival success. The determination of survival success requires information on the total number of larvae hatching in each period. Furthermore, for fishes such as pollock with a long spawning season, inferences about survival based on hatching dates would be biased towards the most recently spawned fish, as fish spawned earlier would be subjected to mortality for a longer period. Finally, the two years of Walline's study are likely not representative of conditions in all years.

Clarke's (1984) analysis of samples from 1980 and 1981 conflict with some of the results of Walline. Clarke found that the highest growth rates were achieved in the oceanic area, followed by the outer shelf and middle shelf regions, whereas Walline found the reverse order (Table 1). Clarke's estimates of larval growth rates were lower than Walline's and ranged from 0.17 to 0.32 mm/d. These growth rates were apparently related to the

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**Figure 1.** Hypothetical seasonal movements of pollock in the southeastern Bering Sea based on the concept of one stock (adapted from Takahashi and Yamaguchi 1972) and two stocks (adapted from Maeda 1972) (from Francis and Bailey 1983).
Table 1. Comparison of growth rates (mm/d) by area and study.

<table>
<thead>
<tr>
<th></th>
<th>Walline</th>
<th>Clarke</th>
<th>Laboratory</th>
</tr>
</thead>
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<td>Regime</td>
<td>1979</td>
<td>1980</td>
<td>1981</td>
</tr>
<tr>
<td>Oceanic</td>
<td>0.34</td>
<td>0.24</td>
<td></td>
</tr>
<tr>
<td>Outer shelf</td>
<td>0.35</td>
<td>0.32</td>
<td>0.21</td>
</tr>
<tr>
<td>Middle shelf</td>
<td>0.37</td>
<td>0.17</td>
<td>0.19</td>
</tr>
<tr>
<td>Coastal</td>
<td></td>
<td></td>
<td>0.20</td>
</tr>
<tr>
<td>Laboratory (5-10 mm)</td>
<td></td>
<td></td>
<td>0.18</td>
</tr>
</tbody>
</table>

abundance of copepod nauplii in the different regions.

The size specific growth rates for these two studies are plotted in Figure 2. Walline presented raw data from different stations, whereas Clarke did not present her data, but only presented regression equations for growth of larvae. The growth rates found by Clarke and Walline are compared with those of pollock from northern Japan (Nishimura and Yamada 1984) and with our own growth rates of laboratory reared larvae (Bailey and Stehr, unpubl. ms.), feeding ad libitum at 8-9°C. This graph clearly shows that growth rates of pollock are extremely variable between the studies, years and areas, with differences of up to three-fold. These differences have several possible explanations. First, as Clarke indicated, the abundance of Pseudocalanus was much greater in 1979 (and in 1978) when Walline did his study compared with 1980 and 1981. Second, Clarke does not give collection dates for her larvae, but they were apparently collected from April-June, whereas Walline collected larvae in June-July. In most years the plankton bloom and resulting increase of larval food occurs first over the slope and later over the shelf. Thus larvae collected in June-July (Walline's study) may have been exposed to higher food concentrations over the shelf, and consequently larvae of the middle shelf domain in Walline's study were growing fastest. In contrast, during May-June, copepod naupliar production was apparently highest over the oceanic domain; and growth rates of larvae in Clarke's study were higher there compared with growth rates over the inner and middle shelf. Third, temperatures in June-July would be warm relative to April-May, and this could have contributed to high growth rates in Walline's study. Finally, differences in otolith reading techniques could account for these differences.

Another approach to examine larval feeding success is to calculate the energy intake needed to satisfy growth and metabolic requirements and to compare these estimates to rations determined from stomach contents. Several studies have used either the energetic or stomach analysis method to...
determine the ration of larval pollock (Clarke 1984; Incze et al. 1984; Dagg et al. 1984). The results are conflicting, therefore further work is required on the energetics of larval pollock.

The existence of a "nursery layer" for pollock larvae is an intriguing concept presented by Nishiyama et al. (1983). The two-layer vertical structure of the water column develops in May due to isolation and dilution of the surface layer by freshwater input from ice melt and runoff. Between the upper and lower layers exists a boundary layer where copepod nauplii and pollock larvae are aggregated. Thus this "nursery layer" aggregates prey and protects larvae from mechanical disturbance. These factors provide favorable conditions for larval development and survival. Although Nishiyama and coauthors attributed the successful production of pollock to these hydrographic conditions, they did not speculate on how interannual variability in the formation or composition of the layer could influence relative recruitment strength.

We conclude from the above studies that the question of whether or not starvation is a factor affecting larval survival remains unresolved. It appears evident that more precise information on the energetic requirements of larvae and whether they are meeting these requirements in nature is needed.

PREDATION

Hunter (1984) indicates that mortality of gadid eggs and larvae is high and that predation may be the dominant source of mortality for these stages. Experiments done in our laboratory indicate that few invertebrate organisms are able to effectively prey on pollock eggs, with the exception of predators with large grasping arms, such as gammarid amphipods (Table 2). Eggs may be prey to certain gelatinous zooplankton with armour-piercing nematocysts or entangling threads. Gelatinous zooplankton are very abundant in the eastern Bering Sea. Cooney (1978) reported densities of Aeglethna at 6-7/m² in May-June 1977. Purcell (pers. comm.) reports that Aeglethna probably prey fish larvae as they readily feed on large crustaceans. Hamner (unpubl. ms) reports high densities of many medusae over the outer and middle shelf. These medusae include many species of known predators on fish eggs and larvae, such as Chrysaora, Aequesia, and Phialidium.

In contrast to eggs, early stage larvae are vulnerable to a host of small invertebrates including euphausids, mysids, hyperiid and gammarid amphipods, and many gelatinous zooplankton (Table 2).

Due to the abundance of potential predator populations, predation on eggs and larvae may be a significant factor affecting variability in year class strength. However, at present there is no field data on predation; consequently, much work remains to be done.

PREDATION ON JUVENILES

More is known about predation on juvenile pollock. Juvenile pollock are prey of many fish species (Smith et al. 1984, Livingston 1985), birds and mammals (Kajimura and Fowler 1984) in the eastern Bering Sea. The predation potential of birds, mammals, pollock and other fishes can represent a significant force on the dynamics of the pollock population. Kajimura and Fowler (1984) estimate that marine mammals may consume about 330 thousand tons of pollock annually and seabirds may consume 270 thousand tons. While these biomass may be small relative to the estimated biomass of adult pollock in the Bering Sea (8-12 million tons), most of the prey pollock are young juveniles (0-1 year olds for birds and 1-3 year olds for mammals). Therefore, these tonnages consumed represent enormous numbers. The most complete studies of predators on juvenile pollock are those of Mito (1974, 1980), Livingston et al. (1985) and Dwyer et al. (1985). These studies have examined predation on juvenile pollock by predator size, season and area. Livingston and co-workers found that juvenile pollock are the major prey of Pacific cod, Greenland halibut and Arrowtooth flounder, and a minor prey of Flathead sole. Flathead sole appear to feed mainly on 0-year-old juveniles. Arrowtooth flounder feed on 0- and 1-year-old juveniles, and Greenland halibut and Pacific cod feed on these ages and older pollock.

Cannibalism of pollock is extensive and may play a major role in determining the abundance of year classes. Dwyer (1984) and Dwyer et al. (1985) have discovered that cannibalism is highest on 0-year-old fish in autumn (Fig. 3). These findings have led to a hypothesis that the timing of the transition from juvenile pelagic larvae to the demersal habitat is critical in the predator-prey interaction, and perhaps this transition occurs with mixing of the water column during autumn cooling and storms (Francis and Bailey 1983).

Although cannibalism on juvenile pollock can be extremely high, can it account for the great year to year variability in recruitment that has been observed? Available historical data on stomach contents of adult pollock do not indicate any clear relationships between the degree of cannibalism and resultant year class strength (Table 3). In fact, cannibalism appeared to be extremely high on 0-year-old juveniles of both the 1972 and 1982 year classes; the 1972 cohort developed into a strong year class, and the 1982 may be strong (Bakkala et al. 1985). Cannibalism appeared to be relatively low on the 1977 and 1981 year classes, which were of weak to moderate abundance. These data are qualitative and conclusions drawn from them should be considered tentative. One such
Table 2. Results of laboratory studies on potential predators of pollock eggs and larvae. Each experiment was done in a single one-liter jar with 2 predators and 10 eggs or larvae. Duration of each experiment was 24 h.

*** 80-100% of prey consumed  
** 50-80% of prey consumed  
* 20-50% of prey consumed  
less than 20% of prey consumed

<table>
<thead>
<tr>
<th>Species</th>
<th>Eggs</th>
<th>Early yolk sac larvae</th>
<th>First-feeding larvae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thysanoessa raschi and Euphausia pacifica mixed</td>
<td>-</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Neptacarpus tenuissimus</td>
<td>*</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Parathemisto pacifica</td>
<td>-</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Calliopius laeviusculus</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Pugettia gracilis</td>
<td>-</td>
<td>-</td>
<td>*</td>
</tr>
<tr>
<td>Pleurobrachia dacei</td>
<td>*</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Phialidium sp.</td>
<td>*</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Microcomella sp.</td>
<td>*</td>
<td>**</td>
<td>***</td>
</tr>
<tr>
<td>Sarisia tubulosa</td>
<td>-</td>
<td>***</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 3. Comparison of extent of cannibalism (% of adult stomach contents comprised of juveniles—predominant age class cannibalized in parentheses) with year class strength.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Area of Study</th>
<th>Cannibalism Extent</th>
<th>Year class Consumed</th>
<th>Year class Strength</th>
</tr>
</thead>
<tbody>
<tr>
<td>1970</td>
<td>Summer</td>
<td>SE</td>
<td>50% (1's)</td>
<td>1969</td>
<td>Strong</td>
</tr>
<tr>
<td>1972</td>
<td>Autumn</td>
<td>SE</td>
<td>70-80% (0's)</td>
<td>1972</td>
<td>Very Strong</td>
</tr>
<tr>
<td>1978</td>
<td>Winter</td>
<td>NW</td>
<td>50% (0's)</td>
<td>1977</td>
<td>Moderate</td>
</tr>
<tr>
<td>1978</td>
<td>Winter</td>
<td>SE</td>
<td>10-30% (0's)</td>
<td>1977</td>
<td>Moderate</td>
</tr>
<tr>
<td>1981</td>
<td>Autumn</td>
<td>SE+NW</td>
<td>50% (0's)</td>
<td>1981</td>
<td>Weak</td>
</tr>
<tr>
<td>1982</td>
<td>Autumn</td>
<td>SE</td>
<td>60% (0's)</td>
<td>1982</td>
<td>Strong (?)</td>
</tr>
</tbody>
</table>
conclusion is that possibly the degree of cannibalism reflects the abundance of a year class rather than the impact. Thus, larval or post-larval survival of a strong year class could be so high that the predatory capacity of adults is overwhelmed.

If cannibalism regulates recruitment, one might expect stock biomass and recruitment to be negatively correlated, as in a Ricker type spawner-recruit relationship. This tenet is not supported by a simple plot of recruitment versus stock biomass (Fig. 4), both being determined from cohort analysis (Bakkala et al. 1985). Evidently there is no simple relationship between stock biomass and recruitment. For example, the strong 1972 year class arose from one of the highest levels of stock biomass and the strong 1978 year class arose from a moderate level.

Figure 4. Recruitment versus stock biomass for pollock in the eastern Bering Sea. Dotted lines are mean values for recruitment and biomass (data derived from Bakkala et al. 1985).

TRANSPORT PROCESSES

Transport of eggs' and larvae by currents can influence larval distribution and their presence in suitable nursery areas. Little is known about transport of eggs and larvae in the eastern Bering Sea and its effect on recruitment, although Francis and Bailey (1983) suggest an interaction between spawning location, transport and recruitment. In warm years (such as 1978), spawning should extend over the middle shelf, an area of limited net transport. By contrast, in cold years (such as 1972), spawning should be limited to the open ocean and outer shelf where net transport would be to the northwest. The interaction between transport and location of spawning could be related to the observed strong recruitment of the 1972 year class northwest of the Pribilofs and the strong recruitment of the 1978 year class southeast of the Pribilofs.

In the western North Pacific, several attempts to understand the effects of transport on year class strength have been made. Fadeyev (1980) and Kachina and Sergeyeva (1981) (both cited in Vasil'kov and Glebova 1985) attributed fluctuations in recruitment of pollock in the Okhotsk Sea to geostrophic transport of eggs and larvae. According to these authors, in warm years eggs and larvae are transported hundreds of kilometers into the northern region of the Sea where conditions are poor for survival. By contrast, in cold years eggs and larvae are transported southward into more favorable nursery areas. Vasil'kov and
Glebova (1985) criticized these findings, reporting that there is actually a positive correlation between year class strength and temperature, and furthermore that transport of hundreds of kilometers is impossible. This later assertion is, however, based on the assumption that actual movement of eggs is one-tenth of that inferred from current speeds, due to fine scale circulation. Vasil'kov and Glebova believe that spawning location is more important than transport in determining egg distribution. They hypothesize cold temperatures result in poor recruitment due to effects on egg and larval survival, and in particular they consider low temperatures to be related to poor egg hatching success.

Nakatani and Maeda (1981) report that fluctuations in pollock catches in northern Japan are caused by variations in year class strength caused by mortality of early stages. They concluded that transport of eggs and larvae by currents was responsible for their distribution in suitable nursery areas.

Actual transport of pollock eggs and larvae, much less the effect of such transport, is undocumented in the eastern Bering Sea. A particularly important question in this regard is whether eggs that are spawned over the Basin contribute to recruitment of the more productive shelf stocks.

FORMATION OF THE 1978 YEAR CLASS

There are many possible interactions between abiotic and biotic conditions of the eastern Bering Sea that can influence year class strength. In this section we will deduce how conditions in 1978 may have given rise to an exceptionally strong year class in comparison with the development of the 1979 year class. Although gross environmental features in 1979 were similar to 1978, the 1979 cohort developed into a weak year class. We will also compare conditions during 1978 to those of the 1971 and 1972, years of contrasting environmental conditions which developed into weak and strong year classes respectively.

Using bulk indicators of the physical environment, the years 1978-79 were similar to each other. Pease et al. (1982) reported ice extent for the months of February and March of 670 km and 750 km for 1978 and 560 km and 650 km for 1979. These years both had low anomalies of percent of ice cover years (Nebauer 1983). Both years were warm, with temperature anomalies of about +1°C.

Wind data from St. Paul Island in the Pribilof's are shown in Figure 5 as wind speed and component of wind speed resolved along an axis of 315°T. A negative value of the latter index infers offshore transport. The data have been averaged over 24 h and the wind speed resolved along an axis of 315°T to indicate on/offshore Ekman transport. We can interpret wind speed as an index of mixing, although mixing power is actually a function of the cube of the wind speed. Following Incze (1983) we identify strong mixing events with periods when wind speeds exceed 10 m/s.

Figure 5. Index of offshore/onshore transport as inferred from wind speed resolved along an axis of 315°T (top: positive value is onshore transport), wind speed (middle) and temperature (bottom) for St. Paul Island in a) 1978 and b) 1979.

During the period March-May, when most eggs are spawned, winds which generate offshore transport were more prominent in 1979 than in 1978 (Fig. 5). If such transport conditions can remove early life stages of pollock from the shelf, then this could be a significant factor in the dynamics of the stock.
Strong mixing events were less frequent from March 1 to June 1 in 1978 compared with 1979, numbering 4 and 11 events respectively (Fig. 5). Less mixing in 1978, combined with an unusually low surface salinity compared with the years 1979-81 (Incze 1983), caused a shallow and strongly developed mixed layer in April. Figure 6 shows that the mixed layer in 1978 was especially shallow over the middle shelf compared with 1979, and mixing was all the way to the bottom in 1980-81. Since these were all relatively warm years, spawning of pollock occurred primarily over the middle shelf. Furthermore, we expect that due to warm temperatures, eggs hatched early and yolk reserves were utilized quickly. These conditions would initiate an early demand for larval food.

![Figure 6. Monthly mean mixed layer depth (MLD) during April, 1976-81. The shelf depth to which the water column was isopycnal during the first half of April is shown by arrows in the lower right of the figure. No stations were found mixed to the bottom in April 1978 (from Incze 1983).](image)

Sambroto and Goering (1983) indicate that turbulence in the wind mixed layer is very important in the timing and intensity of the spring bloom. Usually, net phytoplankton growth begins when the critical depth exceeds the mixed layer depth, thus mixed layer shoaling is an essential factor in bloom development. The early shoaling of the mixed layer depth in 1978 probably resulted in the occurrence of an early bloom. In fact, the spring bloom appeared to be about 2 weeks earlier in 1978 than in 1979-81 over the middle shelf (Walsh 1981).

The major food of pollock larvae, at least over the shelf, appears to be nauplii of Pseudocalanus (Nishiyama et al. 1983, Dagg et al. 1984). The population of Pseudocalanus is able to respond quickly to bloom conditions: adult females produce nauplii about 1 week after a bloom at a rate of about 7 nauplii/female/day. Comparison of zooplankton levels is difficult to make from the existing literature (Cooney and Coyle 1982) because different units of measurement are presented and different nets were used to sample zooplankton in 1978 and 1979. Qualitatively it appears, however, that a bloom of Pseudocalanus was present over the middle shelf in April 1978, but was not present in April 1979 (Fig. 7). In 1979 this bloom of Pseudocalanus was detected later in May. In 1978, Pseudocalanus was at its highest peak of abundance near the 2°C isotherm, about the same region where pollock eggs are most abundant (Nishiyama et al. 1983). Maximum concentrations of small particulates (50-330 μm, a size range that includes nauplii and other larval prey) also occurred here.

![Figure 7. Cross shelf abundance of copepods in April 1978 (upper) and April 1979 (lower) (from Cooney and Coyle 1982).](image)

We suggest that a favorable set of physical factors existed in early 1978 leading to a phytoplankton bloom, which in turn resulted in the timely production and concentration of nauplii as larval prey. Incze (pers. comm.) suggests that the overwintering abundance of Pseudocalanus over the middle shelf is also an important factor in the early spring production of copepod nauplii. These conditions were favorable for the feeding and survival of larval pollock. This synthesis supports the concept of a "nursery layer" (Nishiyama et al. 1983), but also implies that interannual variations in timing, spatial scale and composition may cause variations in larval survival.

Other biological factors need to be considered in the development of the 1978 year class. The abundance of copepod nauplii in 1978 may have decreased rates of predation by invertebrates on eggs and larvae. For example, in laboratory studies, the presence of copepods decreases rates of predation on fish larvae by chaetognaths.
Variations in the abundances of apex predators apparently cannot explain the differences in recruitment between the 1978 and 1979 year classes. Birds (Craighead and Oppenheimer 1982, Springer et al. 1982) and fur seals (Fowler, unpublished) were at similar levels in these years. One biotic factor that may have contributed to the 1979 recruitment failure is predation by the 1978 year class of pollock (as 1 year olds) and the 1977 year class of cod (as 2 year olds). However, the 1977 cohort of cod as one year olds in 1978, should have been capable of feeding on 0 year olds of the 1978 cohort of pollock. Furthermore, the concept that heavy interspecific predation by one strong year class on the following year class significantly influences recruitment suggests that adjacent strong year classes do not exist. This is apparently not the case (Bakkala et al. 1985). In fact, the 1978 year class of pollock was preceded by a stronger than average year class.

Warm years are not a prerequisite for recruitment success, as noted by Bakkala et al. (1985). For example, the strong 1972 year class was spawned in an anomalously cold year. We have compared the bulk features of the physical environment in 1972 with those in 1971, a similar year which resulted in a recruitment failure. These were both years of extensive ice cover, so we can assume that buoyancy flux from ice melt was important in establishing stratification and the resulting spring bloom. Both were years of high fur seal abundance and adult pollock stock biomass. As in the 1978/79 comparison, what was apparently different between these years was the frequency of strong mixing events from March to June, numbering 10 in 1971 and 6 in 1972 (Fig. 8). However, there is no plankton data available to test the effects of mixing on phytoplankton production in these years. Furthermore, since spawning most likely occurred over the outer shelf in these cold years, larval food available may have been dominated by nauplii of the large calanoids living there. These copepods have a different life history strategy from Pseudocalanus over the middle shelf and do not produce nauplii in response to bloom conditions.

As we have illustrated in this paper, the production of weak and strong year classes of pollock in the eastern Bering Sea is a complicated process. In our attempts to deduce a posteriori the factors influencing year class strength, we have greatly oversimplified the behavior of the environment. The value of this attempt has been to illustrate that bulk environmental factors may not be successful predictors of recruitment levels. However, analysis of environmental features that currently vary may resolve some of the important processes causing year class fluctuations.

Although the recruitment process is complicated, great progress can be made in our understanding of this component of stock dynamics. New developments in technology are now being applied to processes influencing survival during early life history stages. We suggest that particularly useful applications will be made in the use of satellite tracking to study transport, high resolution lipid profiling to study feeding condition and microscopic otolith analyses to study growth and predation.
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ABSTRACT

The production rate of juvenile Pacific halibut during the last fifty years exhibits a periodic pattern with high points occurring around 1937 and again in 1976, and a low point occurring around 1956. This pattern of annual juvenile production is essentially opposite to the time trend for estimates of adult spawning biomass, which leads to a hypothesis that juvenile production is density-dependent (as argued in Deriso, 1985). An alternative hypothesis about the cyclic pattern in production of young halibut is that it is due to some, as yet unknown, exogenous factor. Consequences of these two hypotheses to management of the halibut resource are investigated.

An addendum to our two hypotheses about production of juveniles concerns whether the shifts in production are due solely to changes in survival or whether growth rates have also changed. We show that consequences to management of a given hypothesis about production are similar qualitatively irrespective of whether growth rate has changed, although the amount of potential yield is highly dependent on halibut growth rates.

INTRODUCTION

Maximum sustainable yield (MSY) and the stock size that produces it are widely recognized as being important measures of potential long-term productivity. This has been recognized throughout the history of IPHC management and, in fact, the Halibut Convention of 1953 explicitly required that IPHC regulations be designed to "...develop the stocks of halibut in the Convention waters to those levels which will permit the maximum sustained yield and to maintain the stocks at those levels...".

The 1979 Protocol amending the Convention changes the words "maximum sustained yield" to "optimum yield". The concept of optimum yield is vague and means different things to different people. Our current philosophy is still to seek to maximize sustained yield, but the emphasis now is on sustainable and not necessarily maximum. We try to avoid causing a boom and bust type of fishery, as has occurred in the past.

The simplest concept of MSY is based on a static environment where the relationship of production to stock size is a dome-shaped curve. Here the sustainable yield increases from near zero in a very small stock to some maximum level at an intermediate stock size and then decreases again to near zero in a stock approaching its maximum size. Competition for limited food and habitat are among the biological mechanisms thought to cause such effects. The problem with this simple concept of MSY is that the environment is not static. Here again it can be shown, theoretically at least, that random uncorrelated changes in the environment do not change the basic result in MSY theory that there is a desirable intermediate stock size for maximum stock production. Unfortunately for fisheries management, the assumption of uncorrelated random changes has been shown repeatedly to be incorrect in recent literature, perhaps most forcefully by Cushing (1982). Walters (1985) argues that auto-correlated environmental changes can be due to either abiotic or biotic factors. The Thompson-Burkenroad debate (Skud 1975) centered largely on the relative importance of auto-correlated environmental variation versus management measures in the decline and subsequent growth of the halibut population in the 1920's and 1930's.

