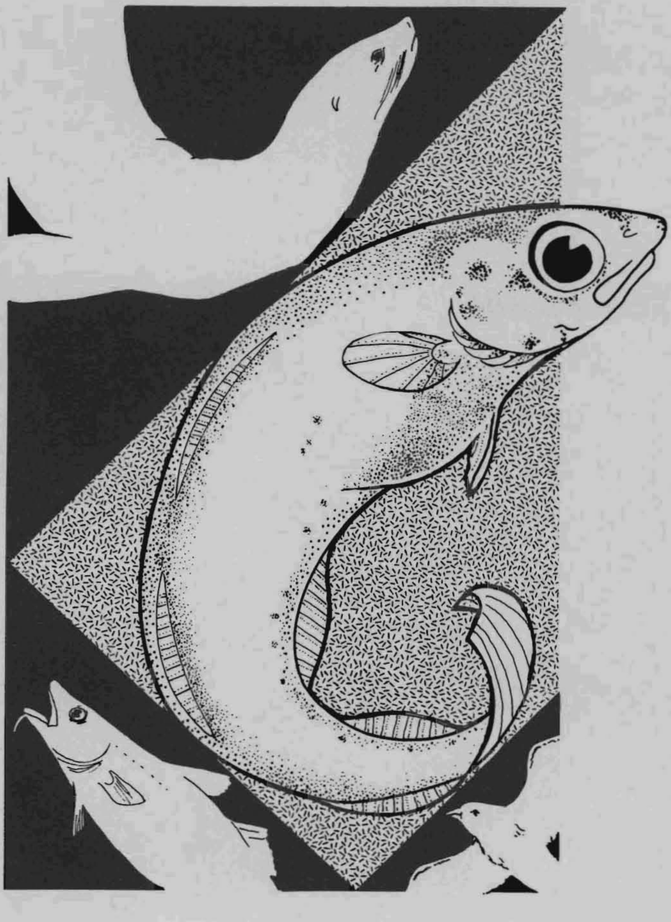
NOAA Technical Report NMFS 126 December 1996

Ecology of Juvenile Walleye Pollock, *Theragra chalcogramma*



Papers from the workshop
"The Importance of
Prerecruit Walleye
Pollock to the Bering
Sea and North Pacific
Ecosystems"
Seattle, Washington,
28–30 October 1993

Edited by
Richard D. Brodeur
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U.S. Department of Commerce

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NOAA Technical Report NMFS 126
A Technical Report of the *Fishery Bulletin*

Ecology of Juvenile Walleye Pollock, *Theragra chalcogramma*

Papers from the workshop "The Importance of Prerecruit Walleye Pollock to the Bering Sea and North Pacific Ecosystems"
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Sponsored by:

Alaska Fisheries Science Center
National Marine Fisheries Service
U.S. Dept. of Commerce, NOAA
Seattle, Washington

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Introduction

RICHARD D. BRODEUR, PATRICIA A. LIVINGSTON,
THOMAS R. LOUGHLIN, and ANNE B. HOLLOWED

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The Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service (NMFS), hosted an international workshop, "The Importance of Prerecruit Walleye Pollock to the Bering Sea and North Pacific Ecosystems," from 28 to 30 October 1993. This workshop was held in conjunction with the annual International North Pacific Marine Science Organization (PICES) meeting held in Seattle. Nearly 100 representatives from government agencies, universities, and the fishing industry in Canada, Japan, the People's Republic of China, Russia, and the United States took part in the workshop to review and discuss current knowledge on juvenile pollock from the postlarval period to the time they recruit to the fisheries. In addition to its importance to humans as a major commercial species, pollock also serves as a major forage species for many marine fishes, birds, and mammals in the North Pacific region.

This workshop originated in 1990, as we lamented how little we knew about the juvenile phase of walleye pollock relative to the larval and adult phases. Although this generality may apply to almost any marine fish species, we thought that the lack of knowledge was particularly acute for pollock, considering their importance to the North Pacific ecosystem. As an example of the underemphasis on the juvenile phase of pollock life history, the published proceedings of the last major workshop on walleye pollock held in 1988 in Anchorage, Alaska, contained almost 800 pages, of which only about 30 (less than 5%) pertained to juvenile pollock. We were aware that scientists throughout the North Pacific were interested, as we were, in juvenile pollock, not only for its biology, but also for its importance as prey for a wide diversity of marine organisms. We thought that much could be gained by gathering these researchers together to discuss what is known, and also—perhaps more important—what we still need to learn about juvenile walleye pollock. We believed that the timing of this workshop was particularly appropriate because the North Pacific ecosystem has undergone some extensive changes in the last two decades because of both natural and human-induced perturbations.