Intermediate term environmental cycles that occur on time scales of 20-40 years can completely confound interpretation of any observed production changes. Further, the choice of appropriate management strategies for obtaining high stable catches varies depending on the cause of major changes in recruit production rate of Pacific halibut. In this paper, we propose the following two alternative hypotheses about production variation: survival is dependent on the density of parent stock size (as argued in Deriso 1985) or alternatively, it is driven solely by a long-term cycle caused by some exogenous factor. We develop a simulation population model for halibut and look at consequences to the fishery of the two hypotheses. We also show how the effect of incidental losses of pre-recruit halibut to the halibut fishery can differ with the two hypotheses. Sub-hypotheses for the two main ones are also considered whereby observed changes in size of halibut is taken to be either a density-dependent phenomenon or due to a cyclical exogenous factor, or else it is a permanent change and fixed into the future. Our comparison of management policies in this paper is a preliminary analysis and we intend to expand the analysis in subsequent research.
METHODS

At the last INPFC Symposium, Quinn et al. (1984) described IPHC methods for estimation of historical abundance and productivity. In this paper we have followed similar catch-at-age analyses, updated in Deriso et al. (1988) to produce estimates of abundance by age (8-20-year-olds) and year (1935-1984) for the Pacific halibut stock. The index of spawning in this paper is the sum over age of age-specific abundance times average weight times fraction of individuals that are sexually mature. Average weight estimates are smoothed averages based on otolith measurements from sampling the commercial catch. Sexual maturity estimates assume the average percent mature females, combined over regions, as listed in Table 2 of St. Pierre (1984). It is important to note the sex composition of the commercial catch is unknown and that average weight estimates are not based directly on fish measurements.

We are especially interested in examining changes in the natural production of halibut. Therefore, we adjusted our estimates of abundance of eight-year-olds upward to account for incidental catch losses. A three-year moving average of incidental catches lagged by four years (to account for the younger mean age of incidental catches) was first multiplied by 1.58 (to adjust for lost net growth to age 8: c.f. Quinn et al., 1984) and then added to our biomass estimates for eight-year-olds. The natural production rate of young halibut is then found by dividing the adjusted biomass of eight-year-olds by the spawning index eight years earlier. Adjusted numerical abundance of eight-year-olds is found by dividing the adjusted biomass by average weight. An index of survival of the young is calculated as the ratio of adjusted abundance of eight-year-olds to the spawning index eight years earlier. Resulting estimates of survival, production, and abundance are similar to those given in Deriso (1985).

A major weakness of estimates produced by the above procedures is that they do not account for temporal changes in the sex ratio of the halibut population. Evidence for such a change is presented in Deriso and Quinn (1981) for TG regulatory Area 2B (British Columbia, Canada). Shifts in the sex ratio over time will primarily affect our estimates of spawning and average weight, which in turn cause potential errors in our estimates of the production rate and survival of the young. Preliminary sex specific data obtained from research cruises are provided in this paper, but we do not yet have enough data from research cruises to properly adjust our estimates of production, survival, and spawning. Adjustments, at least, for changes in sex ratio, may be available after completion of an ongoing project involving discriminant analysis of otoliths.

Management consequences of our alternative hypotheses about factors controlling production are investigated with an age-structured population model. The model accommodates all our hypotheses about factors controlling survival and growth of halibut within the mathematical framework of a generalized Leslie matrix. Age selectivity of fishing mortality and growth rates are based on results from the 1984 stock assessment of Pacific halibut (IPHC unpublished report). Growth rate is defined as the fractional change in weight from one age category to the next with the base weight of eight-year-olds being specified by which particular hypothesis is being examined. Age-specific fishing mortality is the product of an age selectivity factor times full-recruitment fishing mortality (Deriso et al., 1985). Spawning biomass is calculated following the same procedure used to calculate our historical index of spawning. Natural mortality rate is fixed at M = 0.2 and the range of ages considered in the model for adults is for 8- to 20-year-olds. Incidental catch mortality is included only in scenarios where specifically stated.

RESULTS FROM HISTORICAL DATA

Figure 1 shows estimated numbers, biomass, and smoothed average weight of eight-year-olds (the recruits) every year since 1935. These estimates have been adjusted upward, as discussed in the last section, to account for pre-recruit mortality due to incidental catch and, thus, indicate natural changes in recruitment strength. Biomass and numbers of eight-year-olds both were low in the mid-1950's, which adversely affected stock productivity for another ten years or so. Numbers of recruits continued to decline irregularly.

![Graph showing biomass, numbers, and average weight values over years](image)

Figure 1. Biomass, numbers, and average landed weight of eight-year-olds. Numbers and biomass estimates from catch-age analysis are adjusted upward to account for incidental catch losses. Biomass values are given in metric tons and weight is in kilograms.
until 1974 with some recovery evident since then. Biomass recovered much sooner than recruitment and from 1960 to 1975 fluctuated around the long-term average. Since 1975, biomass of recruits has increased substantially. To a large extent the stability of our estimates of biomass between 1960 and 1975 is due to major increases in the average weight of eight-year-olds, the reliability of which is questionable (as discussed in the previous section).

Estimates of production and survival of young halibut are negatively correlated with spawning biomass (Figure 2). Production rates and survival are high from 1935 to 1943 and from 1967 to 1976, when mature stock was low, and vice versa for the years 1944 to 1966. The major change in survival and production rates of the young over time accounts for most of the changes in annual surplus production of the adult stock (Deriso, 1985) with changes in incidental catch accounting for the remainder (Quinn et al., 1984).

One hypothesis to account for the temporal pattern in survival and production of the young is a density-dependent stock and recruitment relationship where high spawning stock densities suppress the production of young (Deriso 1985). We extend Deriso’s analysis here to give results of a least-squares regression of the logarithms of survival against a mature stock biomass, as recommended in Ricker (1975) for a Ricker spawner-recruit curve. With 40 degrees of freedom, the slope estimate is statistically significant ($R = 11.2$). The tight correlation, $R = 0.87$, is somewhat misleading though, as our index of spawning stock is surely measured with error and it appears as a component in both the dependent and the independent variables in the analysis.

An alternative hypothesis to density dependence is that survival and production rates of the young exhibit a cyclic pattern due to some exogenous factor. Many fish populations are thought to exhibit long-term fluctuations due to changes in the environment, as discussed in the Introduction. Changes in survival (Figure 2) appear more indicative of a complete cycle than that for production rate, although both show a definite systematic pattern in time from high to low, then back to high again.

Density-dependent growth is supported by a significant negative correlation, $R = 0.66$, between the smoothed average commercial weight in Figure 1 (through year 1982) and estimates of the number of eight-year-olds similar to those in Figure 1 (Deriso 1985). As discussed in the Methods section, those commercial weights may not be indicative of true changes in sex-specific weights. Table 1 shows sex-specific estimates based on research cruises in the Kodiak region, which indicate that growth increased sharply prior to 1960, (based on the average weight of 10-year-olds for year classes before 1950). Since then, average weight has been stable. The limited time period of estimates available for juvenile five-year-olds shows no systematic changes for either males or females. Research cruise data from other regions are currently being analyzed, but it is clear already that Southward (1967, Page 19) was incorrect about the date in his assertion, ”since the early 1950’s the average weight of halibut of all ages has increased on all grounds from Goose Island to the Bering Sea.” Our results support a change in weight although the exact year of change differs by sex, age, and region.

A refinement of our two hypotheses about production of juveniles is whether the change in average weight of halibut (Figure 1) is a real phenomenon or whether it is perhaps grossly exaggerated because of various sources of errors. We therefore can subdivide our two major hypotheses about production of the young into four hypotheses:

**Hypothesis I(a):** rate of production of juvenile halibut is density-dependent due to both growth and survival being density-dependent

**Hypothesis I(b):** rate of production is density-dependent due to density-dependent survival and growth rates of halibut are constant.

![Figure 2](image-url)
Table 1. Average weight of halibut from the Kodiak region. Weight is given in kilograms and sample size is given in parentheses.

<table>
<thead>
<tr>
<th>Year Classes</th>
<th>Males Age 5</th>
<th>Females Age 5</th>
<th>Males Age 10</th>
<th>Females Age 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre 1920</td>
<td></td>
<td></td>
<td>3.40 (101)</td>
<td>4.49 (67)</td>
</tr>
<tr>
<td>1921-1925</td>
<td></td>
<td></td>
<td>5.62 (91)</td>
<td>12.97 (136)</td>
</tr>
<tr>
<td>1926-1930</td>
<td></td>
<td></td>
<td>5.85 (95)</td>
<td>10.61 (272)</td>
</tr>
<tr>
<td>1931-1935</td>
<td></td>
<td></td>
<td>8.80 (170)</td>
<td>13.65 (333)</td>
</tr>
<tr>
<td>1936-1940</td>
<td></td>
<td></td>
<td>8.66 (251)</td>
<td>16.24 (344)</td>
</tr>
<tr>
<td>1941-1945</td>
<td>1.32 (16)</td>
<td>1.32 (19)</td>
<td>9.98 (67)</td>
<td>19.78 (73)</td>
</tr>
<tr>
<td>1946-1950</td>
<td>1.36 (229)</td>
<td>1.54 (104)</td>
<td>8.48 (70)</td>
<td>19.96 (65)</td>
</tr>
<tr>
<td>1951-1955</td>
<td>1.00 (72)</td>
<td>1.32 (58)</td>
<td>10.07 (375)</td>
<td>16.01 (499)</td>
</tr>
<tr>
<td>1956-1960</td>
<td>0.95 (86)</td>
<td>0.86 (64)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1961-1965</td>
<td>1.00 (56)</td>
<td>1.18 (30)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1966-1970</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1971-1975</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976-1980</td>
<td>1.09 (27)</td>
<td>1.54 (13)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Hypothesis II(a): production has changed due to cyclic exogenous factor(s) which affects both growth and survival.

Hypothesis II(b): production has changed due to cyclic exogenous factor(s) which affects only survival and growth rates are constant.

CONSEQUENCES OF ALTERNATIVE HYPOTHESES TO MANAGEMENT

Simulation results

A computer simulation model was constructed to examine consequences of our four hypotheses to commercial fish yields. Only a small range of possible management strategies are developed so that we can focus on what we consider to be the fundamental differences in fish yields generated by the alternative hypotheses. Forty-two-year scenarios (the length of our entire historical time series of production estimates) were considered for each hypothesis. Catches shown in Figures 3(a) through 3(d) are totals from which adjusted incidental catches must be subtracted.

Constant harvest rate policies are argued to be desirable in Quinn, Deriso and Hoag (1985), so we limit our analysis to these. Three values for full-recruitment fishing mortality (F = 0.1, 0.5, 0.7) were chosen as our options for management because they span the plausible range. F = 0.5 corresponds approximately to F at MSY in Quinn, Deriso, and Hoag (1985) and F = 0.1 is a little below F0.1 (=0.38) from yield per recruit analysis.

Results of hypothesis II (the cyclic exogenous scenarios) are presented in Figure 3(a) for the sub-hypothesis that growth is also cyclic and in Figure 3(b) where growth is assumed fixed at 1984 values. A low fishing mortality rate (F = 0.3) is favored here since it prevents substantial yield declines during the low end of the production cycle. The amount of yield obtained with low exploitation differs widely between hypotheses II(a) and II(b) and shows the importance of growth to the amount of commercial catch available in the future.

Results of hypothesis I (the density-dependent scenario) are presented in Figure 3(c) where size is also assumed to be density-dependent and Figure 3(d) where size is assumed fixed at 1984 values. Those simulation results indicate much less sensitivity to changes in fishing mortality, as compared to results from hypothesis II. A high fishing mortality (F = 0.5 for hypothesis I(a) and F = 0.7 for hypothesis I(b)) are favored here, although stable catches are indicated throughout the ranges of F values. The stability of those catches is somewhat misleading since results are based on a deterministic model where recruitment is precisely that predicted by a Ricker stock-recruitment function. Uncorrelated random perturbations of the recruitment process will naturally generate random changes in setline catch, although the average catch for a given year (generated by averaging several simulations) should give results similar to those in Figures 3(c) and 3(d).

The impact of incidental catch on the future commercial catches varies with which of the hypotheses is true because estimates of incidental catches are not precise. If we knew incidental catch precisely (in terms of 8-year-old biomass lost) then we could adjust setline mortality to precisely offset that loss, and therefore the effect of the incidental loss on the commercial fishery would be the same irrespective of which hypothesis about production of young is true. Since incidental catch estimates are imprecise, we assumed F = 0.2 for the directed setline fishery, irrespective of amount of incidental catch, and looked at two extremes: (i) a 30% annual loss of recruits due to incidental mortality—which is the average loss over the 1960's and 1970's (Quinn, Deriso, and Hoag 1985), and (ii) no
Figure 3(a) and 3(b). Forecasts of total catch as a function of fishing mortality rate and year for hypotheses II(a) and II(b).

loss of recruits from incidental catches. The difference in amount of setline catch between the two extremes (i) and (ii) is the estimated loss due to incidental catches occurring to year classes recruited in 1985 and beyond. Results in Figure 4 show that the loss will differ widely between the two hypotheses I(a) and II(a). High losses in the exogenous scenario II(a) occurred in the later years because the stock will grow much larger when there is no incidental catch losses. Density-dependence prevents large stock growth in hypothesis I(a), irrespective of incidental catch losses.

Optimum Fishing Mortality and Potential Yield

A fishing mortality of 0.5 results in the highest long-term yields under the scenario where both growth and survival are density-dependent (Figure 3(c)). This corresponds to an MSY of about 33 thousand mt (Quinn, Deriso, and Hoag, 1985). If only survival is density-dependent and growth remains constant at present rates, then long-term yields are similar for F's of 0.5 and 0.7; MSY would be higher (about 40 thousand mt) if present growth rates continue (Figure 3(d)).

A low fishing mortality of F = 0.3 provides more stable yields and higher total yields under the scenario where exogenous factors cause cyclical changes in survival and growth (Figure 3(a)). Annual yield declines from 26 thousand mt to about 20 thousand mt over the next 20 years before increasing to about 30 thousand mt in about 40 years. If F is 0.5 or 0.7, potential yield is high during the mid-1980's (over 40 thousand mt) but declines sharply to less than 10 thousand mt in about 30 years; there is also very little increase
stocks prior to 1930 were related to fishing or other factors and whether the increase in stocks from 1930 to 1940 were the result of management. Burkenroad (1948, 1950, 1951, and 1953) claimed that stock changes could not be attributed primarily to the effects of fishing as concluded by Thompson, Dunlop, and Bell (1931). Thompson (1950, 1952) rejected Burkenroad’s arguments and maintained that the fishery was the dominant factor. Huntsman (1953), Ketchen (1956), and Fukuda (1962) argued in support of Burkenroad’s theory that the environment may have been a significant factor in stock changes, but Bell and Pruter (1958) discounted this explanation. Skud (1975) revised estimates of abundance and concluded that Burkenroad rightly questioned Thompson’s interpretations of the early data, but that the revised estimates gave credibility to the thesis that fishing mortality was the major cause of the decline in stock abundance.

Our study shows that even after another 40 years of data we still do not know whether exogenous, environmental factors are the primary cause of changes in natural production rates of the young. The additional hypothesis of density-dependent production is also consistent with our estimates. On the side of Thompson, however, we have shown that, irrespective of whether a long-term environmental cycle or density-dependence occurs, the level of fishing mortality can have a substantial effect on long-term yield. Indeed, it was the exogenous scenario (similar to Burkenroad’s hypothesis) where the amount of fishing mortality had the most effect on stock changes and long-term yields.

Management Implications

We did not thoroughly examine the effect of management action on testing the effect of density-dependence and exogenous factors, but we note that forcing the stock out of phase with the long-term cycle would provide the most information for testing hypotheses. If stocks are allowed to remain high for the next several years, and there is a subsequent decline in survival or growth, there will not be a way of distinguishing between the two effects. On the other hand, sharply reducing stocks over the next few years would provide the data for testing: a subsequent increase in survival or growth would support the density-dependent hypothesis whereas a reduction in survival or growth would support the exogenous hypothesis. However, the cost in terms of future yield of forcing stocks out of phase could be high if exogenous factors turn out to be critical, i.e., stocks would be forced lower at a time when survival and growth would be declining. Hence, the yield available to the setline fishery would be even lower than would have otherwise occurred. The next step in our research will involve looking at these types of "feed-back" effects and actively adaptive policies (Walters, 1985b).

Figure 4. Projected reduction in directed commercial catch for two hypotheses when incidental catch mortality is 30% per year class.

in yield following this decline even though survival and growth are improving. As with other scenario’s, potential yield is much higher if growth remains constant and only survival varies (Figure 3(b)). Potential annual yields of about 40 thousand mt are projected during the 1990-2015 period with an F of 0.3; annual yield then increases sharply to 70 thousand mt by 2025.

These results clearly show that a wide range of potential yields is possible over the next 40 years, depending on changes in survival and growth. Changes in survival and the relationship between survival and density have been examined, but further study is needed to examine changes in growth.

The effect of incidental catch on potential yield was briefly examined in this paper (Figure 4). The results point out the importance of having good estimates of the amount of incidental catches. Without such information, targeting total fishing mortality to some desired level is not possible and, as we have seen, such targeting is especially critical under Hypothesis II, the exogenous scenario. Our analysis also shows the compounding effect incidental catch losses can have under Hypothesis II. The compounding occurs because the incidental catch of juvenile halibut prevents them from reaching sexual maturity and thus reduces potential progeny in subsequent generations. The compounding effect is illustrated in Figure 4 where loss in commercial catch can increase almost exponentially with time.

Thompson-Burkenroad Debate

The Thompson-Burkenroad debate (described by Skud, 1975) involved the question of whether declines in halibut
A low fishing mortality around $F = 0.3$ is supported by results in this paper. It produces higher and more stable yields under the exogenous hypothesis II than those obtained with $F = 0.5$ or $F = 0.7$. A low $F = 0.3$ produced the lowest yields (compared to $F = 0.5$, $0.7$) under the density-dependent hypothesis I. However, the loss in yield with $F = 0.5$ and $F = 0.7$ is much more substantial under hypothesis II than the loss in yield with $F = 0.3$ under hypothesis I.

ACKNOWLEDGEMENTS

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REFERENCES


EFFECTS OF TRANSPORT, TEMPERATURE, AND STOCK SIZE ON RECRUITMENT OF PACIFIC COD (Gadus macrocephalus)

by

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ABSTRACT

During January, February, and March of each year the newly spawned cohort of Pacific cod is in the water in Hecate Strait, British Columbia, Canada as demersal, adhesive eggs and probably bathypelagic larvae. During this period, the water is isothermal from surface to bottom, and characterized by northward water-mass transport. With a 23-year time series of landings-per-unit effort and hydrographic data, we examined the hypothesis that stronger northward transport in some years decreased year-class strength by carrying larvae away from Hecate Strait; that water temperature influenced survival of eggs and larvae; and that stock size influenced recruitment. Multi-variate linear regression did not give a significant fit to the data, but a multi-variate, second-order equation explained 67% of the variance of the recruitment time-series. Transport accounted for most of the variance, with temperature and stock size each accounting for lesser amounts, in that order.

INTRODUCTION

The stock of Pacific cod (Gadus macrocephalus) in Hecate Strait exhibits strong fluctuations in abundance. A population index was previously developed as landings per unit of effort, with fishing effort standardized after studying the influence of vessel tonnage and horse power (Westrheim and Foucher 1985a and b). The time series of 23 years is particularly interesting because the stock has changed not in just one direction as many fished groundfish stocks do, but has gone through two major increases and three major decreases during the period (Westrheim and Foucher 1986). Our purpose in this study is to attempt to explain these fluctuations with hypotheses about the possible effects of hydrographic variables on egg and larval survival. In addition, we looked for effects of stock size on subsequent recruitment.

Our initial work and hypothesis formulation was carried out at a workshop organized jointly by the Fisheries Research Branch (Pacific) of the Canada Department of Fisheries and Oceans and the University of British Columbia to examine the basis for productivity in the biologically productive area of the Hecate Strait (Tyler et al. 1986). The participants formed into two groups, one to consider the effects of species interactions and the other, the influence of physical oceanographic factors on interannual variation in natural production. The objective was to determine whether the two sets of relationships might form a basis for alternative explanations. It emerged that the predation of Pacific cod on Pacific herring (Clupea harengus pallasii) could statistically explain the decreasing and increasing trends in the stocks of both species in Hecate Strait (Walters et al. 1986). The alternative explanation is now provided in this paper.

METHODS

Biological basis for model development

We used the time-place factor method for developing hypotheses rather than developing a matrix of correlation coefficients by systematically exploring a series of monthly time lags between dependent and independent variables. We decided that our modelling should proceed from a priori biological hypotheses rather than exploratory fitting and subsequent rationalization of likely causability. The latter is more likely to give spurious results. In particular, we asked where and when are cod when they spawn, for what period of time and in what place are they larvae. What physical oceanographic phenomena dominate the time-space windows for spawning, and egg, and larval occurrence. We would have extended our hypothesis generation to the juvenile stage, but we have almost no information on that phase. We also ignored factors that might contribute to changes in fecundity and spawning timing in the parent stock, though we decided to consider whether stock size influenced subsequent recruitment. After deciding on time-place factor, we searched for appropriate time series to use in multi-variate statistical fitting.

The stock of Pacific cod under investigation is limited to Hecate Strait (Fig. 1) and international fishery statistical areas 5C and 5D (Westrheim 1984). The fish are in the fishery from age-2 to age-9, but age-6 and older fish are so scarce that catch-at-age analysis cannot be carried out at these ages. Age-3 fish are probably fully recruited to the fishery. Because there are high levels of error associated with age determinations for ages 4 and older, we decided to express recruitment, our response variable, as age-3 fish.

A previously conducted study determined the best way to express change in
stock size, and in relative abundance at age (Westheim and Poucheley 1975b). The method calculated landings per unit effort (LPUE) as kg per hour of trawling, and subsequently uses age-composition to decompose the overall index into age-classes. The landings statistic (LPUE) is used rather than an estimated catch (CPUE), because discards at sea are not recorded regularly, and vary from year to year depending on the markets and abundance of cod. The stock-size index does not represent just potential spawning biomass, since very few age-2 individuals are mature, about 50% of age-3 are mature, and almost all (96%) age-4 are mature (Westheim 1977). The range of the index of spawning stock sizes used in this study is 226 to 1887 kg/hr. Strictly speaking, to study the effect of spawning on recruitment we should estimate egg production, and to measure the effect of intraspecific competition and density dependence we should estimate the biomasses of ages with similar feeding habits. We are not able to make these refinements at present. Trends in age-3 recruitment expressed as year-classes, and the spawning sizes associated with their production, are given in Fig. 2. The age-3 abundances in this figure are plotted against year of birth, not against the year they were caught, so that year-class strength is shown at the year of its production.

Regarding spawning time and location, there is evidence Pacific cod spawn on sandy gravel in the area of Bonilla Island on the eastern side of Hecate Strait, and Reef Island on the western side. Most spawning likely occurs in February and March (unpublished data). The eggs are more dense than sea water and slightly adhesive, indicating they should be found on bottom (Thomson 1963). The larvae are in the water during January, February, and March, most likely near the spawning sites, or to the north of the Strait since prevailing net transport in the area is to the north (Dodimead 1980).

Physical oceanographic basis for model development

The relationship between temperature, salinity, and percentage egg hatch was carried out as a laboratory investigation several years ago (Alderdice and Forrester 1971), and other investigators carried out a resource surface analysis of the data recently (Schunke and McKinney 1984). The recent analysis showed a dome-shaped relationship between percentage hatch and temperature at any salinity level. Peak survival occurred at 4 to 5°C, with decreasing survival at either colder or warmer temperatures.

The most appropriate temperature time-series to use in seeking a relationship between temperature and year-class strength is Bonilla Island Lighthouse surface water data near the cod spawning grounds. Sea surface temperatures are useful because the water in the Strait is isothermal through depth in winter (Dodimead 1980). The coldest water temperature at Bonilla Island for the entire series of data was 4.4°C in January and February 1972. Except for one other year the water temperature was above 5°C. The Bonilla series does not go back as far (only to 1960) as the cod data series and so instead we used another Hecate Strait surface temperature series from the McInnes Island Lighthouse 75 nautical miles to the south at the southern end of Hecate Strait. The mean water temperature in February for each entire series was 5.1°C at Bonilla and 6.3°C at McInnes, and the correlation coefficient shows a very close fit between the two series (r = 0.96). We decided to use this mean temperature because February is the middle of the period for which cod were eggs and larvae (Fig. 2).

We used the above information to formulate a biological hypothesis. If we assumed that eggs and larvae have similar temperature-survival statistics, it is that the laboratory observations apply to the field situation, then we would predict that year-class strength is inversely related to mean February temperatures for the temperature range experienced during the 1958 to 1980 period (4.8-7.7°C).

Another oceanographic phenomenon that might influence year-class strength is net northward water-mass advection during winter. Winds blow strongly from the south at this time, often at gale force (Dodimead 1980). There is dramatic inter-annual variation in wind speed and duration. The winds bring about Ekman Transport towards the coast in the Queen Charlotte Sound area. This advection is northward through Hecate Strait with non-tidal current of about 10 cm/sec -1 in the southern portion of Hecate Strait and sometimes 50 cm/sec -1 in the north where the Strait is narrow (W. Crawford unpublished data). The advection can be measured over the period of interest by using a transport index calculated from the wind field at 51°N, 131°W off Queen Charlotte Sound (Bakun 1973).

Our hypothesis is that high northward advection rates decrease year-class strength by carrying cod larvae away from Hecate Strait with consequent loss to the stock. By looking at plots of the advection time series for January, February, and March, we found that strong transport may occur in any one of the months, or in each of the three months. To develop a time series index of surfactant the three monthly advection times were summed the on-shore transport rates for January, February, and March since any one month is not representative. Mean rates can be calculated by dividing the numbers given in the figures by 3. Since the few away-from-shore advection events would produce no northward advection in the Strait, we set these values to zero when taking the sum (Fig. 2). The range of transport values in the data set is 14 to 449 t/sec/100 m.

Statistical fitting techniques

Data were initially examined by eye as scatter plots of age-3 recruitment against the factors that we selected: Feb-
ruary temperature, the water advection
index, and total stock size. We also ex-
amined the plot of temperature against ad-
vection. Linear least square fitting was
ple means, but we tentatively accept the in-
carried out with Minitab software (Ryan et
dependence.
which indicated that if linear functional rela-
al. 1982) including multiple regression with
relationships exist they are obscured by large vari-
pairs of independent variables, and the
iances. In the plot of recruits against stock
three independent variables. The usual lin-
size, recruitment was low at high
early transformed model of $\log_{e}$ recruits
stock-sizes, but was either low or high at
per unit stock-biomass as a function of
low stock-sizes (Fig. 4). Alternatively, a
dome-shaped curve may be indicated with a
maximum near the relative stock-size of 800
kg/h.

Second-order curvilinear fitting
was carried out using technique and com-
puter programs developed by Schnute and McKinnell
(1984). The method used an 'A' statistic
based on likelihood theory as an objective
function. One-factor, two-factor, and
three-factor curve fitting was carried out.
We did not use Schnute and McKinnell's
(1984) F-distributed B statistic for hypoth-
esis testing on model parameters for two
reasons. First, we were using time-series
data for which adjacent yearly values are
not strictly independent events as would be
laboratory data with well considered exper-
imental design. Second, we carried out stat-
istical fitting to a series of models.
Repeated testing invalidates interpretation
of F-Table probability levels in the sense
that if a test is repeated often enough the
null hypothesis will eventually be rej-
ected. Instead we used the likelihood stat-
istic as an index of relative fit of the
second-order response surface to the vari-
ous models. We also used the $r^2$ statistic as
an index of relative fit to the linear rela-
tionship (slope = 1, intercept = 0) between
estimated (measured) values and values pre-
bicted by the model. Comparisons were made
within a group of one-factor models and
within a group of two-factor models to seek
which factors would give a better fit.
Models with the same numbers of factors
could be ranked by $r^2$ value meaningfully be-
cause they all were equal in their degrees
of freedom. However the interpretation of
variance reduction was not clear in compar-
isons of models with different numbers of
factors because degrees of freedom is re-
duced for models with more factors. The B
statistic, useful in some cases for these
comparisons, could not be used. Therefore
we cannot interpret whether, for instance,
our three-factor model is significantly
different than the best two-factor model.

RESULTS

Linear models

Before using temperature and trans-
port as independent variables we looked for
a relationship between the two. A scatter
plot (Fig. 3) showed that high transport
values might be associated with high tem-
perature values, but that either high or low
temperatures would result in lower transport
values. The correlation coefficient is not
significant ($r=0.46$). The test is not
strictly unbiased because the variables
are means, but we tentatively accept the in-
dependence.

Scatter plots between recruits and
each of the three independent variables in-
dicated that if linear functional relation-
ships exist they are obscured by large vari-
ances. In the plot of recruits against stock
size, recruitment was low at high
stock-sizes, but was either low or high at
low stock-sizes (Fig. 4). Alternatively, a
dome-shaped curve may be indicated with a
maximum near the relative stock-size of 800
kg/h.

The plot of recruits against tem-
perature indicated that greater recruit bio-
mass was associated with higher tempera-
tures, except for an outlier point at 6.0°
(Fig. 5). Both high and low recruitment
levels occurred at low transport values, but
high recruitment did not occur at high
transport values (Fig. 6). Though the
relationships were not well defined, they
were to some degree consistent with the hyp-
otheses that were developed relating phy-
sical factors to recruitment, if we allowed
for the possibility that some of the low
recruit values at high temperatures might be
due to concurrent inhibiting effects of high
transport, and that low recruit values at
low transport levels might be due to con-
current inhibiting effects of low tempera-
ture.

To investigate these possibilities
a multi-variate, linear fit was attempted.
Simultaneous linear fitting of recruits ver-
sus three independent variables did not
reduce variance significantly. The multi-
variate correlation coefficient and the re-
gression slopes were not significant at the
10% probability level.

Curvilinear models

Because of the possible non-linear
relationships between recruits and stock
size, and also recruits and temperature,
multi-variate, second-order (quadratic)
curve fitting was attempted. Our approach
was to fit a series of models of increasing
complexity: a series of three one-factor
models of recruits versus each of the indep-
dendent variables separately; a series of
two-factor models of recruits versus temper-
ature-stock, transport-stock, and trans-
port-temperature; and finally recruits
versus the three independent factors simult-
aneously.

The models were arranged in Table
1 by increasing goodness-of-fit. As the
A-statistic decreased the $r^2$ value in-
creased. Comparing the single-factor models
one can see that transport has far more pre-
dictive power than either temperature or
stock size. Transport alone explains 36.5%
of the variance in the observed versus pred-
icted relationship (Table 1). Stock size
alone could account for the least amount of
variance (1.84%), indicating that a dome-
shaped stock-recruitment curve cannot be
supported as a one-factor model.
Two-factor models were far better in accounting for variance. Stock-size and temperature together accounted for only 13% of the variance, but stock-size and transport accounted for 44%, and transport and temperature together accounted for 60.9% (Table 1). Putting temperature and transport together had a strong effect in reducing residuals and gaining predictive power. Finally, adding stock size to the two-factor temperature-transport model to form a three-factor model improved the predictive power of that two-factor model by only a small degree. The $r^2$ value was 67.3%.

The shape of the 4-dimensional response surface can be examined by a sequence of three drawings in which one of the independent variables is held constant, and isopleth contours of the dependent variable are given on the plane of the axes of the other two independent variables. When stock size is at the index value of 800 kg/h, increase in recruitment is associated with progressively decreased transport from levels of 100 to 20 t/sec/100 m coastline (Fig. 7). The temperature is cool (4.5 to 6.5°C). At less cool temperatures for which there is data (6.5 to 7.5°C) the detracting effects of transport are ameliorated—the highest recruitment levels being associated with the warmest temperatures. When transport is strong enough recruitment levels are somewhat reduced even at the higher temperatures.

The recruitment isopleths for stock size and transport are given at the temperature for best recruitment, 7.4°C (Fig. 8). At transport indices above 100 t/sec/100 m, recruitment increases with decreased stock size, indicating strong density dependence. At stock sizes of larger than 600 kg/h, increases in transport above 80 t/sec/100 m decrease recruitment. At low stock sizes the negative effect of high transport is ameliorated.

The recruitment isopleths for the stock size and temperature variables are given with transport held at the intermediate level of 170 t/sec/100 m (Fig. 9). The density-dependent effect of higher recruitment associated with lower stock size is visible mainly at high temperatures as a drop from the 250 to the 210 isopleth.

The predictive power of the 3-factor model is seen in the time-series plot of the observed (estimated) versus predicted (from the model) values (Fig. 10). The two sets of points are generally very close. The major upward and downward trends are followed by the model. Over the 23-year series, there is overestimation in 12 years and underestimation in 11. Use of the Schnute-McKinnell equation to calculate predicted recruitment from factor values of the three-factor model is given in the Appendix.

DISCUSSION

Of the five years for which there was a poor fit between the observed and predicted values of recruitment, 1977 was particularly interesting because the 3-factor model predicted a much greater recruitment than did the observed series. The unusually high effort directed toward the stock in the late 1970s (Burnham and Foucher 1985) might have resulted in high discards for pre-recruits from the 1977 year-class. Since abundance data were not corrected for discards at sea, the year-class might have been reduced in importance in the statistics through heavy fishing on the young.

To check on the possibility of high discards we examined the weekly narratives filed by groundfish port samplers for the years of 1978 and 1979, when the 1977 year-class should have been partially vulnerable to trawling effort. On May 27, 1978 an entry was made in the port sampler's report that large quantities of small cod were being discarded by the fleet. Again on May 25, 1979 and June 1, 1979 entries were made about large quantities of small cod being discarded. Since 1980 no entries have been made about cod discards. In addition, logbooks for Hecate Strait and Queen Charlotte Sound reported 302 t of cod discarded in 1979 but less than 105 t in all other years for the period 1978 through 1981 (Stanley 1985). We interpreted these records as evidence that a particularly large brood was produced in 1977, that there were heavy discards, and that the model may be more correct in this year than the LPUE series.

The recruit-temperature relationship from the 3-factor fit was different from the original hypothesis, which predicted an optimum temperature in the range of 4 to 5°C and an inverse relationship for the January through March temperatures. Instead highest recruitment occurred above 6.5°C and a positive relationship between recruitment and temperature was evident. One could rationalize the difference as an artifact of working with cod eggs, or else imagine that though egg survival maximizes at 5°C, larvae survival optimizes at higher temperature levels, and that this latter survival rate overrides the former.

Water-mass transport was the most important of the three factors chosen for the model. We supposed that if larval cod were carried away from Hecate Strait they would be lost to the stock. It seemed consistent that when both temperature and stock-size were at levels enhancing survival, the negative influence of strong water advection is reduced in its effect on year-class strength. The size of the spawning stock did not explain as much of the recruitment variance as did the physical factors. One might question whether density dependence was actually exhibited. Supporting our tenuous conclusion is the point that the predator-prey model of cod and herring (Walters et al. 1986) required a density-dependent term for cod in order to fit the Hecate Strait time series. Additional support comes from the shape of the response surface of the three-factor
model (Fig. 8). As described in the results, progressively decreasing stock sizes are associated with progressively larger cohorts. This indicates that density dependence is strong, even though not accounting for much of the variance. To give an example of weak versus strong density-dependent relationships, a species with a stock-recruitment curve that rises from the origin and then becomes flat-topped with further increase in stock size has relatively weak density dependence, whereas a dome-shaped relationship indicates relatively strong dependence. This is because for a flat-topped relationship the compensatory survival rate will only maintain the level of recruitment, not increase the level of recruitment as occurs in the dome-shaped case. The Pacific cod's response surface (Fig. 8) is apparently the right-hand limb of a dome-shaped stock-recruitment relationship. It is difficult to dismiss this shape of response surface as spurious.

An implication for fisheries management is that the stock can sustain the levels of fishing effort that it experienced during the period 1958 to 1980 so long as the physical factors are favourable. Any effect of the historical fishing rate in decreasing the size of the stock did not result in reduced recruitment over the range of spawning stock-sizes in the time series. However, should stock size fall below the level reached in 1971 and 1972 (minimum for the series) stock-recruitment capability that recruitment overfishing could occur. There is evidence that high levels of fishing effort in 1978 and 1979 prevented the main portion of the 1977 year-class from reaching a large enough body size to be commercially valuable. This is a case of growth overfishing without recruitment overfishing. The implication is that use of larger mesh in the trawls would allow larger numbers of young fish to survive and gain weight.

We began this study with an interest in developing a possible physical factor alternative to the cod-herring, predator-prey model put forward by one group of investigators during the Hecate Strait Project workshop (Walters et al. 1986). Our 3-factor model seems a viable alternative. In addition, the effect of physical oceanographic factors on herring recruitment is under investigation. Preliminary findings are that a linear fit to sea surface temperature can explain fluctuations in herring recruitment (pers. comm). Therefore there is a possibility that the herring and cod are simultaneously influenced by warming and cooling. Whether they are produced by favourable oceanographic conditions or an abundance of prey-herring, strong cohorts of adult cod should be fished with maximum historic effort levels. If the predator-prey model is correct strong herring recruitment will be an additional benefit from the fishery on cod. We may be able to distinguish among these models only by capitalizing on a major natural or fishery-induced perturbation that affects herring and cod differentially. Until then the models should be viewed as viable, alternative hypotheses.

ACKNOWLEDGMENTS

We are indebted to Jon Schnute and John W. Glasser for reviewing the manuscript and making constructive suggestions.

REFERENCES


APPENDIX

The equation used to calculate the predicted values of recruitment, \( n \), was:

\[
\begin{align*}
Y^n &= p \cdot q_1^n \cdot r_1 \cdot q_2 \cdot r_2 \cdot t_2 \cdot q_3 \cdot r_3 \cdot t_3 \\
&= q_1^n \cdot r_1 \cdot q_2 \cdot r_2 \cdot t_2 \cdot q_3 \cdot r_3 \cdot t_3 \\
&= q_3^n \cdot t_3 \cdot q_2 \cdot r_2 \cdot t_2 \cdot q_1 \cdot r_1 \cdot t_1 \\
&= q_3^n \cdot t_3 \\
&= q_3^n \\
&= q_3
\end{align*}
\]

(1)

Transformations are necessary between \( Y \) and \( n \); \( x \) and \( q \). The relationship between \( n \) and \( Y \) is:

\[
\begin{align*}
Y &= 2^n \cdot V \cdot V \cdot \bar{V} \\
&= 2^n \cdot V \cdot V \\
&= 2^n \cdot V \\
&= 2^n
\end{align*}
\]

(2)

The relationship between \( q \) and \( X_i \), where \( i = 1, 2, \) or \( 3 \), indexing the independent variables:

\[
\begin{align*}
q_1 &= 2X_1 - U_1 - u_1 \\
q_2 &= 2X_2 - U_2 - u_2 \\
q_3 &= 2X_3 - U_3 - u_3
\end{align*}
\]

(3)

The procedure for using the equation, for example to calculate a predicted recruitment from a set of the independent variables, is to transform each \( X_i \) to \( q_i \) (eq 3), calculate \( n \) (eq. 1) using the parameters given below, then solve for \( Y \) (eq. 2). The model is unstable for \( X_i \) values outside the range of \( X_i \)’s used to estimate the parameters. We used this equation to predict the year-classes as age-3 recruits from 1981 to 1985, inclusive, with the following exceptions: the year-class for 1982 could not be predicted because of a stock size below the fitted range, and the year-class for 1983 could not be predicted because temperature was above the range. Estimated values are not yet available for 1984 and 1985 because the year-classes have not been recruited to the fishery yet.

<table>
<thead>
<tr>
<th>Year-class</th>
<th>Estimated</th>
<th>Predicted</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981</td>
<td>247</td>
<td>58</td>
</tr>
<tr>
<td>1984</td>
<td>-</td>
<td>124</td>
</tr>
<tr>
<td>1985</td>
<td>-</td>
<td>58</td>
</tr>
</tbody>
</table>

The values of the parameters were:

- \( a_1 = 2.2902 \)  
- \( a_2 = -1.4414 \)  
- \( a_3 = -0.4858 \)  
- \( b_3 = -0.25391 \)

\[
\begin{align*}
p &= q_1 \cdot q_2 \cdot q_3 \\
&= 1.8093 \cdot 0.8092 \cdot (-0.9374) \\
&= -1.5414 \\
&= -0.9652 \cdot -0.4741 \cdot -0.2971 \\
&= 0.1231 \cdot 0.5339 \cdot 0.3285 \\
&= 1887 \cdot 226 \cdot 449 \\
&= 357.0 \cdot 26.1 \cdot 7.7 \\
&= 4.8 \cdot 14 \\
&= u_1 \cdot u_2 \cdot u_3 \\
&= 357.0 \cdot 26.1 \cdot 7.7 \\
&= 4.8 \cdot 14 \\
&= u_1 \cdot u_2 \cdot u_3 \\
&= u_1 \cdot u_2 \cdot u_3 \\
&= u_1 \cdot u_2 \cdot u_3 \\
\end{align*}
\]

The table gives the percentage of variance explained by the linear regression of the original estimated values versus the values predicted by the model. The A-statistic is for the minimized residuals around the curvilinear response surface (Schnute and McInnis, 1984).

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>( r^2 )</th>
<th>A-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>One-factor models</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stock size</td>
<td>1.8%</td>
<td>362237</td>
</tr>
<tr>
<td>Temperature</td>
<td>10.2%</td>
<td>305493</td>
</tr>
<tr>
<td>Transport</td>
<td>36.5%</td>
<td>301788</td>
</tr>
<tr>
<td>Two-factor models</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature - stock</td>
<td>18.0%</td>
<td>299463</td>
</tr>
<tr>
<td>Transport - stock</td>
<td>44.0%</td>
<td>262545</td>
</tr>
<tr>
<td>Transport - temperature</td>
<td>60.9%</td>
<td>193234</td>
</tr>
<tr>
<td>Three-factor models</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transport</td>
<td>67.3%</td>
<td>166338</td>
</tr>
<tr>
<td>Stock size</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1. International (Pacific Marine Fisheries Commission) Major Statistical Areas along the west coast of Canada. The fishery time series used in this study are for combined Areas 5C and 5D.
Fig. 2. Time series used in the statistical analysis. The top panel is the relative abundance index of age-3 recruits taken in the fishery, recorded as landings per unit effort (LPUE), and plotted on the year of their birth. The second panel is the index of total stock size, age-2 to age-7. The third panel is the surface temperature in February recorded at McInnes Island Light. The bottom panel is the water-mass transport index in t/sec/100 m along a north-south coastline for the period January, February, and March, as calculated by A. Bakun (1973) from the wind field at 51°N 131°W.
Fig. 3. Scatter plot of February temperature and January, February, March transport index values for each of the 23 years of the time series.
Fig. 4. Scatter plot of stock and recruit levels for each of the 23 years of the time series. The number 2 on the graph field indicates two nearly coincident points.
Fig. 5. Scatter plot of recruitment and February temperatures of each of the 23 years of the time series. The number 2 on the graph field indicates two nearly coincident points.
Fig. 6. Scatter plot of recruitment and transport index values for each of the 23 years of the time series. The number 2 on the graph field indicates two nearly coincident points.
Fig. 7. Isopleth contours of the recruitment response surface (kg/h) against transport and temperature axes with the stock size index held at 800 kg/h. The data ranges can be seen in Fig. 3.
Fig. 3. Isopleth contours of the recruitment response surface (kg/h) against stock size and transport axes with temperature held at 7.4°C. The data ranges can be seen in Figs. 3 and 4.
Fig. 9. Isopleth contours of the recruitment response surface (kg/h) against stock size and temperature axes with transport held at 170 m$^3$. The data ranges can be seen in Figs. 4 and 5.
Fig. 10. Observed and "predicted" recruitment indices (kg/h) over the 23-year time period.
ABSTRACT

Sablefish populations in the northeast Pacific Ocean produce occasional large year-classes. The production of these year-classes is correlated with oceanographic conditions, particularly onshore Ekman transport and high sea surface temperature, at the time of egg and larval development. We propose that large year-classes occur when these favourable oceanographic conditions produce an above average source of food at the time most larval sablefish initiate feeding.

INTRODUCTION

Fish, like other animals and plants, have evolved to optimize their survival in their environment. The size of a population is determined by biological and physical controls. In the absence of a fishery, biological factors may be more important. In the presence of a fishery, physical conditions may become more important because the population may not be able to adjust biologically to the fishery in a relatively short time.

Successful management requires both an understanding of the effects of the fishery on stock size and recruitment as well as how the "fishing effects" interrelate with the animals inherent abilities to optimize its survival. In this study we examine the relationship of sablefish abundance with environmental factors and propose an hypothesis for the relative success of year-classes.

I. EARLY LIFE HISTORY OF SABLEFISH

In 1980, spawning occurred in the Canadian zone from January to March, with 50% of females having spawned by early February (Fig. 1). Mason et al. (1983). The observation by Kobayashi (1957), of larval sablefish off the Aleutian Islands in July and August, was difficult to relate to the timing of spawning because of the possibility of slower larval growth rates in this area. If larval growth rates were similar to rates of growth off British Columbia then maximum spawning may have occurred in March. There are no studies that compare inter-annual variation in spawning time, however, spawning times observed off California in the early 1950s (Phillips and Imamura 1954) and off Vancouver Island (unpubl. data) in 1985, were similar to the timing of spawning off Vancouver Island in 1980.

During 1980, sablefish spawned almost simultaneously in all areas over the Canadian continental slope (Mason et al., 1983, Fig. 2). While there have been no other studies of the distribution of spawning sablefish, tagging studies (Beamish and McFarlane 1983; Dark 1983) have indicated little movement of adult sablefish. For example, it was shown that 81% of the fish tagged from February to September, 1977 to 1980, were recaptured in spawning condition within 100 km of the capture and release location (Mason et al. 1983), indicating no extensive migration although localized movements occur. Thus, it is probable that most sablefish spawn in local areas throughout the continental slope.