The workshop was opened by William Aron, Director, AFSC, who challenged us to see beyond our own research and to work together to understand pollock's importance to the ecosystem. Warren Wooster, Chairman, PICES, next spoke on how this workshop fit into the overall objectives of PICES. Michael Sissenwine, Senior Scientist, NMFS, Silver Spring, Maryland, presented a keynote address on the general importance of juvenile fishes to the productivity and management of marine ecosystems. Sissenwine has long been a proponent of studying the juvenile phase as a way to understand recruitment of marine fishes, and he brought to the workshop much experience with juvenile gadids.

The workshop continued with sessions on abundance and distribution, ecology and growth, predator–prey relations, and population dynamics and modeling, with invited experts from each field serving as session moderators. Overall, 70 authors contributed to 29 oral and 7 poster presentations. All contributors were invited to submit their papers for this publication, and 14 full articles were submitted. Each manuscript was reviewed by at least two anonymous referees consisting of both workshop participants and "outside" reviewers. When papers were to be published elsewhere, the authors were given the option of publishing an extended abstract in these proceedings. These abstracts and the comments of the session chairpersons did not receive extensive peer review.

As workshop conveners, we would like to thank all those who contributed to the success of this meeting. In particular, our Research Center and Division Directors—William Aron, Jim Balsiger, Gary Stauffer, Richard Marasco, and Howard Braham—provided financial support to convene the meeting and edit the proceedings. The PICES Secretariat provided logistical support throughout the workshop. We are indebted to the numerous AFSC personnel who helped with registration,

audiovisual presentations, and other technical aspects of the workshop. We thank Ron Hardy and his editorial staff for their assistance in the review process, Martha Jackson and Gary Duker for assistance in editing the proceedings, and also the many reviewers who helped improve the manuscripts. Finally, we thank the session moderators—Don Gunderson, Ian Perry, George Lilly, and Bill Overholtz—for keeping the workshop on schedule and for offering insightful comments on their sessions both in their talks during the workshop and in their written reports for these proceedings. Their generous giving of time contributed significantly to what we consider a very successful workshop.

Distribution and Abundance of Age-0 Juvenile Walleye Pollock, *Theragra chalcogramma*, along the Pacific Coast of Southeastern Hokkaido, Japan

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ABSTRACT

Age-0 juveniles of walleye pollock, *Theragra chalcogramma*, were studied along the coast of southeastern Hokkaido in autumn in order to describe interannual variations in distribution and abundance and to evaluate the feasibility of using juvenile abundance to measure year-class strengths. The shishamo trawl net surveys for the assessment of shishamo smelt, *Spirinchus lanceolatus*, were conducted in 1978–92, and bycatch data for walleye pollock were collected. Age-0 walleye pollock juveniles were found mainly in the 50-m and the 60-m depth strata, with the highest abundance off Ohtsu. This indicates that juvenile pollock move from the surface layer to the bottom layer, deeper than 40 m off southeastern Hokkaido, as they grow. An age-0 abundance index was calculated by summing the CPUE's of all 10-m depth intervals for each year. There was no significant relationship between abundance indices and estimated numbers of age-0 fish from VPA. Before 1987, however, abundance indices were significantly correlated with estimated numbers from VPA (r=0.76).

Introduction

A key issue in fisheries biology is determining when the relative strength of a year class is to be established. In a management context, this information is useful for predictive purposes, revealing when prerecruit surveys should be conducted. In order to give fisheries managers maximum lead time for establishing harvest levels, surveys should be conducted as early as possible (Bailey and Spring, 1992). Walleye pollock, *Theragra chalcogramma*, is important for commercial fisheries around Japan. Its annual catch from the Pacific Ocean off Japan was 166,304 t in 1990, and 50,000–80,000 t from off southeastern Hokkaido.

Recruitment appears to be the major factor that drives change in the biomass of this stock. Bailey and Spring (1992) found that age-0 juvenile surveys can detect relatively strong or weak year classes in the western Gulf of Alaska. Many studies of the egg, larval, and early juvenile stages of walleye pollock in the Pacific coast population of Hokkaido have been undertaken (e.g.,

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Kanamaru, 1985; Nakatani and Maeda, 1987; Nakatani, 1988), but little is known of the biology of age-0 juveniles of walleye pollock around Japan in autumn (e.g. Ishigaki et al., 1960; Hayashi, 1976).