Largest catches of both eggs and newly-hatched larvae were taken at sampling depths exceeding 400 m where temperatures were less than 6°C and salinities ranged from 33.7 to 34.4 ppt. In the laboratory, sablefish eggs reared at a temperature of 4°C and a salinity of 34‰ hatched in an average time of 15 days and a size of 4-5 mm (Alderice, pers. comm.). Neutral buoyancy measurements of eggs incubated at 4°C indicated that eggs would float freely at salinities of approximately 32 ppt at fertilization (early blastodermal cap) and 33.25 ppt after 80 h. Just prior to hatching (2 to 3 days) egg density increased, indicating that eggs in the ocean would sink, corroborating the interpretation of Mason et al. (1983) that during late embryonic development the eggs sink in the water volume. Hatching probably occurs at depth and it is likely that the early development of yolk sac larvae takes place below the relatively more dynamic upper waters, since no early yolk sac larvae were captured in the upper water column (Mason et al. 1983).

In the laboratory, time to 1/2 yolk utilization at 4°C was 13 days and at the termination of the experiment (25 days) some yolk was still present. At this stage larvae were 7 mm in length. It is unknown at what point yolk sac larvae move up in the water column, however since some larvae were found in the surface waters at 7-9 mm (Kendall and Clark 1982; Shaw et al. 1985) it is likely that migration towards the surface begins in the late yolk utilization stage. Since ocean temperatures average from less than 6°C at 400 m to 7-10°C at the surface during February-March, it is probable that as the yolk sac larvae move...
up, the rate of absorption would be faster than observed in the laboratory. Based on the pattern of "daily growth ring" formation in juvenile sablefish, Beamish et al. (1983), concluded that there was a period of constant growth after hatching which lasted 19 days. This period of constant growth was believed to be the period of yolk sac utilization. These studies indicate that if maximum spawning occurs by early to mid-February, then early yolk sac larvae would be present near the bottom by late-February. One half yolk sac utilization stage would occur by early March and full yolk sac utilization stage by mid to late March. Unfortunately, it was not possible to verify the depth distribution of larvae in the Mason et al. (1983) study because of the use of oblique hauls and small catches.

The abundance of larval sablefish in the surface waters was studied off the west coast of Vancouver Island during 1984 (Shaw et al. 1985) and 1985 (unpubl. data) using a neuston sampler. During April 1984, 122 tows were made and 722 larvae were captured and in April 1985, 295 tows were made and 2480 larvae captured. Larvae captured during these surveys ranged in size from 7 to 38 mm with a mean size of 16.6 mm (Fig. 3). During each survey, larvae were captured in approximately the same area and relative numbers, and only at night (Shaw et al. 1985). Since only surface sampling gear was used it was not possible to examine the vertical distribution of larvae.

A similar study off Washington, Oregon, and California (Kendall and Clark 1982; Clark 1984) reported that large numbers of larval sablefish occurred on the surface at the same time of year.

The rate of larval growth was not studied during the period of larval abundance in the surface waters, however the range in size of larvae does indicate that growth was rapid. Larval fish captured in 1985 that were transported to the laboratory and fed 2% dry ration/day body weight/day, grew quite rapidly. The average daily growth rate of 5 individuals fed this ration was 1.4 to 2.5%/day until a length of 100 mm. These fish were brought into the laboratory at an average size of 26 mm (April 1984) and by July 11th, 1984, had reached 124 mm and 17.5 gm. Fish that were fed until satiation for 3 weeks and then starved, survived from 2 to 16 days. Fish were cannibalistic when fed a reduced diet.

Stomach contents from larvae less than 12 mm (8-12 mm) collected off Vancouver Island in April 1984 and 1985 indicated that the majority of these fish were feeding primarily on copepod nauplii ranging in size from 80 to 100 um (Table 1). This is similar to results reported for larval sablefish off Washington and Oregon in which copepod nauplii were predominant in larvae less than 12 mm (Grover, J. and Olla, B. pers. comm.).

If the wild fish grew at rates similar to those in the laboratory, they would average approximately 7 to 8 mm, the smallest size found at the surface, by mid-March. Studies of other species (Rosenthal and Hempel 1970; Alderdice and Velsen 1971; Alderdice and Forrester 1974) have reported that the initiation of feeding occurred at approximately 1/2 yolk utilization. If larval sablefish feed in a similar manner, then initiation of feeding would occur between late February and mid-March.

II. RELATIVE YEAR-CLASS STRENGTH

The method for ageing sablefish was first developed in 1977 (Beamish and Chilton 1982). The method has since been validated (Beamish et al. 1985) and it is now known that the interpretation of annuli can be difficult for older fish. This reduced level of precision makes it difficult to identify the exact year in which previous strong year-classes were produced. It is assumed that mortality has been relatively constant since the inception of the fishery and that the fishery did not target on any particular year-class, then it is possible to reconstruct relative cohort strength and develop a year-class index. This was done for the 1967-1978 year-classes by standardizing the sample size for each year of age composition data to 1000 individuals. The numbers of individuals in each age group were adjusted to estimate year-class strength using a natural mortality rate of 0.1. This calculation was made for all year classes from each of the 3 samples. The 3 estimates of year-class strength were then averaged to produce a relative year-class index (Table 2). It is evident that strong year-classes were produced in 1977 and 1967, and that year-classes were extremely poor from 1970 to 1975.

Length frequency data has been collected from the commercial fishery and from research surveys since 1977 (Fig. 4). Samples were collected in all areas from trap and trawl gear. The 1977 year-class first appears in the trawl catches in 1978 and is evident in the length distributions until 1981. Because sablefish growth is extremely variable after a length of approximately 50 cm for males and 55 cm for females (McFarlane and Beamish 1983), it was not possible to monitor the growth of this year-class after age four. Immature fish do not again appear in the length frequency distributions until after 1981. These samples indicate the possible presence of larger than average year-classes in 1980, 1981, and 1983. It is unknown if these year-classes will continue to appear productive as they enter the fishery. The percentage of above average year-classes in 1980 and 1981 has been reported in the Gulf of Alaska (Fujikyo 1985), however, U.S. scientists feel they are much stronger in the Gulf of Alaska than they appear off Canada.
III. RELATIONSHIP TO OCEANOGRAPHIC FACTORS

We examined fluctuations in oceanographic conditions from 1967 (beginning of the fishery) to the present, to identify relationships between oceanographic conditions and relative year-class abundance. The analysis compared relative year-class abundance with Ekman transports, sea surface temperature, sea level, and salinity (Tables 3-7), at the time of spawning.

Weak correlations were found between year-class strength and onshore Ekman transport during the first week of March and sea surface temperature in January and February (Table 8). Although there is a great deal of variability in these relationships, it does indicate the likelihood of producing a strong year-class, such as the 1977 year-class, is increased when onshore Ekman is strong and sea surface temperature is high. The 1967 year-class was produced when onshore transport was average but temperature was above average. The weakest year-classes, identified, 1971-1975, were produced during years of low temperatures and weak onshore or strong offshore transport (Fig. 5). In no case were strong year-classes produced during a year of weak onshore transport and low temperatures.

IV. RELATIONSHIP TO ZOOPLANKTON PRODUCTION

Three species of large copepods, Neocalanus plumchrus, Neocalanus cristatus, and Eucalanus bungii, constitute most (80-90%) of the zooplankton biomass in the epipelagic zone of the subarctic Pacific (Miller et al. 1984). From observations conducted at Ocean Station P during 1980 and 1981, it was reported that the two Neocalanus sp. spawned below 250 m and as deep as 1200 m during the entire year. Most spawning occurred from August through February, resulting in the production of large numbers of eggs and nauplii. After hatching, nauplii moved to the surface and the copepodite stages were at their greatest abundance from April to July (Miller et al. 1984). It is apparent that the reproductive cycle of these two species, as described at Ocean Station P, coincides with the spawning cycle and early development of larval sablefish. The third species, E. bungii, reproduces mainly in May and July, with eggs and nauplii peaking in mid to late July, and would have little importance as a food source for larval sablefish.

Fulton (1973) described the life history of N. plumchrus in the Strait of Georgia and reported that spawning took place in water deeper than 300 m in January, February, and March, and that eggs hatched and nauplii moved towards surface waters from February through April (Fig. 6).

At present, there is no information on copepod reproductive behaviour or egg and nauplii development over the continental slope. However, if the observations at Ocean Station P and the Strait of Georgia apply, it is likely that eggs and nauplii would be present in the deeper water from January through March.

V. HYPOTHESIS FOR THE PRODUCTION OF STRONG YEAR-CLASSES

We believe that favourable oceanographic conditions enhance the amount of food for sablefish larvae. The production of abundant food must coincide with the initiation of larval feeding, possibly as early as the 1/2 yolk sac utilization stage as observed in other species.

Favourable oceanographic conditions could increase survival directly by transporting eggs and larvae into areas of higher production or they may improve the quantity of food for larval sablefish in the spawning area. We have excluded, for the present, the possibility of the physical movement of larvae into more productive onshore areas because our recent biological information indicates that the oceanographic events that were correlated with year-class strength occur prior to the time most larval fish reach the surface.

It is probable that favourable oceanographic conditions increase the amount, and not simply alter the timing of maximum food production. We believe that timing is less important because sablefish probably have evolved to produce larvae at a time and place of optimal food abundance. If abundant food was produced prior to initiation of feeding in most years, there would be selection within the population for earlier spawning and ultimately the initiation of feeding would more closely match the production cycle.

Late February and March are periods of low primary production in waters over the continental slope (Denman, K. pers. comm.). However, at least 2 species of copepods are abundant and are in the period of maximum spawning. Since these species of copepods spawn near the bottom, their eggs and nauplii could provide food for larval sablefish. As shown, the stomach contents of larval sablefish (<12 mm) captured in April off British Columbia contained mainly copepod nauplii and copepodes. Larval sablefish captured off Washington and Oregon also fed predominantly on copepods. Thus it is probable that an increased abundance of copepod eggs and nauplii is responsible for increased larval survival.

It is apparent from the growth rate of larval sablefish that they require large amounts of food to satisfy their metabolic requirements. In the laboratory, starvation of late larval stages occurred in 2 to 12 days. It is likely that starvation would occur faster for earlier larval stages. Starvation has in fact been reported in natural populations. Grover and Olla (in press), reported that, based on body measurements, sablefish larvae...
collected at selected stations off the coast of Washington and Oregon showed evidence of starvation which may indicate the patchiness of larval food resources as discussed by Hunter (1981). Thus, an abundant supply of food at the time of hatching appears to be critical for sablefish survival. Unfortunately, little is known about the factors that affect abundance or timing of reproduction of copepods and changes in species composition. However, it is probable that favourable oceanographic conditions would influence the production of copepods such that abundant production coincided with the initiation of larval feeding.

Other explanations such as predation or cannibalism are also possibilities, however, we believe they are less important than food availability during the larval period. Cannibalism by adults is unlikely to cause fluctuations of the magnitude observed because the adult population is relatively small and stable. Cannibalism by larvae occurs in the laboratory, however, these experiments indicated that the amount of cannibalism was related to the degree of starvation. The abundance of other vertebrate and invertebrate predators is unknown but, considering the relative abundance of sablefish eggs in the ocean at this time (Mason et al. 1983) it is unlikely that this source of mortality causes the fluctuations observed.

It is also unlikely that fluctuations in fecundity as observed for some other species (Ware 1984) cause strong fluctuations in year-class abundance. Sablefish are long lived and extremely fecund and the adult population has not been seriously depleted. Thus small changes in individual fecundity are unlikely to result in major changes in year-class strength.

It is possible that these fluctuations result from predation on post-larval individuals. We suspect that this source of mortality may be important for year-classes following a strong year class but we see no evidence of decreased catches in the commercial fishery of potential predators in the years that strong year-classes were produced.

As mentioned, sablefish have evolved to reproduce at a time and location when primary productivity is low. Obviously, the timing of reproduction has evolved to provide the optimal conditions for egg and larval survival. This should involve minimizing predation on eggs and larvae while maximizing the availability of food for larvae. The timing and location of sablefish reproduction appears closely related to the timing and location of copepod reproduction. Our hypothesis proposes that year-class success is dependent on the availability of food over a relatively short period, however, at present, we are unable to explain the biological relationships between the production of this food and oceanographic conditions.

A population that is dependent upon recruitment from infrequent strong year-classes must have low natural mortality and turnover rates. The large number of year-classes in the sablefish population is a consequence of low natural mortality and ensures that the population survives when oceanographic conditions are marginal or unfavourable. The period between strong year-classes is variable and would select against animals that were short lived, thus it is no coincidence that sablefish are long lived, reproducing for up to 30-40 years in the ocean. If our hypothesis is correct, then proper management may have to ensure that sufficient eggs are available following extended periods of unfavourable environmental conditions. This means that it is important to understand how the natural mortality rate is affected when sablefish are subjected to an intensive commercial fishery.

REFERENCES


Fulton, J. D. 1973. Some aspects of the

Table 1. Stomach contents of larval sablefish (5-12 mm) captured in surface waters off the west coast of Vancouver Island, April 1984-1985.

<table>
<thead>
<tr>
<th></th>
<th>1985</th>
<th>1984</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. examined</td>
<td>30</td>
<td>19</td>
</tr>
<tr>
<td>No. empty</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>No. with food</td>
<td>19</td>
<td>15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Prey</th>
<th>No. (%)</th>
<th>No. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods</td>
<td>7 (12)</td>
<td>4 (19)</td>
</tr>
<tr>
<td>Copepod nauplii</td>
<td>40 (69)</td>
<td>15 (71)</td>
</tr>
<tr>
<td>Copepod eggs</td>
<td>1 (2)</td>
<td>-</td>
</tr>
<tr>
<td>Limacina</td>
<td>10 (17)</td>
<td>-</td>
</tr>
<tr>
<td>Invertebrate eggs</td>
<td>-</td>
<td>2 (10)</td>
</tr>
<tr>
<td>Digested matter</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*65% of stomachs examined from 1984 samples contained unidentified digested matter.

Table 2. Year-class index (YCI) for sablefish (1967-1978 year-classes) formed from the contribution in numbers of each age group to age composition, 1980-1982 from the commercial fishery off the west coast of Canada.

<table>
<thead>
<tr>
<th>Year-class</th>
<th>1980</th>
<th>1981</th>
<th>1982</th>
<th>YCI</th>
</tr>
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### Table 8. Results of correlation analysis\(^a\) relating sablefish year-class abundance to oceanographic conditions. (+) significant correlation.

<table>
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<th>Year-class abundance</th>
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<tr>
<td>Ekman transport-March</td>
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<tr>
<td>Ekman transport-1st week March</td>
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<tr>
<td>Temperature-March</td>
<td>-</td>
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\(^a\)Correlations were developed by assuming that the 1980, 1981, and 1983 year-classes were above average.
Fig. 1. Maturity states for female sablefish sampled daily between January and March 1980, on the British Columbia coast.

Fig. 2. Capture locations of spawning sablefish.
Fig. 3. Length frequency of larval sablefish captured off the west coast of Vancouver Island, April 16-May 10, 1984.
Fig. 4. Length and age composition of sablefish captured off the west coast of Canada, 1977-1985.
Fig. 5. Oceanographic conditions off the west coast of Vancouver Island, February-March 1967-1985. (A) Ekman transport in February (+ indicates onshore; - offshore). (B) Ekman transport, first week of March. (C) Mean sea surface temperature in February. Bottom of panel shows anomalies. (D) Adjusted mean sea level. (E) Surface salinity.
Fig. 6. Schematic diagram of *C. plumchrus* life cycle in the Strait of Georgia. (After Fulton 1973.)
TEMPERATURE FLUCTUATIONS IN THE NORTHEAST PACIFIC FROM 1954 TO 1985 IN RESPONSE TO EL NINO/SOUTHERN OSCILLATIONS AND LONGER PERIOD FORCING

by

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ABSTRACT

Ocean temperatures at various depths in the Northeast Pacific have evidence of a subsurface response to some El Nino/Southern Oscillation (ENSO) forcing since 1970. Warnings of more than 1.5°C have been observed. These relatively brief warming events of several months' duration are superimposed on longer period temperature fluctuations with amplitudes of up to 2°C. In contrast with ENSO warming, the low frequency changes are evident at the sea surface and throughout the water column.

Over the past 30 years, sea surface temperatures were greatest in the late 1950s and least in the mid-1970s. Since 1976, there has been a subsurface warming trend of more than 0.1°C/year. The North Pacific Ocean has experienced decreased sea level atmospheric pressure and increased wind stress curl since 1975. These long period fluctuations in the atmosphere and ocean are possible indicators of changes in the ocean circulation which could influence the distribution and intensity of oceanic productivity.

Hydrographic measurements near Seward, Alaska (Fig. 1) have been made on an irregular basis since 1970 (Xiong and Royer, 1984). Estimates of salinity and water temperature exist now for 57 different months. The salinity and temperature measurements have accuracies of ± 0.02‰ and ± 0.02°C, respectively. From the individual cruise data, monthly means have been determined for salinity and temperature at the depths of 0, 10, 20, 30, 50, 75, 100, 150, 200, and 250 m (Xiong and Royer, 1984). The monthly means are subtracted to determine the anomalies at the surface (Fig. 1, upper panel) and at 150 m (Fig. 1, middle panel). The temperature anomalies at 150 m are used to represent the temperatures from 50 to 250 m because of the good coherence of the temperature anomalies at 150 m with the anomalies at the other depths.

From 1970 until 1976, the surface water temperatures were less than the 1970-84 average with the exception of a brief warming from late 1973 to mid-1974. The temperature at 150 m follows a similar pattern and since 1976 the temperature anomalies at both depths have generally been positive. There are some important differences between temperature anomalies at the surface and 150 m. Warming of more than 2°C at 150 m in 1976-77 does not appear at the surface, whereas in late 1979, surface warming does not appear in the 150 m record. The elevation of temperature at 150 m in 1980 coincides with the downward propagation of the 1979 surface warming. The 1983-84 warming is clear in both time series and through October 1984, the temperatures continue to be above normal (Fig. 1). It is suggested that the subsurface warmings observed in 1975 and 1983-84 are the consequence of El Nino-Southern Oscillation (ENSO) events which occurred about 8-9 months prior to these observations (Royer and Xiong, 1984). The 1972 ENSO event is not apparent in either of these records and it has been reported that this particular event did not propagate to high latitude regions (Enfield and Allen, 1980).

The correlation between the temperature anomalies at the 0 and 150 m is 0.607 (P<0.01 for n = 57) and a linear regression fit indicates an average temperature increase at 0 m of 0.116°C year⁻¹ which accounts for 22% of the variance. At 150 m the time rate of the temperature increase is slightly greater (0.126°C year⁻¹) and accounts for more of the variance (31%). With the possible exception of the small 1979-80 warming, the temperature anomalies are coherent with depth and apparently they do not propagate downward from the surface since they are in phase and are often larger at depth. This suggests that they are the result of horizontal advection. The variations in the water column salinity anomalies are not as consistent as those in temperature, however, there is a tendency for increasing temperatures to be accompanied by decreasing salinities (Xiong and Royer, 1984).

Both the vertical and horizontal extent of these temperatures anomalies are of interest to fisheries researchers. However, there is a scarcity of coastal hydrographic measurements in the Northeast Pacific and coastal sea level measurements here are not good indicators of water temperature since they do not respond significantly to thermal changes but instead respond primarily to local runoffs (Royer, 1979). Instead, sea surface temperature (SST) data (J. Namias, Scripps Institution of Oceanography, La Jolla, California) are used to determine the horizontal extent of
Figure 1. Temperature anomalies at Station 1 (upper and middle panels) and average sea surface temperature for the Northeast Pacific (bottom panel).
the surface temperature anomalies for the Northeast Pacific. The SST data used here are monthly means from a 6° grid with temperatures averaged for all grid points from 45°N northward to the coast and from 170°W eastward to the coast. Temperature anomalies were determined in a manner identical to the hydrographic observations.

The trend of SST anomalies (lower panel, Fig. 1) for the period (1970-1983) is similar to the temperature trends at 0 and 150 m, though the slope is less (0.065°C year^{-1}) with 26% of the variance explained by a linear regression. The correlations between SST and the temperatures at 0 and 150 m are 0.484 and 0.351, respectively, both of which are significant (P<0.01, n=57). While SST reproduces the broad trend in the temperature anomalies including the 1979 warming, it does not contain the subsurface warming events that are consistent with the ENSO events of 1976 and 1983-84. Thus, SST can reveal low frequency changes but does not display shorter, subsurface events attributed to ENSO.

The vertical extent of these temperatures fluctuations is limited by the upper layer density structure which is controlled in the Northeast Pacific by vertical salinity gradients. Generally, this does not allow the formation of intermediate or deep water in winter, so surface cooling causes mixing downward only to the top of the pycnocline (200 m near the coast and 100 m elsewhere). Thus, temperature anomalies in the upper layers in the central gulf could be similar to anomalies within the shelf water column at the coast, especially on time scales longer than seasonal. The temperature anomalies seen at the coast appear to be representative of the temperature anomalies in the upper (0-100 m offshore, 0-250 m over the shelf) throughout much of the Northeast Pacific Ocean.

The record of sea surface temperature (SST) is available from 1947 through 1984, much longer than the Station 1 record. The SST data (Fig. 2) reveal that the surface warming trend (1976-84) observed at Station 1 and in the SST data is a reversal of a long cooling period that began in 1957. The rate of SST warming in 1976 is not as rapid as that in 1956, but the two amplitudes are similar. These SST fluctuations are in general agreement with the surface temperature observations at Ocean Station P (50°N, 145°W) reported by Tabata (1981). It is clear that we now have emerged from a decade of cooler than normal surface temperatures for the Northeast Pacific, and are experiencing surface warming that is similar to the 1957 warming. The December 1984 anomaly of 1.7°C is the greatest since 1957. The long period temperature fluctuations are not evident in the other quadrants of the North Pacific (Chelton, 1984), so the effect does not extend over the entire ocean basin.

The atmospheric forcing in the Northeast Pacific displays some regular fluctuations which are evident in the eastward wind stress (Fig. 3, upper panel)
Figure 1. Atmospheric conditions for Northeast Pacific with 25-month averaging. Eastward (top panel) and northward wind stress curl (bottom panel).
with 5-6 cycles occurring over 30 years of the record. The wind fields have been determined using monthly mean sea level atmospheric pressure from a 3° grid available from Fleet Numerical Oceanography Center (FONC) in Monterey, California. While the northward wind stress (Fig. 3, middle panel) has fluctuations that are similar to the eastward wind stress, it also contains longer period changes such as the gradual increase in northerly wind stress from 1972 to 1977. There are also regular fluctuations in the wind stress curl (Fig. 3, lower panel) with maximum curl following the 1957 warming and leading the 1976-77 warming. The size of these fluctuations in wind stress curl is about three-fold, from about 30 x 10^10 dyne cm^-3 to 90 x 10^10 dyne cm^-3. The curl fluctuations will influence the vertical transports in the Northeast Pacific, causing upwelling in the oceanic region and downwelling along the coastal boundaries.

To investigate the relationships of SST and wind stress curl, cross-correlations between the two time series have been made (Fig. 4). Disregarding the correlation at -16 months, SST and curl are significantly correlated at -1 to -3 months (SST leads curl) and +1 month (SST lags curl). The situation was SST leads wind stress curl suggests that the ocean is heating the atmosphere, creating an upward velocity and low pressure system and hence increased wind stress curl. SST lagging wind stress curl (with a negative correlation) could be the result of the winds altering the SST either by upwelling-downwelling or increasing the northward heat transport. Neither of the two generalized scenarios of 1) the ocean driving the atmosphere and 2) the atmosphere driving the ocean, can be eliminated or preferred from this particular analysis.

The long period fluctuations of SST, wind stress and wind stress curl should influence primary production and fisheries. In a recent study, Willette (1985) finds that odd and even-year pink salmon (Oncorhynchus gorbuscha) populations in Prince William Sound respond to the odd-year ocean temperature anomalies at Station 1. With longer period responses of biological communities to ocean temperature cycles or events, phasing plays an important role. For example, the 1976-77 ENSO warming probably did not have the biological impact of the 1983-84 event because in 1976 the upper waters in the Gulf of Alaska were experiencing a trough in the long period temperature cycle. Our knowledge of ENSO events allows an approximately 9-month advance notice of an ENSO warming entering the Northeast Pacific and in combination with the slowly varying background temperature variation, some predictions of upper water temperatures in the Northeast Pacific can be made. For example, for the next several years there will probably be above normal temperatures in the Northeast Pacific Ocean.

![Figure 4. Cross correlation between sea surface temperature and the vertical component of the curl of the wind stress over the Northeast Pacific between 1954 and 1984.](image_url)
Attention must be made to the response of the biological communities and especially fisheries in the Northeast Pacific to these observed temperature fluctuations. Temperature measurements must also continue to be made. It is evident from Figure 1, that the satellite measurements of temperatures, which are restricted to the surface, are inadequate to measure the subsurface influence of ENSO. While the irregular sampling at Station 1 will probably continue, a more reliable and continuous measuring program should be installed, such as a radio telemetered thermistor chain with meteorological sensors. These observations, when combined with a better understanding of the dynamics of ENSO event propagation to high latitudes in the Pacific, should enhance the development of basin scale circulation models.

The influence of the cyclic upper ocean temperatures in the Northeast Pacific on biological communities must be investigated with statistical analysis of environmental conditions and populations and with laboratory studies of thermal responses of biological organisms. The immediate question is, "How are these temperature fluctuations important to fisheries?"

I thank those colleagues who have taken the time to occupy the hydrographic station at the mouth of Resurrection Bay as they venture forth or return from oceanographic cruises. Without such a cooperative effort, this time series would be impossible to maintain. The support for cruises from April 1983 through March 1985, and the analysis of these data has been provided by NSF through grant OCE-8208306. Contribution 619 from the Institute of Marine Science, University of Alaska.

REFERENCES


ABSTRACT
The abundance of cod and pollock have increased in the Gulf of Alaska, especially in the last decade, and the abundance of numerous independent stocks of the pink shrimp, Pandalus borealis, declined drastically. The shrimp stock declines were not simultaneous but each was temporally associated with increased abundance of cod and pollock. Analysis indicated that fishery harvests, presence of cod and pollock, and higher water temperature were associated with decreased shrimp stock growth. Predation was inferred to be important in the shrimp declines. Characteristics of the predacious interaction are discussed and speculations are made that declines of other species may be due to predation.

INTRODUCTION
Most current fisheries thinking assumes that the survival rate is constant and fluctuations of populations are a result of fluctuating recruitment. Investigating the effects of fluctuating predator abundance may explain prey population fluctuations in the Gulf of Alaska.

During the last 30 to 40 years very large changes have occurred in the marine fisheries of the Gulf of Alaska. Untailored resources were developed into important fisheries and many of these subsequently declined to a fraction of the former level. Population abundances have changed drastically; some species increased in abundance while others decreased.

The biomass of pollock (Theraerga chalcogramma) in the Gulf of Alaska increased six fold between surveys conducted in 1961 and 1973-76 (Ronholt et al. 1978). Most of this increase was in the central and western gulf, where, in the Kodiak, Chirikof and Sanak regions the increase ranged from 8 to 17 fold (Ronholt et al. 1978). The pollock stocks in the central gulf (the Shelikof Strait spawning population) increased between 1977 and 1982 as a result of five strong year-classes (1975-79). Since 1982 the population has declined considerably (Alton and Rose 1985).

Cod (Gadus macrocephalus) abundance in the Gulf of Alaska did not change significantly between the surveys conducted in 1961 and 1973-76 although point estimates of abundance were two to three fold higher in the 1970's (Ronholt et al. 1978). Large 1977 (possibly 1978) and 1980 year classes of cod were documented in the central gulf (Blackburn 1984; Zenger 1985). A fifteen year time series of cod incidental catch rates in king crab pot surveys conducted by the Alaska Department of Fish and Game (Fig. 1) indicates that the abundance has increased since the early 1970's and that it is quite variable between years.

Growth of cod is relatively rapid (Blackburn 1984). Their diet changes with size (Clausen 1981), and they do not seem to survive in abundance beyond age eight or nine (Owen and Blackburn 1983). Based on Clausen (1981) cod would be expected to prey heavily upon smaller items such as shrimp beginning when they are about age 3 or less until they are about age 4 or 5. Then they would consume larger fish for a year or two until they died out.

The fishery for shrimp in the Gulf of Alaska began in 1958 in the Kodiak area and grew to a peak of nearly 32,000 mt in 1971 (Fig. 2). In 1968 the fishery expanded west to fish areas south of the Alaska Peninsula. In the Kodiak area there were nine consecutive years in which harvest exceeded 18,000 mt and 14 consecutive years in which it exceeded 9,000 mt. The Kodiak area catch fluctuated from 21,000 to 37,000 mt through the 1970's, until it declined abruptly beginning in 1977 and less than 1,400 mt were harvested in 1984 (Alaska Department of Fish and Game 1985).

![Figure 1. Catch of cod per crab pot by year from crab pot surveys conducted by the Alaska Department of Fish and Game in the Kodiak area.](image-url)
Shrimp surveys were conducted at various times throughout the year to develop growth and life history information, identify seasonal changes in distribution, and identify the best time of year to obtain accurate abundance estimates. Surveys were routinely conducted in May-June and again in August-September. Additional surveys were common so that most of the important areas were surveyed two to four times each year.

RESULTS

Four case histories are presented which represent a variety of environmental conditions in the area. The locations of these areas are depicted in Figure 3.

Marmot Island and Twoheaded Island Stocks

The Marmot Island and Twoheaded Island stocks were selected as examples of stocks which occur outside of bays or offshore. Both these stocks produced 5,400 to 7,400 mt per year for a number of years prior to 1975 (Figs. 4 and 5). These two offshore shrimp stocks declined in abundance from 1975 to 78 (Figs. 4 and 5). Simultaneously, fish abundance generally increased.

In the first few years of the surveys, fish caught were not identified due to their low abundance but the weight caught was recorded as part of the sampling protocol. Beginning in 1975 the fish catch was speciated.
Figure 5. Landings of shrimp in metric tons and annual average catch rates of shrimp, cod, and pollock in kg/km from all surveys conducted each year from 1975 through 1984 in the Twoheaded Island area.

Figure 6. Landings of shrimp in metric tons and annual average catch rates of shrimp, cod, and pollock in kg/km from all surveys conducted each year from 1975 through 1984 in the Ugak Bay area.

Ugak Bay

The Ugak Bay shrimp stock was harvested heavily during the development of the shrimp fishery and was closed to fishing in the early 1970's. It was an experimental closure in an attempt to obtain information on stock rebuilding rate. The fishery was reopened in 1979 for harvest of stock above an agreed upon threshold. The stock supported fisheries in 1980 and 1981 but when surveyed May 22, 1982, prior to a fishery, the shrimp stock was the lowest ever seen. The survey was repeated June 3 out of disbelief of the initial results. The second survey also showed a low shrimp stock but found an extremely high abundance of cod, 160 kg per km trowaled with peak catches in excess of 2.8 mt/km trowaled. Survey catches of shrimp have not been greater than 2.8 kg/km trowaled since that time, while they had been 200 kg/km trowaled in 1981 (Fig. 6).

Ugak Bay is on the east side of Kodiak, adjacent to the continental shelf. It has a maximum depth of 55 fathoms and the 50 fathom contour is continuous from the shelf to the inner portion of the bay. It is easily accessible to fish such as cod which are most abundant deeper than 40 fathoms in this area. Cod have historically been present rarely and in small numbers.

Alitak Bay

Alitak Bay was chosen here as an example of a bay with a broad shallow sill separating it from the continental shelf edge. The mouth of the bay has a maximum depth of about 25 fathoms while the inner portion of the bay is over 95 fathoms. For cod to enter the bay they would need to cross a broad area which is shallower than the depth range they inhabit in abundance. Juvenile pollock are common in this bay.

The shrimp fishery in Alitak Bay was producing about 1,300 mt per year throughout the 1970's. Cod penetrated into the bay in 1983, which correlated with a depressed population (Fig. 7). The harvest decreased because of a reduced quota due to the low survey estimates (Fig. 7).

The decline in both the offshore stocks, Marmot and Twoheaded islands, was several years earlier than the decline in the bays. In protected bays such as Alitak, the decline was much less extreme and current harvests come largely from such enclosed areas. This generalization suggests that the accessibility of each area to predators was important in the time and extent of shrimp stock declines.
Figure 7. Landings of shrimp in metric tons and annual average catch rates of shrimp, cod, and pollock in kg/km from all surveys conducted each year from 1975 through 1984 in the Alitak Bay area. The landings for 1975-78 were from the Southern District, which includes Alitak Bay and two other minor areas.

DISCUSSION

Jackson et al. (1981) studied the size/age group abundance from successive surveys from all stocks throughout the Kodiak, Chignik and Alaska Peninsula areas during the period of stock decline. They found that all size/age groups of shrimp in each stock declined equally over a relatively short time period. Predation, environmental change, and disease were considered as possible causes. Evidence supported only non-size selective predation, such as that by cod (Albers and Anderson 1985) and cod abundance increased at the time of stock decline.

Thompson (1984) examined the shrimp survey and commercial catch data using multiple regression and stepwise procedures for selecting the most important variables. He concluded that the following factors were significantly related to shrimp stock fluctuations: shrimp fishery exploitation rates, cod and pollock abundance in the shrimp surveys, and water temperatures averaged over July, August and September. He found that high catches of cod and pollock were each associated with lower than expected catches of shrimp, but low cod catches occurred at the same time as high cod catches and one year after high pollock catches. Cod prey upon shrimp of all sizes fairly equally (Albers and Anderson 1985). Size of shrimp in pollock diets is not known but pollock prey heavily upon planktonic size organisms such as euphausiids (Somerton 1979) which are about the same size as shrimp less than a year old and most of the pollock in the bays have been juvenile. Shrimp are recruited to the survey gear at about one year of age, thus the temporal relationship between predation by these species and its effect upon shrimp populations is consistent with auxiliary information.

Albers and Anderson (1985) examined cod food habits, estimated consumption of shrimp by cod from Pavlov Bay, and compared the estimate to shrimp stock decline between successive surveys. In an 112-day period between surveys in late May and mid-September 1981, the estimated pink shrimp biomass decreased by 1501 mt. Estimates of pink shrimp consumed during the same period, based upon stomach contents and published estimates of evacuation rate, were 875 mt from the May survey and 142 mt from the September survey. Albers and Anderson (1985) estimated that cod consumed between 24% and 54% of their weight in shrimp during the 112-day period.

In Ugak Bay the shrimp stock declined from 237 kg/km in May 1981 to 40 kg/km in May-June 1982. Cod abundance at this time was 22 and 30 kg/km in May and Sept. 1981 and peaked at 456 kg/km in early June 1982. The peak abundance of cod could have consumed more than the 194 kg/km of shrimp lost, using the spring figure from Albers and Anderson (1985) of cod consuming 54% of their weight in shrimp. In the other three areas, however, the observed cod abundance was not high enough to account for the loss of shrimp. However, there are several considerations which suggest that such a calculation is an underestimate of the effect of predation. The shrimp trawl apparently catches a higher proportion of the shrimp present than it does of cod (Albers and Anderson 1985). Cod and pollock are more mobile than shrimp and those outside the area surveyed may also be significant predators; or more simply stated, the effective predators are probably more widely distributed than the prey. This would seem to be a very important factor since the shrimp that have survived best have been those within bays where the effective area from which predators may come is restricted by the sides of the bays. The time of summer shrimp surveys has been May and early June, with fall surveys in September. From work with the fishery it appears that cod abundance within bays is greatest in June and July. Therefore, the shrimp surveys would be expected to underestimate the summer abundance of cod. And, the predation calculations have been based entirely upon cod while other predators have been important and did increase during this time period, notably pollock and juvenile sablefish (which had an extremely large 1981 year class) which have been taken in shrimp surveys feeding on shrimp at age 1 (25 to 35 cm).
The decline of the shrimp stocks of the Gulf of Alaska was very large. In some cases it was over two orders of magnitude. The fishery did have an effect upon the stocks but predation was extremely influential. Stocks declined when fishing was not permitted. The large change in the abundance of shrimp certainly contrasts with the probable change in abundance of cod of about two to three fold. Pollock stocks seem to have increased more than cod but not as much as shrimp stocks declined.

This illustrates a basic characteristic of predation on a resource. Prey species may fluctuate widely in abundance due to comparatively small fluctuations in predator year class success. The relatively minor change in the abundance of a predator would also make it difficult to believe that increased predation was an important factor. And, conversely, relaxed predation due to predator year class failure or increased fishing pressure on the predator would rarely appear important to people reaping benefits of increased abundance of a valuable species.

Heavy predation by cod on shrimp seems to have been ephemeral, due to highly mobile predators; it took a second survey in Ugak Bay in 1982 before the extremely large concentration of cod was encountered. Predatory activities were somewhat difficult to document. The relatively frequent survey schedule and the high number of areas routinely surveyed contributed to the success.

Cod seemed to be increasing in abundance by the middle 1970's, at which time they were resident on the continental shelf but were completely absent or rare in bays. Beginning in 1980 they appeared in most of the bays around Kodiak and in Pavlof Bay (Albers and Anderson, 1985). When they did reach the bays they apparently reduced the stocks of shrimp considerably. This scenario suggests that they were consuming food resources and spreading in search of more. And, conversely, it suggests that a lower population level would have not invaded the bays for food; a slightly lower population may have had a much smaller impact upon resources in bays.

Cod are known to feed on other important fishery resource species, for example Tanner crab and king crab. Predation on Tanner crab is considered fairly intensive based on observations by AD&F&G staff. Hunter (1979) documented Tanner crab as more than 8% of the diet of 139 cod in the Kodiak area. AD&F&G observations indicate that juvenile Tanner crab, less than about 4 cm shell width, are subject to predation. Unpublished AD&F&G observations have also identified cod predation on king crab. From a large number of stomachs examined during summer, some work in early spring, and reports from fishermen, it appears that cod feed upon softshell king crab. The most frequently found parts include the egg bearing abdomen of females, suggesting sex selective predation. During the softshell period, crab are relatively concentrated in areas shallower than that occupied by cod. Cod abundance has been found to be low in the vicinity of molting king crab. The incidence of king crab in cod stomachs has also been low, about 10% at the highest. The potential impact of cod predation on king crab is debatable, but considering the correlations from shrimp, it should not be discounted.

Powell and McCrory (1982) point out that the largest recruitment and commercial catches of red king crab in the Bristol Bay area of the Bering Sea were produced by low brood stocks at the same time that the groundfish fishery was the most intense in history.

The surveyed stock of pollock in Shelikof Strait is declining and has been since about 1981 or 82 (Alton and Rose 1985). Increased predation on pollock may be a contributing factor in this decline, but the abundance of halibut has also increased considerably since the late 1970's (International Pacific Halibut Commission 1977-84) and they feed heavily upon pollock (Hunter 1979; Alton and Rose 1985). The 1976 year class of cod was large in the Gulf of Alaska (Blackburn 1984; Zenger 1985). The modal size of this year class passed 60 cm in 1982 (Blackburn 1984 and unpublished data from AD&F&G) and the abundance of 70 cm and greater cod began to increase in 1983 (unpublished data from AD&F&G). Clausen (1981) reported that large cod, 70 cm and larger, feed heavily upon fish while those between 60 and 70 cm feed increasingly on fish. Hunter (1979) found that pollock were the most important by biomass, of fish identifiable in the food of cod in the Kodiak area. The large 1977 cohort of cod may be at least partially responsible for the decrease in the abundance of pollock.

The following anecdotal evidence is also of interest. In 1981 the shrimp fishery encountered unusually high levels of fish abundance in the Twoheaded Island area during the summer fishery. Fishermen were, for the first time, resorting to elaborate mechanical means to separate fish and shrimp, such as floatation or inclined netting on which the catch was dumped. The port sampler in Kodiak brought in a bottle of otoliths recovered from the shrimp processing line; they had been mixed in with the catch and were all over the decks of the fishing vessels. The otoliths were identified as coming from pollock about 80 mm in length using Morrow (1977) and Frost and Lowry (1981). The otoliths were smaller than the mesh of the shrimp nets so the only way they could have come aboard in quantity was in the intestines of predators. The 1981 cohort of pollock has since been identified as low in abundance (Alton and Rose 1985).

Shrimp stocks in the Gulf of Alaska have declined considerably, apparently due to increased predation by cod and pollock. Shrimp are only one of the commercially important prey species in the Gulf of Alaska, consequently fluctuations in
other important stocks may be due in part to predation. As stated by May et al. (1979), MSY may be a useful concept only for top predators.

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RELATIONSHIPS BETWEEN ABUNDANCE OF EPipelagic SQUIDS AND OCEANOGRAPHICAL-BIOLOGICAL ENVIRONMENTS IN THE SURFACE WATERS OF THE SUBARCTIC PACIFIC IN SUMMER

by

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National Science Museum, Tokyo

ABSTRACT

Relationships among the distribution and abundance of three dominant epipelagic squids, Ommastrephes bartrami, Onychoteuthis boreali japonica and Gonatus borealis, biomass and species compositions of zooplankton and micronekton, and temperature and salinity during summer along the longitudinal lines from 38°N to 50°N in the northern North Pacific were examined. The distribution patterns of the three squid species coincide well with the oceanographical domains, i.e. O. bartrami in the tropical water, O. boreali japonica in the transitional to subarctic waters and G. borealis in the subarctic water. There is an exception of large sized females of O. bartrami which intrude into transitional water where they can be caught in great numbers. Large catches of O. bartrami are generally associated with high abundance of zooplankton, such as Doliolium, medusae, Salpa, Euphausia pacifica, Calanus plumchrus and pteropods. O. boreali japonica are caught in the water where zooplankton biomass is relatively low in contrast to high abundance of micronekton, such as myctophids and young Berytethus anonyxus. No clear relation has been found so far between catches of G. borealis and zooplankton biomass. There is little evidence of utilizing zooplankton and micronekton by O. bartrami and O. boreali japonica, but it is expected that regional differences in biomass and composition of zooplankton-micronekton will be one of indirect factors to govern their northward migrations and aggregations in certain areas during the summer seasons.

INTRODUCTION

Three species of epipelagic squids, Ommastrephes bartrami, Onychoteuthis boreali japonica and Gonatus borealis are sometimes caught in large number during summer by surface gillnet in the waters around the subarctic boundary. O. bartrami in particular aggregates at certain surface waters and is utilized by squid drift gillnet fisheries. Life history data on these species have accumulated in recent years, accompanying the development of their fisheries (Murakami 1976; Murata et al. 1977; Naito et al. 1977a, 1977b; Murata and Ishii 1977; Murakami et al. 1981; Murata et al. 1982; Fiscus and Mercer 1982; Murata and Shimag 1982; Araya 1983; Murata et al. 1983; Kubodera et al. 1983; Murata et al. 1985).

These studies revealed the different distributional areas, seasonal migrations, population structures, reproductive ecology and prey consumed among the three species. Kubodera et al. (1983) discussed hypothetical mechanism of aggregation of O. bartrami and O. boreali japonica in surface waters in relation to the oceanographical conditions. Biological variables, such as food availability and prey-predator relationships are important factors governing their migrations, regional distributions and abundance. This paper intends to show the relationship between distribution and abundance of the three squid species in the surface waters, and biomass and composition of zooplankton and micronekton along a longitudinal line across the subarctic boundary in the North Pacific during summer. The distribution and migration patterns of these squids from spring to fall seasons are schematically summarized based on previous information.

MATERIALS AND METHODS

This study is based on the catch records and squid specimens caught in the research surface gillnets operated during July to August in the northwestern North Pacific by the Oshoro-Maru in 1978, Hokusai-Maru in 1979 (training vessels of Hokkaido University) and Iwate-Maru in 1978 (research vessel of Iwate Fisheries Experimental Station). Details of net operation and method of analysis are given in Kubodera et al. (1983). Zooplankton and micronekton were collected by a larva net (1.3 m in mouth diameter, 4.5 m in length and mesh 2.0 mm square in the anterior 3 m and 0.3 mm in the remaining 1.5 m) towed at one m surface column for ten min at two knots one hour after sunset at the same positions where gillnets were set (Fig. 1).

Samples taken by the larva net were divided into zooplankton, fish and cephalopod, and each group weighed wet. Relative abundance of species or taxonomic group in zooplankton was roughly classified into five grades. Fish and cephalopod were identified into possible level of taxon and counted.

RESULTS

Relative abundance of O. bartrami, O. boreali japonica and G. borealis, vertical distribution of temperature from surface to 125 m depth and wet weight and composition of zooplankton and micronekton along the longitudinal research line of 175°17'30"W from 39°N to 51°N on 3-20 July, 1978, are shown in Figure 2. Those of the research lines from 38°30'N to 49°N along 175°30'-165°30'E on 26 July-
August, 1979, are shown in Figure 3 together with the vertical distribution of salinity.

Judging from the vertical profiles of temperature and salinity, the subarctic boundary lies at about 41°N in 1978 and 42°N in 1979. In the Subarctic region, there was a boundary between Transitional and Western Subarctic Domains situated at about 45°N in both years (see Dodimead et al. 1963; Favorite et al. 1976).

O. bartrami occurred in the surface waters of the Subtropical Region and Transitional Domain and was highly abundant in the waters just south of subarctic boundary in 1978 and its northern end of distribution in Transitional Domain in 1979. O. borealijaponica appeared in the surface waters of the Transitional and southern part of Western Subarctic Domains. This squid tended to be abundant in its southern part of distribution in 1978 and its northern part in 1979. O. borealis was distributed in the waters of Transitional and Western Subarctic Domains in 1978 and restricted in the Western Subarctic Domain in 1979. It was low in abundance compared to the other two species. No longitudinal differences in sex ratio were seen in O. boreali-japonica and O. borealis. On the contrary, O. bartrami caught in large numbers in the Transitional waters in 1979 were all females, irrespective of sex ratio in the Subtropical waters. Sex ratio of O. bartrami in 1978 was not examined.