We describe the geographical distribution and abundance of the juvenile stage of walleye pollock that have settled to the bottom layer. We then estimate an abundance index of juveniles from the results of surveys that have been conducted in September and October since 1978. Finally, we evaluate the feasibility of using our abundance index for estimating year-class strength.

Methods and Materials

Shishamo trawl net surveys for the assessment of shishamo smelt, *Spirinchus lanceolatus*, stock have been conducted along the Pacific coast of southeastern Hokkaido in September and October since 1978 (Fig. 1). Captain Nahira modified the shishamo smelt beam-trawl net by taking the beam off, changing the net size, making the upper net longer than the ground net, and so on (Fig. 2). A total of 1,152 tows were made at 38 main stations and at some additional points, mainly off Kushiro region. The *No.5 Tensho-maru* was used for all surveys. Bycatch data for age-0 walleye pollock were recorded. We took samples of up to 100 individuals each year for standard length measurements. We were able to discriminate age-0 walleye pollock from older age classes by their length distribution in this season. Almost all age-0 walleye pollock ranged from 7 to 13 cm in standard length, so we classified walleye pollock smaller than 15 cm as age-0 juveniles. A Nansen bottle sampler was used to gather information on the water temperature of the bottom layer at each station.

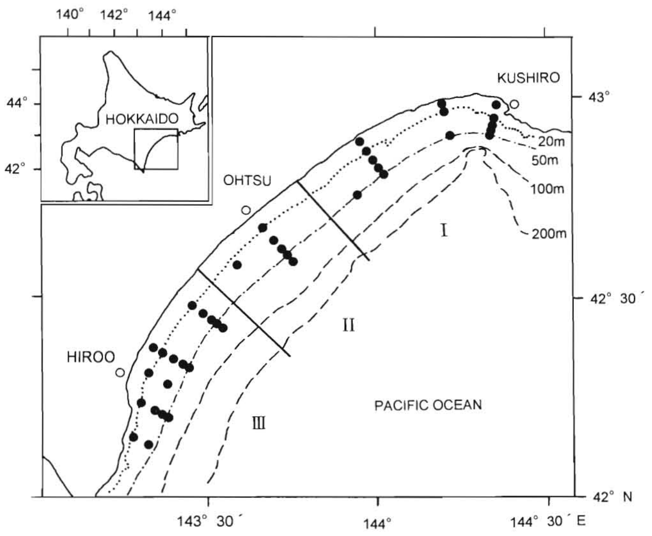

Figure 1
Survey area in southeastern Hokkaido showing the three regions used to calculate local abundance indices.

We estimated the abundance index by summing up the catch per unit of effort (CPUE) of each interval of 10-m depth in each region (Fig. 1) over all areas; 0

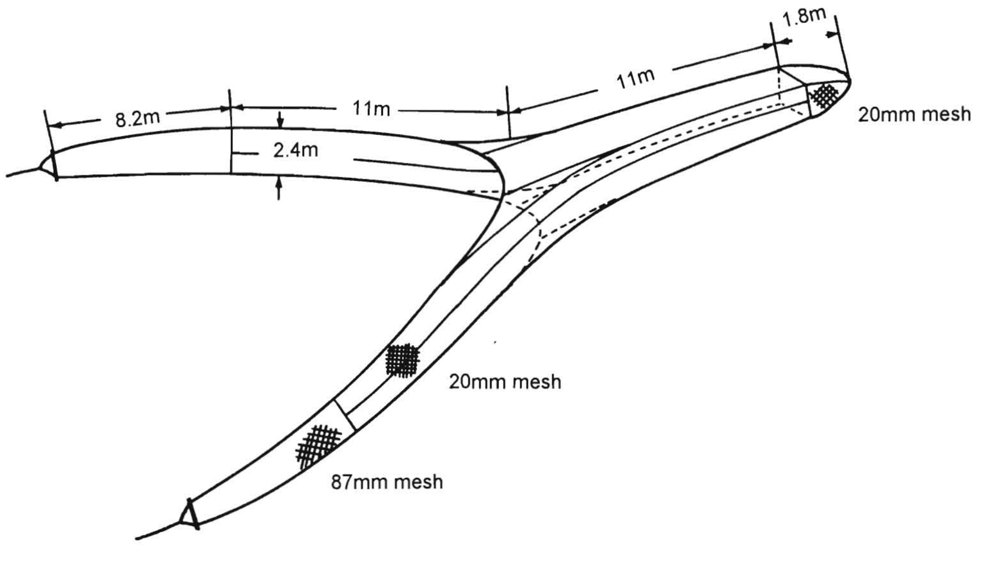

Figure 2
Shishamo trawl net as modified by Captain Nahira.

catches were included. The equation used was

$$Y = \sum_{i=1}^{M}\sum_{j=1}^{N} \frac{C_{ij}}{X_{ij}}$$

where Y is the abundance index, X_{ij} is the number of tows, C_{ij} is the total catch in the ij th area, i is the i th depth stratum, j is the j th region, N is the number of depth strata, and M is the number of regions.