Micronekton in the larva net sample were < 20 individuals in most stations in 1978. However, sample at 46°30'N contained 69 individuals of young squid. Fifteen of Gonatus middendorffi, 2 of Gonatopsis borealis and 52 unidentified small gonatids were caught. Sample at 50°45'N contained many individuals of young fish, 100 of Stichaeidae and 2 of Hemilepidotus sp., while in 1979, 6 stations out of 10 yielded > 50 individuals of micronekton. Among them, station at 38°30'N in the Subtropical waters yielded 107 myctophids and 13 young Cololabis saira. From two stations in Transitional waters, 167 and 78 young squid, mainly Berryteuthis anonychus, were collected.

High abundance of young squid was also seen in the stations at 47°30'N, 48°N and 49°N in the Subarctic waters where 96, 64 and 67 individuals were collected, respectively. Dominant squid in the Subarctic waters was again B. anonychus with a small number of G. borealis, Onychoteuthis cyclostoma and Onychoteuthis type A (Kubodera and Okutani 1981). In general, micronektonic constituents change myctophids-enoploteuthids in the Subtropical waters, myctophids-C. saira-B. anonychus in the Transitional waters and Ammodytes sp. and Stichaeus sp.  B. anonychus-gonatids in the Subarctic waters (Table 1).

No clear relationship was seen between abundance of the three squid species caught by surface gillnets and zooplankton and micronekton biomass and composition. But, high abundance of O. bartrami tended to associate with large biomass of Doliolum-medusa, Salpa, E. pacifica, C. plumchrus, peripods and young squid of B. anonychus. While O. boreali-japonica tended to be caught in the waters where zooplankton biomass was relatively low but with a high abundance of young gonatid squids, mainly B. anonychus and young myctophids, Ammodytes sp. and Stichaeus sp.

DISCUSSION

This paper discusses the longitudinal differences of distribution and abundance of three dominant pelagic squids around the subarctic boundary during summer in relation to regional differences of biomass and species composition of zooplankton and micronekton, which are considered to be important prey for these squids. Before going further, I summarize the general distributional areas, migration patterns, and population structures, mostly based on Murakami (1976), Murata et al. (1976), Nakazato et al. (1979), Murakami et al. (1981), Fiscus and Mercer (1982), Murata et al. (1983), Kubodera et al. (1983) and Araya (1983) (Fig. 4). O. bartrami and O. boreali-japonica are subtropical species and estimated to spawn in the southern part of the Kuroshio Current during winter to early spring. Hatchlings are translocated to the north by the Kuroshio Current or stay in Countercurrent until they get enough swimming ability. After that, they ontogenetically migrate as far north as around the subarctic boundary in early summer, where O. bartrami is sometimes highly concentrated. Due to the different tolerable temperature, O. boreali-japonica migrates further north to the boundary between Transitional and Subarctic Domains. With the rising of the surface water temperature of Transitional and Subarctic Domains during summer, large females of O. bartrami enter the Transitional Domain through northward extensions of warm surface water and concentrate in surface waters around the boundary between Transitional and Subarctic Domains. O. boreali-japonica extends further north to the Subarctic Domain and sometimes aggregates at the northern end of its
distribution. During summer season, they grow and mature. In fall, a spawning migration to the south takes place in both species according to the degree of maturity. Individuals in higher degree of maturity tend to lead migration south. Males of both species mature earlier and are smaller in size than females, and begin a southward migration earlier than females. Large female O. bartramii, which migrated earlier and further north than the other groups during summer, may leave Transitional waters first. On the other hand, G. borealis is a subarctic species and distributes broadly in the pelagic waters north of subarctic boundary in spring. With warming up the surface waters of Transitional Domain during summer, G. borealis disappears in the surface waters of Transitional Domain. However, they distribute in deeper layers of this area where water temperature is suitable. During spring to summer, G. borealis also grow and mature. Spawning is estimated to occur in the broad pelagic area of subarctic Region and continues through the fall to winter (Kubodera and Jefferts, 1984).

From the viewpoint of population structure, size compositions of these squids are very complicated. Murakami et al. (1981) found two different size groups in male and four groups in female in the O. bartramii (Fig. 5). They estimated that the two groups of males and two groups of middle-size females were in a one-year life cycle and the difference in size might be due to the time difference of hatch-out and/or spawning of the year. The smallest size group of females may have originated from the late spawning period and survived over a year. This group may be contiguous to the largest group which migrates north before the middle size groups do. Recently, Murata et al. (1985) reported a growth rate of O. bartramii almost twice that estimated by Naito et al. (1977b) based on the tagging experiments. They mentioned that the largest size group could grow within a year. The two different size groups were also reported in G. borealis (Naito et al. 1977a; Kubodera et al. 1983) which have different geographic distributions and biological characteristics (Fig. 6). Kubodera et al. (1983) considered that the large size group might be survivors of the small size group which did not mature in the previous year. No clear size group was found in G. borealis japonica, however, size range of individuals caught during summer ranged considerably between 15 cm to 30 cm DML (Naito et al. 1977a; Kubodera et al. 1983). These different size groups and/or wide size range in the populations are taken nearly at the same time of the year and same area. They are considered to be affected by two factors. One is a long period and different area of hatching or spawning with some peaks of reproductive activity. The second is a different growth rate that is affected by the food availability during the growing period. Both factors might be inter-connected as well.

Considering the above-mentioned background, longitudinal distributions of O. bartramii, G. borealis japonica and G. borealis shown in Figures 2 and 3 represent the different distributional patterns of three squids in the research lines in early summer in 1978 and of middle summer in 1979. Research was not conducted in the same year nor same latitude, though high abundance of O. bartramii in the waters just south of subarctic boundary in early July shifted to the Transitional Domain in late July. High abundance of G. borealis japonica also shifted from Transitional waters in early July to its northern end of distribution in Subarctic Domain in late July. This indicates northward migrations of both species during summer. High concentrations of both species especially in northern part of distributions are considered to be stressed by the migrants from the south. There is as well a narrowing of their suitable temperature ranges vertically in the northern areas where pronounced vertical thermoclines develop in a relatively shallow layer during summer (Kubodera et al. 1983).

Longitudinal differences of distributions and abundance of these squids in the surface waters during summer are explained by the relations to their northward migration, suitable temperature range and vertical oceanographical conditions. A question is why they migrate into Transitional and/or Subarctic waters crossing the physical barrier of subarctic boundary? Taniguchi (1981) compared noveliative food activity for migrating fishes between the Subarctic, Boundary and Subtropical waters in summer and winter on the basis of plankton productivities (Fig. 7). He pointed out that the Subarctic area is unattractive in winter but highly attractive in summer. On the contrary, the Subtropical waters are attractive in winter and unattractive in summer. The Boundary area is attractive throughout the year. Such seasonal differences in food attractivity might be one of the factors promoting north to south returning migration of Subtropical nektonic animals. Tsujita (1981) also stressed that the utilization of large biological products in the Subarctic waters in summer is essentially necessary for migrants, especially for zooplankton feeders such as saury, mackerel and sardine.

Concerning the prey items of three squids in this study, analysis of their stomach contents is now in progress. Naito et al. (1976b) examined 611 stomachs of O. bartramii taken by squid jigging off northeastern Japan among which 37% were empty. The most important prey was small fishes, occupying 76% of stomach contents, among which Diaphus coeruleus and Engraulis japonicas were dominant. The second was squids (18%) of watasenia scintillans and O. bartramii and the third was crustacea (6%) of Euphausiacea and Parathenmehisto sp. (Table 2). They pointed out the change of prey items with growth from crude fishes and crustacea-small fish-squid feeding of individuals < 30 cm DML to small fish-squid feeding of larger individuals. Araya (1983) briefly mentioned the same feeding habits of O. bartramii. Naito et al. (1976b)
also examined stomach contents of G. boreali-japonica and G. borealis caught by surface gillnets finding that the most of them were empty. However, both species tend to feed on small fishes (Table 3).

Judging from the limited information, all of these species are considered to be nekton or micronekton feeders except for G. bartramii of < 30 cm DML which may depend partially on large zooplankton such as Euphausia pacifica, large copepods and amphipods. In this study, high abundance of G. bartramii was sometimes associated with the large biomass of C. plumchrus, pteropods, E. pacifica all of which are considered to be large enough to be fed by such carnivores as G. bartramii in the waters of Transitional Domain. While, the micronekton feeders G. boreali-japonica and G. borealis tended to distribute in the waters where zooplankton biomass was relatively low but high abundance of young ongataids and young myctophids, ammodytids and stieaeids. There is no direct evidence of utilizing these zooplankton and micronekton by G. bartramii. G. boreali-japonica and G. borealis. However, I expect that regional bias in zooplankton and micronekton biomass and compositions is an indirect factor which governs their distribution and abundance in Transitional and Subarctic waters in summer.

In this paper, the biological environment was only viewed from a small window of larval net samples. Further studies are badly needed for clarifying relationships among nekton and micronekton of migrants from/to Subtropical waters and endemics of Subarctic waters as well as detail analysis of stomach contents of these squids.

REFERENCES


Table 1. Regional differences of species composition of micro-nekton collected by the larva net in the waters of Subtropical, Transitional and Subarctic during summer season in 1978 and 1979.

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<td><strong>Fish</strong></td>
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<td>Stichaeidae spp.</td>
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<td>Ammodytes sp.</td>
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Table 2. Frequency of stomach contents of *Ommastrephes bartrami*
from 1975 to 1976 (after Naito et al. 1977b).

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<th>Euphausiacea</th>
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<td>37.5%</td>
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<tr>
<td>Small fishes</td>
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<tr>
<td>Diaphus coeruleus</td>
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<td>58.0%</td>
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<tr>
<td>Engraulis japonica</td>
<td></td>
<td>26.5%</td>
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<tr>
<td>Sardinops melanosticta</td>
<td></td>
<td>5.9%</td>
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<tr>
<td>Scomber japonicus - young -</td>
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<td>5.0%</td>
</tr>
<tr>
<td>Others</td>
<td></td>
<td>4.6%</td>
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<td>Squids</td>
<td>17.6%</td>
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<tr>
<td><em>Watacenia scintillans, Ommastrephes bartrami</em></td>
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Table 3. Frequency of stomach contents of squids (after Naito et al. 1977b).

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<tr>
<th>Date and location</th>
<th>Number of specimens</th>
<th>Mantle Length (cm)</th>
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<th>Crustacea</th>
<th>Small fishes</th>
<th>Squids</th>
<th>Crustacea fishes</th>
<th>Squids</th>
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*TH: Tohoku Regional Fisheries Research Laboratory, Hachinohe Substation, AM: Aomori, FS: Fukushima, IT: Iwate, WK: Wakkanai, KS: Kushiro - Fisheries Experimental Station.
Fig. 1. Stations at which research gillnet and larva net samplings were conducted.
Fig. 2. Vertical features of temperature from the surface to 125-m depth with CPUE of Ommastrephes bartrami, Onychoteuthis borealijaponica and Gonatopsis borealis caught by research gillnet in the surface layer and biomass of zooplankton and micronekton in wet weight, with their composition and number of fish (solid) and cephalopods (open) in larval net samples along a north-south transect from 39° N to 50° 30' N at 175°-177° 30' W, July 3-20, 1978.
Fig. 3. Vertical features of temperature and salinity from the surface to 125 m-depth with CPUE of Ommastrephes bartrami, Onychoteuthis borealijaponica and Gonatus borealis caught by research gillnet in the surface layer, and biomass of zooplankton and micronekton in wet weight, with their composition and number of fish (solid) and cephalopods (open) in larva net samples along a north-south transect from 38° 30'N to 49°N at 175° 30'-165° 30'E, July 26 - August 5, 1979.
Fig. 4. Schemes of distribution and migration patterns of Omastrephes bartramii (O. b.), Onychoteuthis borealiartica (O. b.l.), and Gonatopsis borealis (G. b.) from spring to fall. F, female; M, male; LF, large female.
Fig. 5. Frequency distribution of mantle length of *Ommastrephes bartrami*, 1978 to 1980. SS: SS mantle-size group; S: S mantle-size group (after Murakami et al., 1981); L: L mantle-size group; LL: LL mantle-size group.
Fig. 6. Distribution and relative abundance of Gonatopsis borealis caught by surface gillnets in July, 1977-1979, separating them into small size group (smaller than 20 cm DML) indicated by solid and large size group (larger than 20 cm DML) indicated by open. (after Kubodera et al., 1983).

Fig. 7. Schematic representation of relative food attractiveness for migrating fishes between the Subarctic, Boundary and Subtropical sea areas of the North Pacific in summer and winter. (after Taniguchi, 1981).
RELATION OF THE MIGRATION OF PACIFIC SAURIES TO OCEANIC FRONTS
IN THE NORTHWEST PACIFIC OCEAN

by
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ABSTRACT

There is a wide distribution of Pacific sauries in the northwest Pacific. These fish migrate from the Kuroshio area in the subtropical zone to the Oyashio area in the subarctic zone. In this report, the author will describe the relation of the migration of Pacific sauries to oceanic fronts.

The larvae of sauries are widely distributed in the Kuroshio area immediately after hatching and most of them emerge in a patchy formation on the surface of eddies which are generated on the southern side of the Kuroshio front zone. It was observed that there tended to be more juveniles than larvae as they proceeded from the warm core to the strong current zone around the Kuroshio front zone. It appears that they proceeded mainly to the transition area during the period of development from larvae to juveniles.

In spring, the pre-northward migration period, juveniles, young fish, and adults, having survived the winter, gather around the upper layer front formed by warm water stretching north from the Kuroshio extension which has a temperature of 14°C to 15°C. In the mid-northward migration period, sauries gather around two thermal fronts in the upper layer around the Oyashio front. Pre-adults and adults with undeveloped gonads gather on the northern side of these fronts, post-young fish mainly gather between the fronts and the pre-young fish, and larvae and adults with developed gonads are found on the southern side of the fronts. In the post-northward migration period, most develop into pre-adults or adults and move to the northern side of the upper layer front created by warm water which spreads from the Oyashio front to form a seasonal thermocline, whereas a smaller number of young fish, juveniles, larvae, and adults with high gonad somatic index (GSI), stay on the southern side.

In summer, a school of sauries migrates for feeding between the two thermal fronts of about 10°C and 15°C that are formed in the upper mixed layer in the Oyashio area.

From the end of August to the beginning of September, the fish begin to migrate in a southwesterly direction. In the pre-southward migration period, sauries gather around the Oyashio front, migrate south to the transition area, and gather at the northern side of the Kuroshio front in the latter part of the southward migration period. During this period, most of the fish start to prepare for spawning.

1. Introduction

Epipelagic fishes which are classified as Belonidae and live in the upper layer of the North Pacific consist of most species of the Scombroidei, which are distributed from the tropical zone to the subtropical zone, and the only species of the Scomberesocoidei, Pacific saury Cololabis saira, which is distributed from the subtropical zone to the subarctic zone (Novikov 1967; Parin 1967; Odate 1977).

In the Tohoku Sea region, which is inhabited by the northwest Pacific population of Pacific saury, the Kuroshio front is in the southern part and the Oyashio subarctic front is in the northern part (Kawai 1972). Seasonal changes in oceanic conditions form thermal fronts in the upper layer. Pacific sauries migrate from the Kuroshio area to the Oyashio area across the various fronts (Fukushima 1979; Kosaka 1980).

In this report, the author will describe the relationship of Pacific sauries in the northwest Pacific to these oceanic fronts.

2. Materials

In this report, the following information has been used: data obtained by research vessels operated by the Tohoku Regional Fisheries Research Laboratory and the Japan Marine Fishery Resource Research Center during the spawning period from winter to spring and during the northward migration period from spring to summer 1979 to 1985; reports on biological characteristics recorded by skippers; and data on the geographical distribution of surface water temperature published by the Fishing Information Service Center during the fishing period.
3. Results

(1) Larval stage—juvenile stage* and the Kuroshio front

The temperature distribution of the 200-m layer water in the area under investigation from February 7 to March 8, 1985, is shown in Fig. 1. The distribution of larvae collected with larval nets is shown in Fig. 2. The larvae were mainly distributed on the southern side of the Kuroshio front which has a temperature of 14°C in the 200-m layer. Figure 3 shows the profile of water temperature, a consecutive record of surface temperature and salinity along the longitude of 137°E, the density of sauriies, and size composition of sauriies at some observed stations. There were large-scale warm water masses consisting of subtropical water having the same temperature from the surface to the 250 layer to the south of the Kuroshio front. There tended to be more juveniles than larvae as they proceeded from the warm core to the stronger current zone around the Kuroshio front zone. It seems that they proceeded mainly to the transition area during the period of development from larva to juveniles. However, some had already reached the young fish stage by the time they arrived on the southern side of the Kuroshio front.

(2) Relation of Pacific sauriies in respective developmental stages to oceanic fronts in the northward migration period

The temperature distributions at depth of 100 m off Sanriku-Jeban from May 26 to June 12, 1979 are indicated in Fig. 4. The isotherm at surface temperature 15°C and the distribution of sauriies collected by high-speed net tows for 10 minutes' duration are shown in Fig. 5. Sauries in all developmental stages from juvenile to adult are distributed around the 15°C isothermal line but have not yet moved to the northern side of the line. Figure 6 shows the water temperature profile, a consecutive record of surface temperature, and the density and size distribution of sauriies collected by high-speed net at intervals of five miles from 39°N to 39°30’N at 152°E. It is recognized from this figure that a thermal front identified by 15°C surface water temperature and 10°C at 100 m depth is formed at the end of the northward warm water mass which extends from the Kuroshio around 39°25’N. Sauries are distributed densely around the center of the warm water mass from 39°10’N to 39°20’N on the southern side of the front and not seen at all on the northern side of the front. At the central part of the distribution most are larvae 4 cm in length while young fish predominate at 39°20’N a little to the north. In this water mass, no pre-adults were collected, but from 39°05’N to 39°15’N, large adults about 30 cm in length were collected although they were small in number. We call the period of such distribution the pre-northward migration period.

From June 23 to July 11, 1981, a hydrographic survey using XBT and a saury investigation utilizing a high-speed net were conducted within the area from 39°N to 43°N and from 162°E to 170°E.

The three-dimensional temperature distribution of the area is shown in Fig. 7. In the figure, two thermal fronts are recognized. The first, slightly to the north, is a subarctic front with a surface water temperature of 9°C. The second, a little to the south and formed by the spread of northward warm water, is a thermal front characterized by temperature of 13°C. Numbers of sauriies collected during this period are shown in Fig. 8. High densities can be seen at the south end of each thermal front. The relation between the two thermal fronts and the saury distribution by developmental stages is shown in Fig. 9. Sauries in both the larval stage—juvenile stage (<5.9 cm) and pre-young fish stage (6.0 to 9.9 cm) are distributed only on the south side of the 13°C front. The latter are relatively higher in density than the former and tend to be distributed a little to the north. In the post-young stage (10.0 to 14.9 cm), the area with high density is seen between the two thermal fronts while there are no post-young fish on the north side of the 9°C front. In the pre-adult stage (15.0 to 19.9 cm) there are relatively many sauriies between the two fronts and some have already reached the northern side across the 9°C front. Quite a few medium-sized small adults (20.0 to 26.9 cm) are distributed also on the northern side of that front. Large adults (27.0 cm+) are distributed over most of the area, though only a few were collected due to inefficiency of the high-speed nets.

Thus, in the migration period from the transition area to the subarctic zone, generally, post-young fish first migrate to the southern end of the subarctic front across the thermal front formed by northward spread of the warm water. The period in which the main school of northward migrating sauriies are thus distributed is herein termed the mid-northward migration period. Subsequently, sauriies which have developed from post-young fish to pre-adults move across the sub-arctic front to the northern side of the subarctic zone. The period from the time the main school of sauriies have crossed the subarctic front until the time when the subsequent northward migrating school has almost reached the subarctic zone is herein called the post-northward migration period.

In the mid- and post-northward migration periods, large adults with undeveloped gonads proceed north across

*The developmental stages of Pacific sauriies were reported by Odate (1977).
these two fronts whereas those with developed gonads stay on the southern side of the subarctic front.

3. Feeding migration period and the thermal fronts in the upper layer area

Sauries which have reached the subarctic area remain there while feeding mainly on zooplanktons, Calanus plumchrus and C. cristatus (Taka et al. 1980). In the north, they are distributed around the Kuril east front (Fukushima 1969) in the upper layer area along the Chishima Islands with a water temperature of about 10°C. They are also distributed in the upper layer of the southern end near the Kuril front (Nakamura and Uda 1973) where the temperature is about 15°C. Both these fronts are formed only in the summer. In this feeding migration period, sauries tend to be dispersed.

4. Relation of transition of sauries and ovary development to the oceanic fronts in the southward migration period

The distribution of surface temperature by five-day period from summer to autumn during 1978 and the distribution of catch per stick-held dipnet effort by growth stages in 20° squares of latitude and longitude are shown in Fig. 10. At the beginning of September, the Kuril front extending from 149°E to 150°E from south to north can be clearly observed. Immediately after that period, the northern side of the front has collapsed in a southwesterly direction. At this time, as suggested by the existence of a few sauries along the east coast of Hokkaido, some of the few sauries which were staying on the eastern side of the front moved towards the collapsed front as a preceded school. During the early half of September, a subsequent school of sauries from the east offshore area migrated to the area of 149°E to 150°E. During the latter part of September, the Kuril front has a low temperature gradient and sauries begin to move rapidly in a southwesterly direction along the front, making a detour through the warm water area in the Oyashio area and subsequently, at the end of September, reach the area off the coast of east Hokkaido which becomes the main fishing ground. Around the southern end of the fishing ground along the east coast, the Oyashio front, with a high temperature gradient, remains until the latter part of early October and sauries stay on the northern side of this front. The period from when the Kuril front collapses and sauries begin to move south, to the period when they stay together at the northern end of the Oyashio front is called the pre-southward migration period.

From the latter part of the first 10 days in October to early mid-October, the spread of cold water in the first Oyashio branch near the coast towards the south increases and the temperature gradient suddenly is dissolved. Meanwhile, sauries begin to proceed across the front from the Oyashio area along east Hokkaido to the transition area along the Sanriku coast. Schools then proceed one after another to the transition area. In the course of this migration they stay primarily at spots where they encounter the secondary front which stems from the Kuroshio front or in isolated areas of cold water. This period is called the mid-southward migration period.

They then migrate south in the transition area and stay together at the northern end of the Kuroshio front which is characterized by a marked temperature gradient. The period in which they stay around the end of the Kuroshio front is called the post-southward migration period.

Changes in the composition of the gonad somatic index (GSI) of females by migration periods and fish sizes are shown in Fig. 11. During the period when they migrate from the Kuril front in the central and southern part off the Kuril Islands to the northern side of the Oyashio front off east Hokkaido, most medium and small sauries are those with GSI under 0.4. Of large fish, those with a GSI over 0.4 represent less than 50%. Percentages of medium and small females with a GSI of 0.4 to 0.9 migrating south in the transition area off the Sanriku coast across the Oyashio front gradually increases and exceed 50%, whereas large adults with GSI over 0.4 are 50% or more from the beginning and then increase. As expected, those with GSI under 0.4 almost disappear. While staying at the north end of the Kuroshio front, medium and small sauries with GSI over 0.4 exceed 50%. Among these sauries, those with values of 1.0 to 1.9 are observed although they are few in number. Large sauries with GSI of 1.0 to 1.9 represent about 20 to 30% at this time.

4. Discussion

The relationship of saury migration in the northwest Pacific to the oceanic fronts is schematized in Fig. 12. It is clearly evident that sauries, the only species among Belonida that migrate as far as the subarctic area, reach at least pre-adult developmental stage during the northward migration when they cross the subarctic front and that their gonads do not develop until they cross the subarctic front during their southward migration. In the latter part of the southward migration period, most of the sauries start to prepare for spawning at the northern side of the Kuroshio front.

As to the relation of the development of sauries to changes of the oceanic fronts in the northwest Pacific, for sauries the front formed by the northward warm water stretching from the Kuroshio in the transition area in spring to autumn is essentially identical with the Kuroshio front. It appears that the southern part of the front is the place...
where they reproduce. Neither the Kuril-east front, which is formed in the surface layer of the Oyashio subarctic area only in summer, nor the Kuril front, are related to the development of sauries. However, the changes in these fronts affect the route of southward migration in terms of distribution and transition.

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Fig. 2. Distribution of saury larvae collected with larval nets from February 7 to March 8, 1985.
Fig. 3. Vertical distribution of water temperature (A), consecutive record of surface water temperature (B), density of sauries (C), and body length compositions at some observed stations, February 22 to 27, 1985, along the longitude of 139°E.
Fig. 4. Water temperature (°C) at a depth of 100 m off Sanriku-Joban from May 26 to June 12, 1979.
Fig. 5. Isotherms at a surface temperature of 15°C and density of sauries of each developmental stage from May 26 to June 12, 1979.
Fig. 6. The vertical distribution of water temperature (A), a consecutive record of surface temperature (B), the density of sauries (C), and body length compositions between 39°N and 39°30'N along the longitude of 152°E.
Fig. 7. The three-dimensional temperature structure down to 150 m depth in the area from 39°N to
43°N and from 162°E to 170°E from June 23 to July 11, 1981.
Fig. 8. The number and isonumbers of sauries collected by high-speed net tows of 10 minutes' duration.
Fig. 9a. The relation between the two surface thermal fronts (9°C and 13°C) and Pacific saury distribution by developmental stages.
Fig. 9b. The relation between the two surface thermal fronts (9°C and 13°C) and Pacific saury distribution by developmental stages.
Medium and small adults (20.0-28.9 cm)

Fig. 10a. The distribution of surface temperature for five-day periods from summer to autumn during 1978 and distribution of catch per stick-held dipnet effort by growth stages in 20° squares of latitude and longitude.
Medium and small adults (20.0-28.9 cm)

Fig. 10b. The distribution of surface temperature for five-day periods from summer to autumn during 1978 and distribution of catch per stick-held dipnet effort by growth stages in 20' squares of latitude and longitude.
Feeding migration period

Pre-southward migration period

Mid-southward migration period

Post-southward migration period

Large adults (29.0-cm)

Medium and small adults (20.0-26.9 cm)

Fig. 11. Changes of composition of GSI (GW/BW x 100) of female saury by size and by migration period in 1978.
Fig. 12. A schema of the correlation between saury migration in the northwest Pacific and the oceanic fronts.
DISTRIBUTION OF THE PELAGIC FISH COMMUNITY AROUND THE SUBARCTIC BOUNDARY IN THE NORTH PACIFIC OCEAN

by

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ABSTRACT

In recent years, research has been carried out from June to July 1983-1985 to determine the distribution of pelagic fish in an area that extends from the Subtropic to Subarctic regions crossing the Subarctic boundary in the western Pacific. Fish were caught with non-selective drift gillnets (stretched mesh sizes from 19 to 204 mm) and their oceanic and biological environments were also investigated.

Some specific fish populations were found to live only in the Subarctic region, north of the Subarctic boundary; some were found only in the Subtropical region, south of the Subarctic boundary; others were distributed widely in both regions.

Species inhabiting both regions have their spawning ground in the Subtropical region, but in summer they move north into the Subarctic region. In this northward migration of all species combined, smaller fish move first, with larger ones following them, but within a single species the larger ones tend to move first. With regard to feeding habits, plankton feeders move first, followed by euryphagous feeders, with carnivores moving last.

These observations indicate that the fish moving north into the Subarctic region are ranked according to their dependence on the high biological production of this region, that is, those with direct dependence and those with indirect dependence.

INTRODUCTION

The Subarctic boundary in the North Pacific Ocean is known as a line of discontinuity of waters between the Subarctic and the Subtropical regions (Dodimead et al. 1963; Favorite et al. 1976). In and around summer, some pelagic fish of the Subtropical region move north past the boundary, becoming evenly distributed in the Subarctic region (Suda 1962; Kawasaki 1963; Odate, S. 1977; Naito et al. 1977; Shimazaki and Nakamura 1981). As such, fish make very active seasonal migrations, the species composition around the Subarctic boundary being quite variable. This northward migration can also be termed a feeding migration; in other words, the fish make use of the Subarctic region with its high biological production, as their feeding grounds. Therefore, it is necessary to consider some ecological factors to assess the significance of this summer expansion of their distribution to their whole mode of life.

MATERIALS AND METHODS

Research was carried out in an area bounded by longitudes 155°E-175°30'E and latitudes 35°N-50°N (Fig. 1). The fishing gear used consisted of research gillnets made of 20 mesh sizes (Shimazaki et al. 1984) as detailed in Table 1. The nets were set in the evening and hauled early next morning. The catch was recorded by mesh size, species, and number, and the length of fish was measured. When an extremely large number of specimens of one species was collected, only 150-300 fish per each mesh size were measured and up to 30 intermediate and large fish were also weighed. Because different numbers of tans were used for different mesh sizes of the gillnet, the values were standardized on a 3-tan-basis for each mesh size, so that "comparable catch per unit effort" (CPUE) could be obtained. In the cases in which the lengths of all fish caught were not measured, values were calculated based on the number measured and collected. When not all fish were weighed, an equation relating the length and the weight was formulated, allowing the calculation of the weight from the measured length. The annual and local distribution of each species was also calculated by considering the number of each species caught at each sampling station as its relative density and the total weight as its biomass. This paper is based primarily on the results of investigations carried out along 170°E and 175°30'E from 1983 to 1985.

RESULTS

1. OCEAN STRUCTURE

To determine environmental conditions, the vertical distribution of water temperature and salinity was examined. Figure 2 shows the vertical distribution of water temperature and salinity measured along 170°E and 175°30'E in July 1984. The Subarctic region was divided into 2 domains (Transitional and Subarctic) according to the method of Dodimead et al. (1963).

Along 170°E the following was found: the Subarctic boundary occurred near 43°N; the subarctic domain was characterized by temperatures below 4°C at a depth of 100 m, or by a salinity of less than 33.4‰ beneath the thermocline (formed in the 100-200 m deep layer), north of
43°30'N; and a narrow Transitional domain existed between the two.

Along 175°30' E, a salinity of 34% was found in the 100 m layer at 44° N, but 43°30' N, was determined to be the Subarctic boundary. The Subarctic domain was formed at approximately 45° N, and the Transitional domain was wider in the north/south direction than along 170° E, however, the salinity structure was complicated and the boundary between the domains was obscured. At each observation point, the water temperature on the surface was higher than that of deeper layers, with a thermocline formed at a depth between 10 and 60 m and becoming shallower in the north.

As in the above example, domains were determined according to the vertical distribution of the water temperature and salinity measured in 1984. Similar results about ocean structure were obtained from the observations made in other years.

2. SAMPLING STATIONS AND OCEANOGRAPIC DOMAINS

Figure 2 shows the sampling stations 1-14 and their domains, classified according to the ocean structure described above. Yearly observations showed that the two longitudes crossed the Subtropic and the Subarctic regions, which include the Transitional and Subarctic domains. Sampling stations occurred in each domain (Table 2).

3. SURFACE DISTRIBUTION OF FISH

3.1 Number of species caught in each domain

Twenty-four species of bony fish, four species of cartilaginous fish, and five species of squid were caught by research gillnets along 170° E and 175°30' E. Pacific salmon and six other species were caught in the Subarctic region; skipjack and nine other species in the Subtropic region; flying squid and five other species in the area from the Subtropic region to the Transitional domain; Pacific saury, pomfret, and two other species were seen in both regions. (Scientific names of all species are listed in Table 3.)

3.2 Numbers caught

The species yielding largest catches from 1983 to 1985 were Pacific saury (49,451), sardine (15,385), pomfret (5,603), flying squid (2,667), and boreal clubhook squid (1,267) (see Table 3). The number of Pacific saury was greatest at 20 of the 41 sampling stations, the number of sardine and flying squid was greatest at five stations each, followed by pomfret (1) and Japanese mackerel (1). At the remaining stations the number of Pacific salmon was greatest.

The largest catches of all species combined were made at Stations 4 and 5 along 170° E, and at Stations 11 and 12 along 175°30' E (Fig. 3). At these stations many Pacific saury and sardine were collected and since these stations all belong to the Transitional domain, it can be concluded that these are the areas where schooling small-sized fish are primarily found during the summer. In the northern and southern areas of the two longitudes, the number of fish caught was small. At Stations 6-9 in the south many neon flying squid were seen, whereas at Stations 1, 2, 13, and 14 many Pacific saury, boreal clubhook squid, and pomfret were seen. These fish reproduce in the Subtropic region.

Thus, many small-sized fish such as Pacific saury and sardine were caught; the former being widely seen both in the north and south, and the latter in more limited areas.

3.3 Biomass

During the three years of study, the biomass of Pacific saury, pomfret, Pacific salmon, flying squid, and blue shark was always large (Table 3). Stations 4, 5, 11, and 12, all in the Transitional domain, showed a high total biomass for all species (Fig. 4). Many Pacific saury, sardine, and pomfret were caught at these stations. The dominant species at the 41 sampling stations were Pacific saury (13 stations), pomfret (9), skipjack and flying squid (4 each), blue shark, sardine, and Japanese mackerel (1 each), with Pacific salmon dominant at the other stations. The southern and northern stations had a lower biomass, with large fish such as skipjack and blue shark dominant in the south, and Pacific salmon and pomfret in the north.

4. LENGTH DISTRIBUTION OF MAJOR SPECIES

The numbers and biomass of fish caught along the two longitudes have already been described. The distribution of a single species is dependent on its developmental stage, therefore, the length distributions of five major species were examined.

4.1 Pacific saury (Fig. 5-A)

The lengths of Pacific saury caught along 175°30' E in 1984 were between 13 and 33 cm, with larger specimens caught in the north and south, and mid- to small-sized specimens in the intermediate zone. This indicates that the larger saury migrate north first (Izutani, S. 1977). The weight of the saury in the north showed that the fish were immature, whereas they were mature in the south, which suggests that ecologically different types occur in the north and south.

4.2 Pomfret (Fig. 5-B)

Pomfret had a wide distribution area, second only to the Pacific saury in
Its northward distribution. Their lengths were between 10 and 50 cm, with small (15-30 cm) and large size (35-45 cm) being dominant. Large pomfret were seen mainly in the Subarctic domain, with small specimens occurring in the southern portion of the Transitional domain. The large pomfret decreased in numbers towards the south. Considering the seasonal migration of this species, it is generally thought that not many pomfret live in the Subtropic domain in July (Shimazaki and Nakamura 1981).

4.3 Sardine (Fig. 5-C)

Many sardines were caught in the Transitional domain, but most were small, 9-18 cm in length. A few specimens longer than 20 cm were caught in June along 155°E. Such large specimens were not seen along 170°E and 175°30'E. The small specimens (9-12 cm) apparently belong to the U-1 age group (Sato and Kaga 1952).

4.4 Flying squid (Fig. 5-D)

Like pomfret, flying squid were distributed widely, with large specimens in the north and small specimens in the south. The large squid in the north are probably females (Naito et al. 1977a). In each year, the smaller squid were seen mainly in the Subtropic region and the large squid were seen as far north as the northern edge of the Transitional domain, but none were caught in the Subarctic domain.

4.5 Boreal clubhook squid (Fig. 5-E)

Although boreal clubhook squid were mainly seen in the Transitional domain, they were also found to the north and south. Their lengths were between 7 and 12 cm, with the larger squid caught in the north.

5. CLASSIFICATION OF FISH COMMUNITIES

The distribution of fish along 170°E and 175°30'E differs from the Subtropic to the Subarctic regions. A dendrogram was made (Morishita 1959; Horn 1966) by obtaining the similarity index between sampling stations based upon the number of fish and the biomass, and by carrying out a Cluster Analysis. In this paper, data obtained in 1984 are used as an example.

5.1 Classification by abundance of individual species (Fig. 6-A)

Three groups had a similarity index of 0.8 or more. They are described as follows:

Flying squid group: Stations 7, 8, and 9 belong to the Subtropic region, where small-sized squid live. Skipjack were seen at Stations 8 and 9, along with Pacific saury at Station 9. The similarity index was 0.9 or more.

Pacific saury group: Stations 3-14 belong to the Subarctic region. More than 90% of the fish caught at Stations 3-10 were Pacific saury, whereas at Stations 2 and 14 saury constituted 67% of the catch, with the remainder being pomfret, boreal clubhook squid, and eight-armed squid.

Sardine group: Stations 5, 11, and 4 had a similarity index of 0.83 or greater. These stations belong to the Subtropic region and the Transitional domain. At Stations 5 and 11, sardines comprised 54% and 63%, respectively, of the catch, with Pacific saury and pomfret forming 19% and 16%, respectively, at Station 5. At Station 4, sardines accounted for 93% and large-sized pomfret for 3% of the catch.

Thus, small-sized fish played an important role in classifying the fish communities by abundance. A secondary role was played by the south by skipjack, and in the north by large-sized pomfret. It has also become clear that abundance of component species in the catch differs in each of the domains.

5.2 Classification by biomass (Fig. 6-B)

Unlike classification by abundance, when classified by biomass, the percentages of major components became smaller, with the number of components often more than one. A similarity index of 0.87 or greater was found at Stations 15-19. Skipjack, with the greatest biomass, were found together with small-sized neon flying squid. At Station 9, blue shark, appearing exclusively in the Subtropic region, formed 29% of the biomass. At Stations 3-11, Pacific saury had a large biomass with a similarity index of 0.7 or greater, with 95% of the biomass at Station 10. At Stations 3 and 12, pomfret made up 31-47% of the biomass, whereas at Station 11, sardines accounted for 37%. This group is seen in the Subarctic region and has a large biomass. At Stations 5 and 6, the major component fish were small-sized pomfret and small-sized flying squid. At Stations 13 and 14, large-sized pomfret with a similarity index of 0.41 was the major component along with Pacific salmon and Pacific saury. At Station 4, pomfret and sardines were the major components with a similarity index greater than 0.6. Like the group found at Stations 5 and 6, pomfret was the major component with a similarity index of 0.54.

Thus, fish communities were classified by abundance and biomass. The fish community found in an area always reflects the existing oceanographic characteristics. The Subtropic region was found to contain the following group: skipjack, small-sized flying squid, and sardine (in some years albacore and blue shark were seen). In the Subarctic region the following main components were found: Pacific saury and sardine, with large-sized pomfret and large-sized flying squid or oho salmon.
DISCUSSION

The investigations were carried out crossing the Subarctic boundary from south to north. As a result, in a short period, fish were collected in three oceanographic areas (Subarctic region, Transitional domain, and Subarctic domain) with differing ecological conditions.

The numbers of fish and biomass values exhibited slight variation during the three years along 17°N and 17°30' E. The data suggest that small-sized and strongly gregarious fish, such as Pacific saury and sardine, were the most abundant, followed by pomfret, flying squid, and boreal clubhook squid. On the other hand, using biomass as the criterion, Pacific saury, pomfret, flying squid, sardine, and blue shark were the main components.

The distribution of these fish is shown in Figure 1. Of the fish with the widest distribution, Pacific saury migrate north the earliest, soon followed by pomfret, boreal clubhook squid, and flying squid. The fish group chiefly composed of Pacific salmon, whose habitat is the Subarctic region, moves further north at this period, and the above mentioned fish group (spawning group is in the Subarctic region) moves into this vacated region, apparently to use it as a feeding ground (Suda 1962; Udate, S. 1977; Naito et al. 1977b; Shimazaki and Nakamura 1981).

As surface water temperature rises, fish groups migrate further north. Albacore, which were seen only in the Subtropic region during this investigation, migrate into the Transitional domain about September. Flying squid and blue shark also spread their habitat to the north (Shimazaki and Nakamura 1981; Nakano et al. 1985). Except for Pacific salmon and eight-armed squid, whose habitat is in the Subarctic region, the main component fish have their spawning grounds in the Subtropic region, and show a northward migration in surface waters as water temperature rises. The data strongly suggest that in this migration the northern (or, Southern) limit (or vertical distribution) is partly determined by water temperature. The distribution and density are also dependent upon predator/prey relationships. Pomfret, for example (Shimazaki and Nakamura 1981), are spread widely from north to south, where the water temperature is between 9 and 21°C. The density, however, is high in the Subarctic region but very low in the Subtropic region. Their feeding index also differs by domain, being highest in the Subarctic region (Fig. 9). Pomfret migrate further north in September, when they have the highest coefficient of condition (Fig. 9), which indicates that they feed most actively at that time on large-sized fish.

Large-sized fish, such as the larger pomfret and flying squid, co-exist with such small-sized fish as Pacific saury and sardine. It appears pomfret are euryphagous, eating both plankton and fish (Kikuchi and Tsujita 1977; Shimazaki and Nakamura 1981). Flying squid, on the other hand, take such small-sized feed as lantern fishes and small-sized squid, whereas Pacific saury are mainly predacious, and Japanese mackerel are plankton feeders (Sato et al. 1968; Shirota 1975; Udate, K. 1977).

From the viewpoint of numbers and biomass, Pacific saury and sardine are the key plankton feeders, and large-sized pomfret and flying squid are the key carnivorous species in the Subarctic region. These communities eat fish and plankton living in the Subarctic region, which indicates that the above fish also have a predator-prey relationship. As shown in Figure 10, large-sized pomfret eat small-sized fish migrating from the Subtropic region, as well as Subarctic squid and lantern fishes. The stomach contents of fish caught in 1982 were closely examined by Kohno (1983), who pointed out that small-sized fish migrating northward from the Subtropic region are important prey for the larger fish following them.

It seems that fish migrating northward into the Subarctic region can be categorized either as those that make direct use of the region's high biological productivity or those that make indirect use of it (Fig. 9). When smaller fishes such as Pacific saury and sardine, which are not stable as resources, are not abundant, larger fishes become dependent on squid or lantern fish, which are distributed mainly in the Subarctic region. Considering the feeding habits of the northwardly migrating fish, clearly the plankton feeders migrate first, followed by euryphagous and then carnivorous fishes. Apparently, the high biological production of the Subarctic region in summer is substantially utilized (Tsujita 1977; Taniguchi 1981).

Since, in this research, fish were caught by gillnets, limitations concerning time and space as well as fishing gear existed. In the Transitional domain, for example, large-sized eight-armed squid were caught by jiggling below the water surface, but few or none were caught by gillnet. Therefore, this collection may not necessarily reflect the actual vertical distribution. Further research is necessary.

SUMMARY

Since 1982, ecological research on the pelagic fish community has been carried out in a given area across the Subarctic boundary in the North Pacific. Many fish were collected by research gillnets. This paper discusses the results of the research carried out in July 1983-1985 along 17°E and 17°30'E, and includes some ecological considerations based on these results. The main points are summarized as follows:

1. Thirty-three species of fish were col-
lected in the investigations carried out along the two longitudes running through three areas that are described as the Subtropic region and the Transitional and Subarctic domains.

2. Small-sized fish, such as Pacific saury and sardine, were the most abundant, followed by pomfret, flying squid, and boreal gunnook squid. With regard to biomass, Pacific saury and pomfret were the largest components, followed by Pacific salmon, flying squid, sardine, and blue shark.

3. The sampling stations that produced the largest values in fish numbers and biomass along the two longitudes were in the Transitional domain. These were coincidentally the stations where Pacific saury and sardines were collected.

4. As to fish distribution, larger fishes were seen in the north.

5. As a result of classification by fish community, Cluster Analyses of fish abundance and biomass for each species show that fish are distributed differently in each domain.

6. As summer advances, pelagic fish communities migrate further northward, feeding actively. Fish that migrate northward from the Subtropic region can be separated into two groups: (1) small-sized fish, which move first and make direct use of the high biological production of the Subarctic region, and (2) those fish that follow, making indirect use of it.

ACKNOWLEDGMENTS

The author expresses his sincere gratitude to Captain S. Yamamoto and his crew of the T/S HOKUSEI MARU for their support and aid in sampling. Thanks are also due to Mr. N. Kohno and Mr. M. Kuruhashi of the Research Institute of North Pacific Fisheries, Hokkaido University, for their cooperation.

REFERENCES


Table 1. Details of research gillnets used for the experiments.

<table>
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<th>Stretched mesh (mm)</th>
<th>Length of float line (m)</th>
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<td>&quot;</td>
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Table 2. Sampling stations and their domains classified according to oceanographic structure. In 1983, Stations 11 was not occupied.

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<th>Year</th>
<th>Long. (°E)</th>
<th>Subarctic domain</th>
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<td>4</td>
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<td>175°30'</td>
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<td>10, 11, 12</td>
<td>8, 9</td>
</tr>
<tr>
<td>1985</td>
<td>170°</td>
<td>1, 2, 3, 4</td>
<td>5</td>
<td>6, 7</td>
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<tr>
<td></td>
<td>170°30'</td>
<td>13, 14</td>
<td>10, 11, 12</td>
<td>8, 9</td>
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Table 3. Total number of fish collected from 1983 to 1985.

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<th>Species names</th>
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<td>312.8</td>
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<td>Coho salmon (Oncorhynchus kisutch)</td>
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<td>Pacific saury (Cololabis saira)</td>
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<td>2619.1</td>
<td>12750</td>
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<td>Lantern fishes (Myctophidae)</td>
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Fig. 1. Map showing sampling stations by research gillnets in 1983-1985.
Fig. 2. Vertical selections of temperature (°C) and salinity (‰) distribution, along 170°E (upper) and 175°10'E (lower) in July 1984. SD: Subarctic domain; TD: Transitional domain; SR: Subtropic region.
Fig. 3. Total numbers of all species caught at each sampling station in 1983-1985.
Fig. 4. Total biomass of all species for each sampling station in 1983-1985.
Fig. 6-A. Dendrogram produced by cluster analysis, using Morishita's similarity index, of the numbers of each species collected in 1984 at the various sampling stations.

Fig. 6-B. Dendrogram produced by cluster analysis, using Morishita's similarity index, of the biomass of each species collected in 1984 at the various sampling stations.
Fig. 7. Schematic distribution pattern of major fish groups for each region in July.
Fig. 8. Relationship between CPUE of pomfret and average feeding indices at each sampling station from September to October 1979.
Fig. 9. Seasonal changes of the mean coefficient of condition (body weight (gm)/length (cm)$^3 \times 10^3$) of large pomfret caught by the RV Shinyo maru (from Shimazaki and Nakamura 1981).
Fig. 10. Schematic food chain of major fish groups migrating northward into the Subarctic region.
ABSTRACT

Landings of Japanese sardine, Sardinops melanosticta, around Japan began to increase around 1910 followed by a period of abrupt increment from 1924 to 1936. Landings peaked in 1936. After 1936 landings rapidly declined and reached a low level in 1965. The low level continued to 1971 but since 1973 the landings increased with the appearance of a strong 1972 year class. This year class may have resulted from good survival during early planktonic egg and larval stages, followed by good recruitment.