We compared abundance indices of age-0 fish with estimated numbers of age-0 and age-4 fish derived from virtual population analysis (VPA) for the Pacific stock around Japan (Watanabe[2]).

Results

Distributions of Juvenile Pollock

The shishamo trawl net tows were made at depths from 5 m to 210 m. After 1983, survey depths ranged from 5 m to 60 or 70 m in most years. The catches by haul of age-0 juveniles ranged from 0 kg to 120 kg. The largest catch was observed in the 60-m depth stratum (Fig. 3). Juveniles ranged from 5 cm to 15 cm standard length; average length was 9.4 cm from 1988 through 1991. Juveniles were found in the 40-m to 100-m depth strata, mainly in the 50-m and 60-m strata; very few were found shallower than 40 m in any year (Table 1, Fig. 4). The highest CPUE was 100.0 kg/tow in the 60-m depth stratum in region II in 1988.

To examine interannual changes in distribution along the coast, we calculated the local abundance indices for each year by the three regions shown in Figure 1. In 1978, 1979, and 1980, the highest index of juveniles was in region I (off Kushiro); in 1981 and 1982 the highest index was in region III (off Hiroo). Region II (off Ohtsu) was dominant from 1983 through 1991. However indices were very low in all three regions in 1992 (Fig. 5).

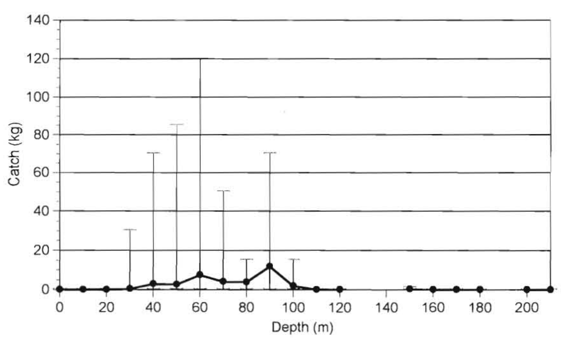

Figure 3
Catches and depths. Dots show mean of catches and bars show range of catches for each 10-m depth stratum.

The bottom-water temperature ranged widely, from 6° to 16°C, in the areas where catches of age-0 juveniles were observed through all years (Fig. 6). We did not catch any 0-age juveniles in the areas where bottom temperatures were lower than 6° or higher than 16°. The highest catch (120 kg) was recorded at the station off Ohtsu, where the bottom water temperature was 13°.

Abundance Indices

The changes in age-0 abundance indices are shown in Figure 7. Age-0 juveniles were relatively abundant in 1978, 1981, 1986, and 1988–91. During 1988–91 the abundance index was very high, but it decreased rapidly in 1992. The age-0 abundance index of walleye pollock ranged over two orders of magnitude, from 175.6 in 1989 to 1.2 in 1992.

The changes in estimated numbers of age-0 juveniles from VPA are also shown in Figure 7. The changes in abundance indices and estimates based on VPA were similar during 1978 to 1986. The relationship between abundance indices and VPA estimates of age-0 fish is shown in Figure 8. The simple correlation coefficient was not significant during 1978 to 1991 (r=–0.03, n=14); however, it was highly significant from 1978 to 1986 (r=0.76, n=9, p=0.018).

Discussion

Abe (1968) reported that larval walleye pollock ranging from 4 to 38 mm total length (TL) are distributed mainly in the surface layer along the coast of southeastern Hokkaido in June. When pollock reach 85 mm TL in July, they move to the bottom layer in Funka Bay (Nakatani and Maeda, 1987). These studies indicate that juveniles migrate offshore and move to the bottom layer as they grow. We found very few age-0 juvenile walleye pollock shallower than the 40-m depth stratum in any year. A shishamo trawl net catches fish in the bottom layer, and thus our results indicate that juveniles move from the surface layer to the bottom layer, which is deeper than 40 m off southeastern Hokkaido in autumn.