Landings of Japanese sardine in the 1980s are greater than those of the high period of the 1930s. The reasons for fluctuations in Japanese sardine stock may depend on survival at early life stages which are affected by environmental conditions such as the meandering of the Kuroshio. This paper describes fluctuations in Japanese sardine stocks and discusses: (1) effect of the Kuroshio on distribution and survival of sardine; a strategy against unpredictable environmental fluctuations; (2) geographic enlargement of spawning and nursery grounds during the period of high abundance; (3) larval recruitment as a result of transport by the Kuroshio from an adjoining sardine population (Ashizuri population); and (4) reasons for the depletion in the 1940s and a perspective on future trends of the sardine stock.

INTRODUCTION

Since the early 1900s, the Japanese sardine has shown repeated long-term fluctuations. Since 1970, abundance abruptly increased with the appearance of several strong year classes. At present, the landings of sardine exceed those taken in the 1930s, the previous years of high abundance. Fluctuations in sardine abundance may be affected by success or failure of survival at early stages of life, such as egg and larva. Sardines release pelagic eggs which, together with larvae, drift on the surface or in the sub-surface layers. Along the Pacific coast of Japan, the distribution and survival at early stages are closely connected with meandering of the Kuroshio. In this paper we discuss the environmental and biological factors that affect recruitment and distribution of the Pacific population as well as the perspective of future trends of the sardine stock.

HISTORY OF FLUCTUATIONS

The landings of Japanese sardine increased from about 1910 with a sharp increment during a period from 1924 to 1936. Landings reached a high maximum level of about 1.5 million tonnes in 1936 followed by a rapid decline to a minimum level of less than 10,000 tonnes in 1965. Low levels continued to 1971 but since 1973 the landings showed a stepwise increase to over one million tonnes in 1976, two million in 1980, three million in 1981, and over four million in 1984. The landings exceeded those of the previous maximum level in 1936 (Fig. 1).

The sardine stock around Japan consists of four local populations having unique distributional and migratory patterns; namely Pacific, Ashizuri, Kyushu, and Japan Sea populations. During the period of large stock size in the 1930s, the major fishing grounds were located in the Japan Sea along the coast of Democratic People's Republic of Korea and the Coast Range of the U.S.S.R., as well as along the Pacific coast of Hokkaido and Tohoku (see Fig. 2). The sardines were caught both from the Kyushu and Pacific populations. The major fishing grounds in recent years also are located in the same regions as in the 1930s.

In recent years, landings from the Pacific population, which constitutes 60 to 85% of the total sardine landings in Japan, have increased, similar to the trends observed in other sardine stock around Japan. Landings exceeded one million tonnes in 1977, two million in 1981, and three million in 1983 (Fig. 3). This increase in the Pacific population reflects the appearance of the strong 1972 year class, followed by several more strong year classes. These strong year classes can be classified (Fig. 4) on the basis of abundance levels: (1) medium level, such as the 1972 and 1973 year classes; (2) strong, such as the 1974 to 1979 year classes; and (3) very strong, such as the 1980 and 1981 year classes. Year classes following 1982 fluctuated between the strong and very strong levels.
GEORAPHIC ENLARGEMENT OF SPAWNING AND NURSERY GROUNDS

The migratory and distributional patterns of sardines depend on stock abundance. Generally, when abundance is low, sardines do not make a seasonal north-south migration but instead are confined mainly to the southern warm waters. In contrast, during the period of high stock abundance, sardines expand their range by making a large scale north-south migration (Fig. 5). During the feeding season, sardines migrate to warm waters and expand their range southward. Such expansion was evident during the recent increase of the Pacific and Kyushu populations when there was a marked tendency for eggs and larvae distributed near the Kuroshio and its southern edge to show a greater distributional range from inshore to offshore (Figs. 6 and 7). On the other hand, the Ashizuri and Japan Sea populations did not show any remarkable expansions during the recent increase in other populations. During the feeding season, the Pacific population migrated into the cold waters of the Oyashio while the Kyushu population extended into the Liman Current off D.P.R. Korea and the Coast Range of the U.S.S.R. The spawning ground of the Pacific population is within the waters from Kashima-Nada to off Kii Peninsula, and that of the Kyushu population from off San' in District to the Satsunan Region south of Kyushu (see Fig. 2 for locations). The spawning areas and the migratory ranges north and south of these populations show similar extensions. It can be said that increasing abundances of the populations spread ranges and migration to both warm and cold waters, respectively (Nakai 1962; Hara 1983). Therefore, sardine stocks, which fluctuate dramatically, also undergo geographic enlargement and shrinkage with changes in abundance.

LARVAL TRANSPORT BY THE KUROSHIO

Generally, sardine larvae disperse mainly by water movement. Sardine larvae are recruited and transported by the Kuroshio into the area where the Pacific population is distributed. As the Kyushu population expanded, the recruitment increased (Figs. 6 and 7). For example, the catches of 0- age fish (2 to 15 cm in body length) increased in Enshu-Nada, Ise Bay, and Mikawa Bay at the southernmost extremity of the Pacific population area. There are two possible reasons for such increments in recruitment: (1) the initial increase in the Pacific population may have occurred through immigration from the upper stream of the Kuroshio (Watanabe et al. 1979). It is not clear, however, whether these transported young fish remained in the Pacific population or later returned to their original spawning grounds; and (2) recruitment, as estimated through the incidence of young fish, could be misleading in the Pacific population because, within this population, only the early stages, such as eggs, larvae, and 0-age fish, were dominant; the dominancy of succeeding stages was not clearly apparent. The high incidence of young stages in the Pacific population is a result of this one-sided invasion or might be indications of the formative period of the Pacific population derived from the adjoining Kyushu and Ashizuri populations (Hara 1983). In general, however, the majority of long distance dispersant by other species do not become established (Nishimura 1970).

EFFECT OF THE KUROSHIO ON DISTRIBUTION AND SURVIVAL

There are two characteristic flow patterns of the Kuroshio as it passes through the spawning ground at the southernmost sector of the Pacific population area, (1) offshore Kuroshio, Enshu-Nada, the "A-type," and the nearshore meander, or "non-A-type." The "non-A-type" can be classified into three sub-types by its degree of meandering (Nitin 1969; Fujimoto 1970): (1) B-type: the Kuroshio flows closely along the coast of Enshu-Nada when there is no cold water mass on the coastal side of the Kuroshio where the coastal area is relatively large (Fig. 8). The coastal temperature in winter is lower than usual. (2) B-type: the Kuroshio flows northward along the west rim of the Izu Ridge across the cold water mass which is smaller than that during A-type (below), coming close to the Izu and Boso peninsulas. This type usually persists for less than six months. The coastal temperature in winter is higher than usual. (3) C-type: the Kuroshio meanders along the cold water mass which lies over and across the Izu Ridge, somewhat apart from the Boso Peninsula. The temperature around Izu Island may drop when C-type persists in the winter season. (4) D-type: the Kuroshio meanders along the cold water mass which lies east of the Izu Ridge, apart from Boso Peninsula, like the C-type. These types usually change from one to another over a short time with sequences such as N-B-C-D-N. The fluctuation of the Kuroshio meandering may influence reproduction of marine animals, including sardine, by flow patterns that alter water temperature during winter and spring seasons.

During periods of A-type flow, the coastal domain of the Kuroshio is depressed and coastal temperature is higher than usual since the Kuroshio comes close to Izu and Boso peninsulas. As a result, spawning of the sardines occurs a little earlier and the spawning area is concentrated in a narrow belt in coastal waters. As the coastal waters are narrowed, the density of eggs spawned may become higher. In contrast, the density and abundance of Clupeoida, on whose prey, sardine larvae, may decrease (Kidachi and Ito 1979). When such a flow pattern is maintained for more than several years, these effects become pronounced. Consequently, sardine abundance tends to
decrease during the A-type meanders.

When meanders shift from the A-type to the non-A-type, the Kuroshio changes to a path parallel to the coastline, such as A-B-C-(D)-N; coastal type waters are expanded with more frequent occurrences of upwelling and mixing. Such oceanographic changes may cause a high production of planktonic organisms on which sardine post-larvae inhabiting the area prey favorably. The 1980 year class was a good example. Egg abundance of this year class was at a lower level than others, but survival during their early life was good, resulting in a strong year class.

The C-type Kuroshio meander usually results in the spawning period of sardines becoming later because of low temperature in coastal waters. The eggs and larvae are concentrated in the coastal water where suitable plankton remains abundant and post-larvae grow favorably in such a food-rich nursery ground. Hence, the conditions for survival depend not only on the abundance of eggs but also the mode of transportation and dispersion at early stages.

During the N-type meander, the sardine spawning grounds are located on the coastal side of the Kuroshio. Plankton is abundant there and conditions for good survival of early life stages are favorable. The Kuroshio changed its course from C-type to N-type during the winter in 1972. Because of this change, the coastal, small type copepoda were abundant (Watanabe 1977; Kidachi and Ito 1979). The egg abundance in this year increased to a level of 18x112x, although this was still lower than in the present prosperous period. Under such conditions of physical and environmental conditions, the dominant year class of 1972 appeared, resulting in the succeeding success of dominant year classes.

If the A-type meander persists, the plankton biomass remains at a very low level. This condition is not favorable for sardine reproduction. During the non-A-type, the survival of early life stages of sardine varies considerably depending upon sub-type. Therefore, a strong year class can occur when the Kuroshio shifts from the A-type to non-A-type and from the C-type to N-type during the spawning season. Thus, the occurrence of a dominant year class is indirectly affected by physical conditions resulting from the flow patterns of the Kuroshio and by sardine abundance. Under a fluctuating environment, a survival strategy in early life, which is characterized as having a high natural mortality, might be to spawn profusely and maximize dispersal of pelagic eggs. Thus, the sardine adapts well to the unpredictable fluctuations of the Kuroshio.

THE DEPLETION IN THE 1940s AND FUTURE TRENDS

In addition to the short-term fluctuations caused by changes in the physical and biotic environment, sardines also undergo long-term fluctuations. There have been many contradictions on the reasons for the depletion of sardines in the 1940s. Nakai (1962) concluded that the depletion was primarily through changes of abiotic environmental factors such as anomalies in the Kuroshio that had an ill-effect on recruitment for the years in question. Nakai's view has been accepted by many scientists concerned with this problem. However, several biotic phenomena related to the reduction of recruitment in the early life stages were not always satisfactorily explained. The biological phenomena that occurred in that depletion were: (1) disappearance of the spawning ground in the Satsuman Region (south of Kyushu); (2) disappearance of the advanced age fish in the northernmost nursery ground in summer; (3) delay of the fishing season on the northernmost fishing ground; and (4) delayed increase of catch at the northernmost range and the earlier decrease of catch than in the southern part of range. It can be assumed that the spawners decreased gradually, resulting in decrease in egg abundance, because of the disappearance of fish of advanced age. This means that overfishing might have played an important role in depletion of sardine catch in those days. We may again observe these phenomena and future depletion. However, the catch of sardine will stay at present high levels at least for several years since the abundance of advanced ages (1980 and 1981 year classes) is at a high level. Depletion is caused through a complex effect of biotic and abiotic environments including fishing and thus it is necessary to continue present and future studies from various standpoints.

REFERENCES


Fig. 1. Fluctuations in sardine catch around Japan.
Fig. 2. Japanese Islands showing major fishing locations.
Fig. 3. Catch of sardines from the Pacific population. Numerals identify the year classes.
Fig. 4. Relationship between spawned eggs and recruitment. Numerals identify year classes (1900s); alphabetical symbols correspond to the type of Kuroshio meandering (see Fig. 8).
Fig. 5. Local catch of the Pacific population.
Fig. 6. Distribution of sardine eggs and larvae based on vertical zooplankton hauls (February-March, 1985, R/V Soyo maru).
Fig. 7. Distribution of sardine eggs and larvae based on vertical zooplankton hauls (February-March, 1971, R/V Soyo maru).
Fig. 8. Flow patterns of the Kuroshio (after Nitani 1969 and Fujimoto 1970).
I had the opportunity of making a presentation of my studies on methods for calculating catch limits at the first INPFC Symposium held in Vancouver in 1981. Thus, this is my second opportunity to participate in the INPFC Symposia series. It is a great honor for me to give the review at the close of this Symposium. I also realize the graveness of my responsibility. I would like to take this opportunity to note some aspects which have impressed me during this three-day symposium.

First, I was impressed with the active research concerning fish stocks in the North Pacific Ocean that is being conducted by each nation. The recent atmosphere in international relations in the field of fisheries in the North Pacific Ocean is not necessarily amicable. Various politically difficult problems have arisen. Nevertheless, or should we say, therefore, the scientific studies are being carried out at high levels which is very gratifying. Through the presentations made here, I have learned that important studies are also conducted which form backgrounds for these presentations. As we can see from the references which are cited in the papers presented, the majority of these studies have been accomplished in the 1980s. I hope these studies will contribute substantially to the solutions of political problems concerning fisheries in the North Pacific Ocean in the future.

I would like to pay my respects to the scientists who are involved in these studies and also to place a high value on the role that is performed by the International North Pacific Fisheries Commission in order to expedite studies in this field.

For this symposium, two topics were adopted: "Biological interactions of fisheries resources" and "Environmental and biological factors affecting recruitment, distribution and abundance." I feel that these topics have been considered as though they were separate problems. However, it is clear that they are not separate at all but have great relevance to each other. For instance, studies concerning the fluctuations in year classes of Pacific cod (Gadus macrocephalus) in Hecate Strait were presented under each topic by Dr. Tyler. It has been clearly learned that fluctuations in stock sizes are affected by those in recruitment levels and it has been stressed by many scientists for many years that species interactions have relevance to the fluctuations in stocks. However, this is a theoretical hypothesis for which there is only little evidence. For example, although many people note the negative correlation between the sizes of sardine stocks and anchovy stocks, no concrete or practical explanation for the mechanism has yet been given. However, in this symposium, data have been presented that indicate that predation by Pacific cod and Pacific hake can cause fluctuations in the sizes of a year class of herring in Hecate Strait. Although further studies are required, because we learned that fluctuations in the sizes of year classes are also explainable by other factors such as sea water transport and water temperature. I would like to note this presentation as an example of the relationship between predation and fluctuations in stock size.

I initially had some fears that a large number of studies dealing with ecosystem modeling might be presented in this symposium since one of the topics concerned interactions between fisheries resources. Fortunately, however, such presentations were not made except for that by Dr. Kitano which discussed an ecosystem model of the Sea of Japan. To me, the ecosystem model is like a nightmare. However, this does not mean that I deny the value of ecosystem modeling. Although its necessity is understandable, the extent of our knowledge is still extremely small.

Under this situation, we should consider our approach in ecosystem modeling. First of all, we should clarify practically the interactions of resources step by step. In this symposium, many studies on food habits of fish were presented. The importance of predation as a factor in interspecific relationships was noted through these presentations. Food habits of fish vary in complexity through a great number of factors such as year, season, area, age or size, time of day, amount of food and the existence of other competitive species. We should identify these factors one by one. This might appear nightmarish to scientists dealing with food habits. However, without overcoming these difficulties there would be nothing else but to look forward to hearing some divine message for developing ecosystem models. Although such studies require much effort and budgetary support and impose a strain on the scientists, I believe that we should promote these studies with all our capabilities.
However, I think that ecosystem modeling can be developed even though studies on food habits are not complete. One aspect of the utility of the modeling is to indicate the direction for further studies. Modeling of interspecific relationships should be attempted taking this aspect into account. I would like to examine those models which are developed based on real data. I think these models would be very meaningful even if they concerned only a part of the whole ecosystem. With respect to the model discussed by Dr. Yeh, still at an elementary stage, it is interesting that the model was developed with the focus on a particular species, such as the lizard fish. I believe that in the future it is necessary to develop models on the one hand while accumulating practical data on the other, and in this manner, it may be possible to find means to avoid the nightmares.

I would like to add a few more words concerning ecosystem models. Accumulation of a great number of further studies is required in order that the complex and comprehensive ecosystem models might be of practical significance in managing the fishery resources. If one constructs a model under conditions where practical interspecific relationships are not sufficiently identified, such a model might be considered an armchair model, and the model originator may not realize how he should incorporate the results and improve the model from future practical studies such as the interrelations between Pacific cod and herring. In developing any ecosystem model, we should structure it so as to allow its development and improvement by incorporation of up-to-date results of studies. And, at present, the original object of developing an ecosystem model should be limited to providing a basis for determining the direction of further study and to re-examine the fundamental standpoint for resource management.

In cases of studies on multi-species relationships and communities, various coefficients and indices are frequently used. Examples are the "Index of affinity," "Schoener's index" and include the "Diversity index." These indices are most effective in describing communities which have complicated structures and functions and in clarifying the status of the communities. However, it is not satisfactory to determine the degree of a relationship only by arriving at some value of a coefficient. It is necessary that the state of interaction between stocks be identified through these coefficients. For that purpose, clear reasons for calculating the coefficients should be defined before the calculations are made. In other words, models which are regarded as the norm and through which we get their thoughts in order are required. Calculations of coefficients which are obtained without referring to such models might invite additional confusion instead of getting our thoughts in order particularly in this age where computers can process an enormous amount of data very rapidly.

Models concerned with species interactions may not be satisfactory at the present time. For example, Dr. Sudo described the spatial or temporal segregation of niches and differences in feeding patterns between species. There is a question of how to develop a model to quantify such phenomena. On the one hand we should expend our efforts to corroborate phenomena with additional data and on the other hand develop practical models. In the course of this process, various indices and coefficients which are elaborately derived can be expected to perform their function effectively.

It is a major problem to evaluate the correlation between fluctuations in resources and those in the physical aspects of the environment. There have been a number of instances where fluctuations in the Kuroshio current or El Nino might have resulted in large fluctuations in stocks. However, the Kuroshio current itself cannot directly kill fish. The direct cause of fluctuations in stocks is the change in mortality rate and in this regard there is no doubt that predation has great importance as repeatedly noted during this symposium. Thus, it is essential to investigate the direct causes of death of fish in order to fully examine the fluctuations in stocks in relation to those in the environment. Further studies on predation and starvation should be conducted. However, this may be difficult. We cannot obtain information for studies on predation unless we collect samples at the site and during the time when death is actually taking place. In order to accumulate such information, we have to begin with a clarification of how and into what we should direct our research. Statistical studies on fluctuations in both the physical factors of the environment and the stocks are of great importance in this context. However, we still cannot say that we understand the mechanism of fluctuations in stocks if only the correlation between the fluctuations in the Kuroshio current and those in stocks is calculated. Even though the meandering of the Kuroshio current might positively affect fishery stocks in one circumstance it might do so negatively in other circumstances.

There were a number of presentations concerning the correlation between distribution of stocks and oceanic conditions. Each presentation describes material derived from both detailed observations of ocean conditions and the collection of samples. It was recognized that ocean organisms show fairly clear segregation depending on the water masses. Furthermore, it is noteworthy that even one species of fish may show different patterns of habitat preference according to the stage of growth. By combining these studies with studies on the distributions of prey items and on the food habits, it is expected that we may comprehend not only
the relationship between distributions of water mass and of fish schools but also situations in situ where predation and starvation are taking place.

There was an important statement that we cannot neglect the influence of fishing even if some fluctuations in environmental conditions exist. I think we can agree that the influence of fishing is not negligible under every situation particularly for such species as Pacific halibut. However, it is not an easy question of how we should take into account the influence of fishing in considering management concerning the sardine stock off Japan whose stock size historically has shown fluctuations of the order where the maximum level is several hundred times as large as the minimum. While there is a danger that intensive fishing may again result in collapse of the sardine stock, we cannot deny the possibility that stock thinning by means of fishing helps maintain the sardine stocks at high levels.

Here I would like to call your attention to the fact that the survival rate from spawning to recruitment is not significantly different under conditions where the stock remains at high levels or at low levels. An extremely high survival rate is observed when a stock has begun increasing. However, this high survival rate does not continue in the period after the stock has reached high levels. This should be taken into account in considering the fluctuations in recruitment levels.

Since the topics for this symposium were interspecific relationships and fluctuations in recruitment levels, there was no discussion of the basic data from which the presentations under these topics were derived. In the process of calculations, the values of the biomasses are frequently used. The biomass is calculated based on CPUE or other data. Although CPUE has been used as a relative index of the stock size for a long period of time, it is also well known that this method raises some questions. When converting the CPUE into the biomass it is often assumed that one hundred percent of the fish which are found in a swept area are captured. However, it is known that capture efficiency is considerably lower than one hundred percent. The virtual population analysis (VPA) method is often used but it is essential to this method that the numbers caught by age are correctly estimated. Taking into consideration the errors of age determination, the conversion of length composition into ages, and the samplings, it is presumed that errors in the estimated numbers caught at each age are not at all minor. Estimates of food consumption might have even a larger range of errors because the weight and composition of stomach contents vary drastically. In the calculation of VPA and in simulating the fluctuations in stocks it is essential that the natural mortality coefficient M be given. However, it is also very difficult to estimate the value of M. In addition, if we assume that predation is the major component of natural mortality, it is questionable to consider the value of M as a constant. The methods of estimation of basic data or the accuracies of the estimates, for which I gave examples earlier, have a critical influence on subsequent analyses. Although this problem was not discussed in this symposium, I hope that this will be intensively examined at another opportunity in the future.

The study of resources has a long history. Japanese studies on the sardine stocks have been conducted for fifty years. Even studies initiated after the Second World War have a history of more than thirty years. This fact poses a serious question to us. The continuation of studies for several decades has not brought about significant changes in the situation. Our knowledge is still quite limited. Even though we continue these studies for another several decades, the problems which we are facing at the present might still remain unsolved. This is a very serious question for all of us.

If our studies have not made visible progress, two possible causes can be identified. One is that the methodologies of our studies are basically incorrect. The other is that actual budgets and personnel that are available for our studies are extremely small. Compared with the complexities of the subject of our investigations our methods of observation are far from satisfactory. Accordingly, we have to rely on data from fisheries that include large biases. In addition, either the types of data which we have collected or the methodologies in analyses do not seem complete.

However, even though we cannot answer, for example, the question of why the stock of sardine has increased or when it will start declining, the current amount of our knowledge is much greater than that of 10 years ago to say nothing of comparison with that of 30 years ago. In this symposium it has been suggested that excellent developments in studies have been attained over the recent several years. However, unfortunately, the information which we can obtain is still fragmented because of limitations of budgets and personnel which are available for us. I believe that we have a responsibility to request a large increase in budgets and personnel. However, since every government is always poor, I suspect that any such request would not be easily accepted. In order to make up for such limitations, we are requested to intensify our efforts.

Although the number of scientists is limited, it is essential that their originality and ingenuity be fully developed and that cooperation and exchange of information among the scientists be most active. And, after all, scientists should be tireless for continuing their studies.

I would like to conclude my symposium review by wishing you every success in the future.