The highest age-0 pollock catches were consistently located in region II (off Ohtsu) from 1983 to 1991. In other years, most fish were found in region I or III. Our survey area was deficient in some strata, mainly those

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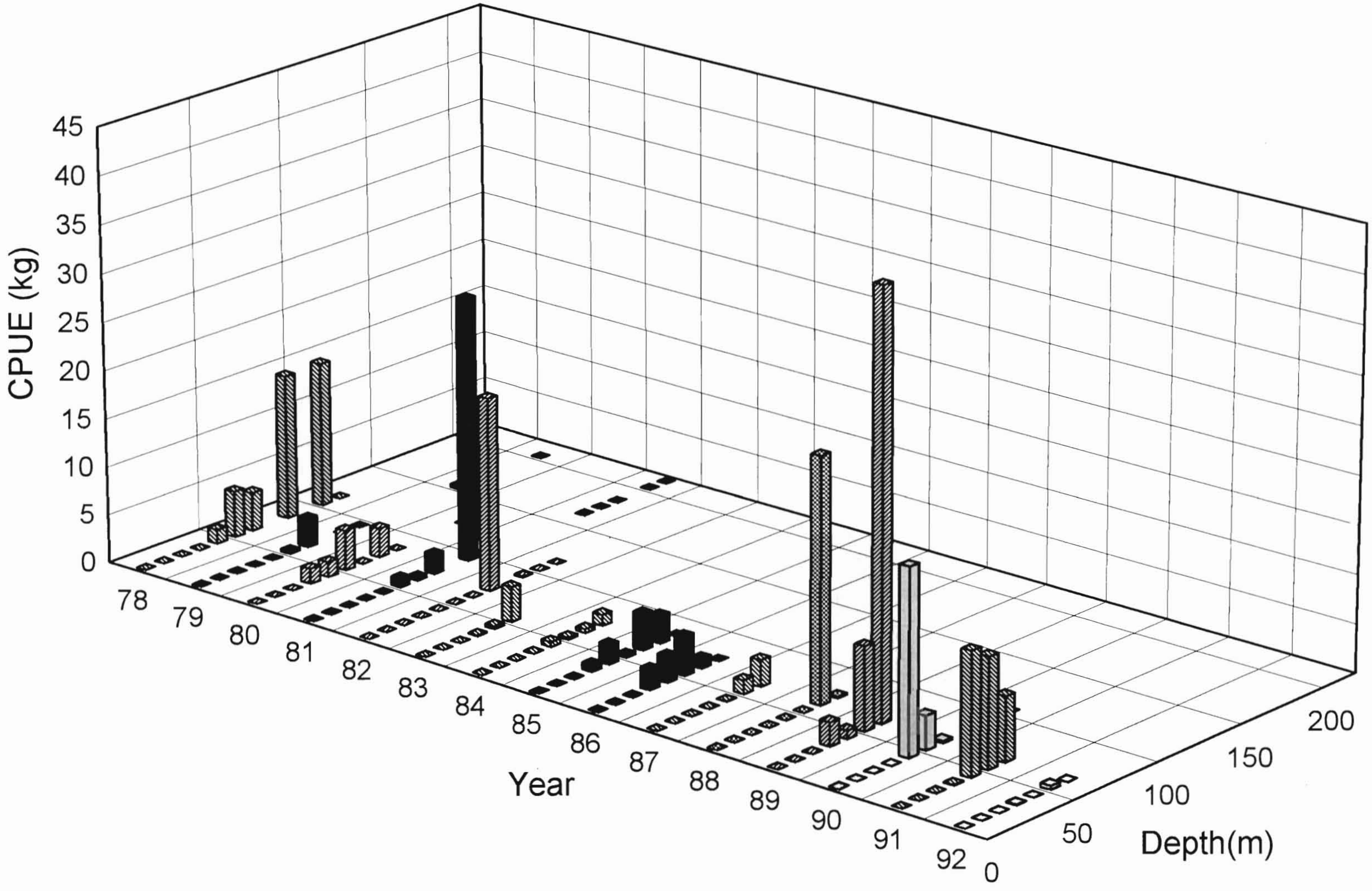

Figure 4

CPUE of age-0 juvenile walleye pollock for each 10-m depth stratum from 1978 to 1992.

Table 1
CPUE of each 10-m depth stratum in the three regions, from 1978 to 1992.

	1978			1979			1980			1981			1982			1983			1984			1985			1986			1987			1988			1989			1990			1991			1992		
Depth (m)	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
0	0.0		0.0	0.0		0.0	0.0		0.0	0.0			0.0		0.0	0.0			0.0			0.0			0.0			0.0			0.0			0.0			0.0			0.0			0.0		
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0			0.0		0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
30	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.1		0.0	0.0	0.0	0.2	1.0	0.0	0.0	0.2	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.8	0.0	0.0	0.8	0.1	0.0	0.0	0.1	0.0	0.0
40	1.2	2.0	1.8	0.0	0.0	0.0	1.5	0.1	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.1	0.0	1.0	0.5	2.9	0.0	0.1	3.3		0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	5.0	1.0	70.0	25.7	17.6	0.0	0.3	0.1	0.0	0.0
50	5.2	2.0		0.4	0.0	0.0	4.2	5.2	3.0	1.1	0.1	0.1	0.0		0.0	3.7	2.7		0.1	1.0	0.2	0.0	0.0	1.0	0.0	40.0		0.6	1.1	4.8	0.0	0.0	0.0	3.0	42.5	7.8	2.9	10.0	3.4	6.2	60.0	1.5	0.6	0.3	0.0
60	4.0			3.0			0.0			0.7	0.0	0.0	0.0						0.0	1.5	0.7	0.0	10.0	2.5			1.0		5.2	0.2	0.0	100.0		42.5	65.0	2.0	0.0	0.5	0.2	0.0	12.0	7.0	0.0	0.0	0.0
70							3.0			1.7	1.0	5.0	0.0		26.7				0.2	1.3	1.5		5.0	0.7		0.0					0.1														
80	15.0			0.0			0.0				0.0												0.0																						
90				0.0						6.0		70.0	0.0		0.2																0.3														
100	15.0									0.0		0.0			0.0																						0.0								
110	0.0												0.0																																
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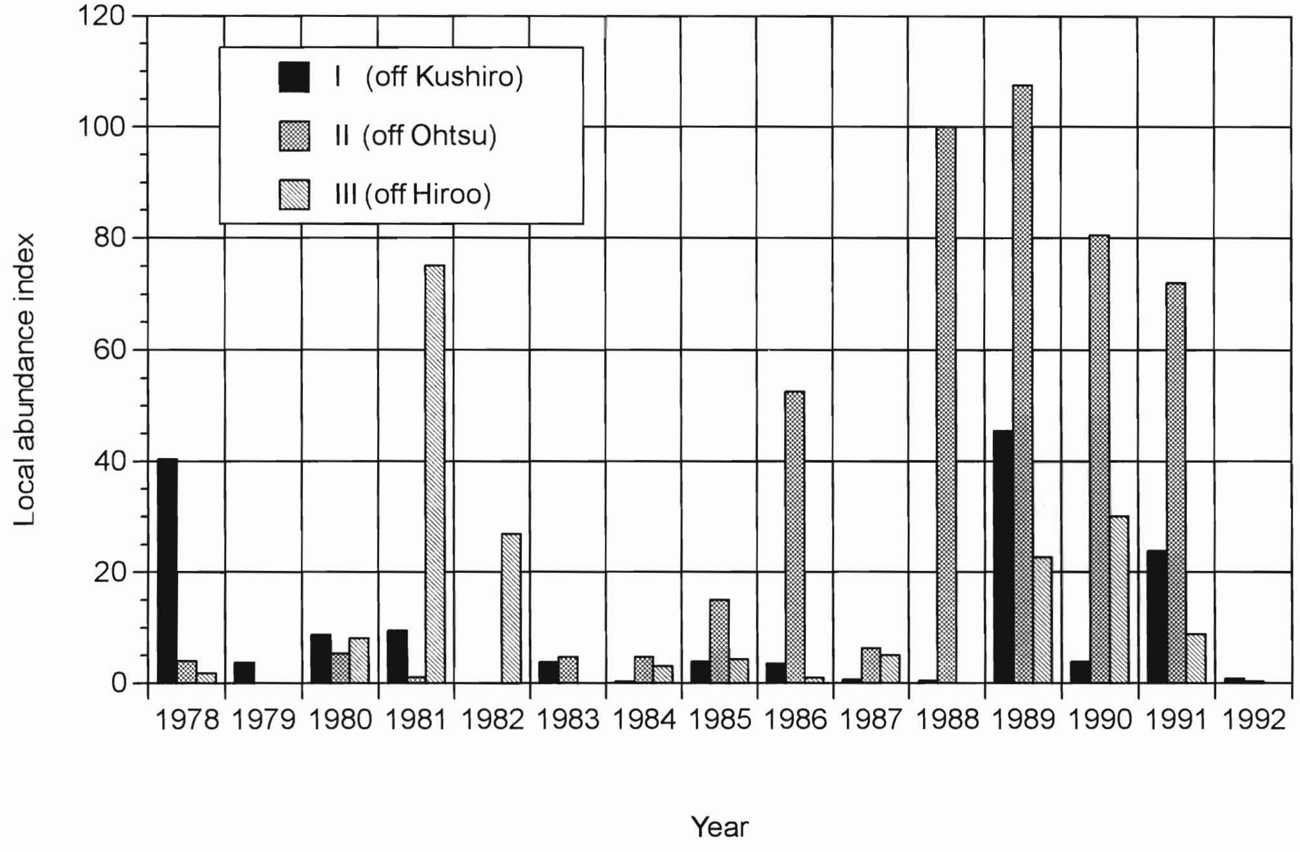

Figure 5
Local abundance indices for the three regions, from 1978 to 1992.

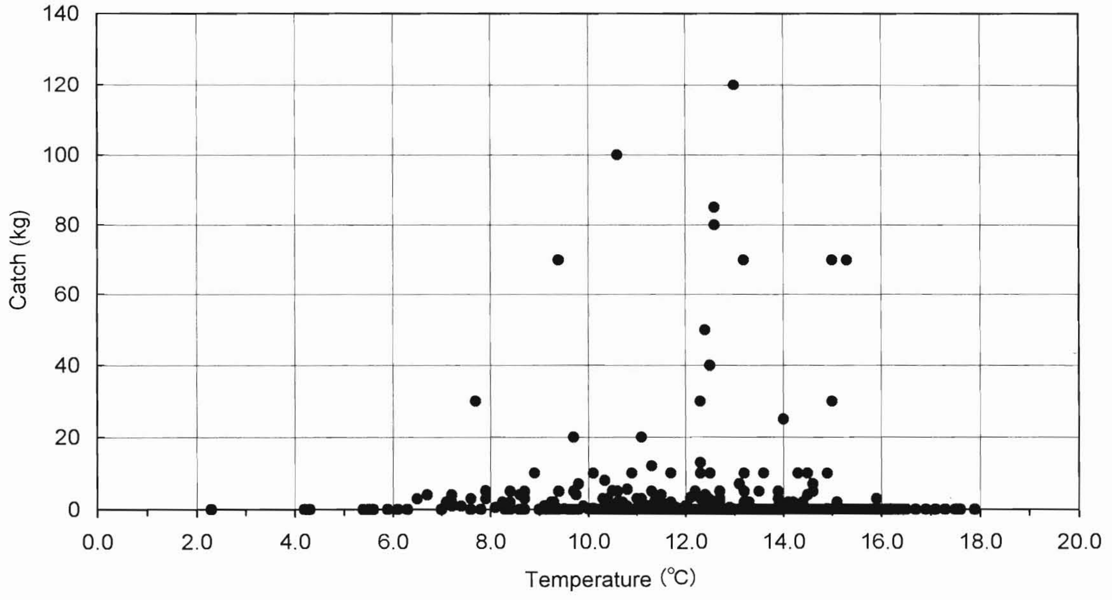

Figure 6
Relation between catches and temperature of bottom layer, from 1978 to 1992.

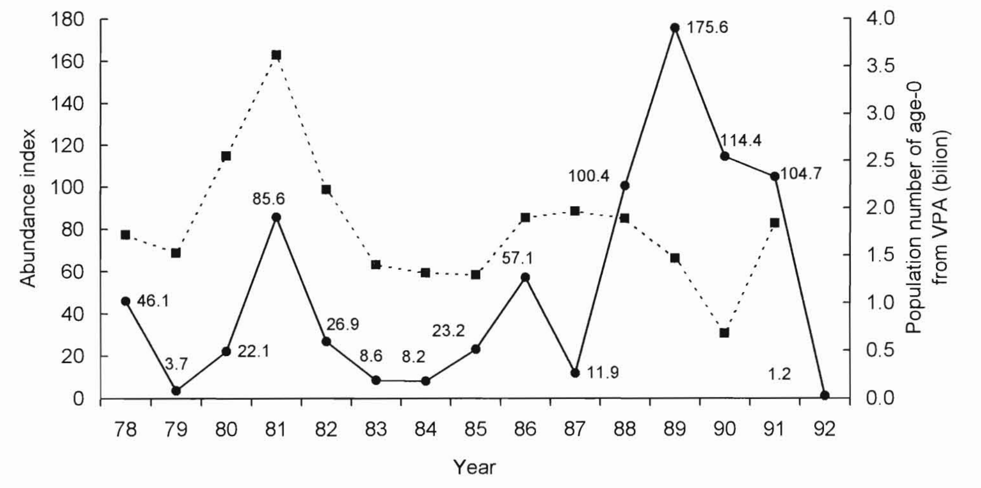

Figure 7

Change of age-0 juvenile abundance index from 1978 to 1992 (solid line) and population of age-0 walleye pollock from VPA (dotted line). Numbers in figure are values of the abundance index.

deeper than 70 m. In cases in which the highest CPUE was in the edge stratum in the survey area, more fish may have been distributed beyond that stratum. However, we observed such cases in only 5 years: 1980, 1983, 1987, 1988, and 1989. In the other 10 years our survey probably covered the main distribution of juveniles after their migration. The highest CPUE occurred most frequently in the 50-m and 60-m depth strata in those 10 years (three times in each). Moreover, the largest catch occurred in the 60-m stratum. Thus we concluded that in autumn, 0-age juveniles were located mainly in the 50-m and the 60-m strata, with the highest abundance found off Ohtsu.

Kanamaru (1985) reported larvae under 10 mm long distributed to the east of Kushiro. Our survey did not cover this area, because this survey's main object was an assessment of shishamo smelt, and extensive surveys are costly. However, survey there may yield further infor-

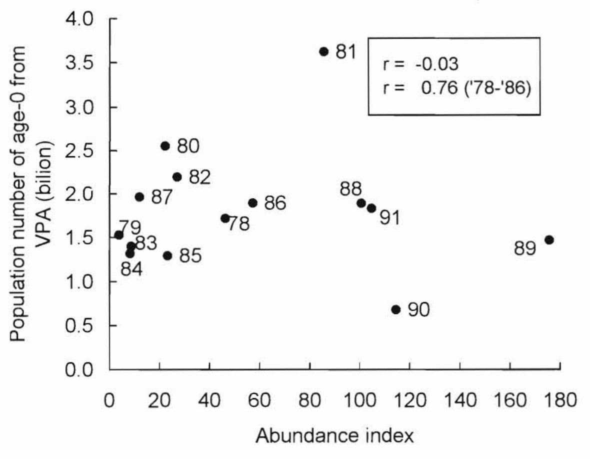

Figure 8

Relation between age-0 juvenile abundance index and population of age-0 walleye pollock from VPA. Numbers in figure indicate years.

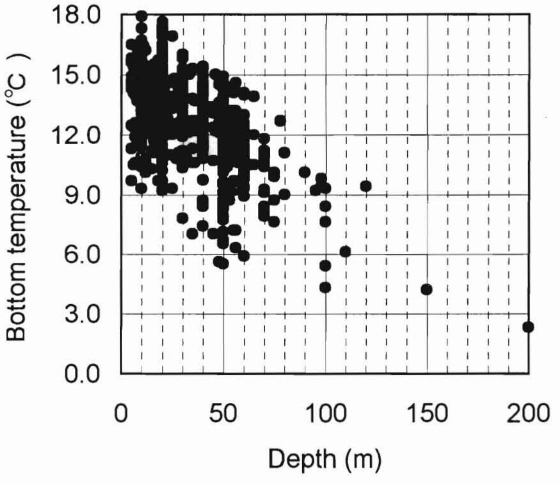

Figure 9

Relation between depth and bottom temperature at survey points.

mation on interannual shifts in pollock distribution. Thus we hope to extend the survey area eastward of Kushiro.

Moreover, age-0 juveniles were observed in bottom water ranging from 6° to 16°C. Olla and Davis (1990) showed that juvenile pollock avoid cold water (3°C) in the bottom of an experimental tank. This indicates that cold water in the offshore bottom layer may be an obstacle to age-0 pollock. Our results show that cold water under about 6°C forms an obstacle. This temperature was observed from 50 m to 110 m depth (Figure 9). Therefore, survey for age-0 walleye pollock should be extended to the 100-m depth stratum.

During 1988–91 this survey overestimated the abundance of age-0 juveniles, compared with VPA estimates. Therefore, we did not find a statistically significant linear correlation between abundance indices and estimated numbers from VPA. However, before 1986 the trends of abundance indices and VPA estimates were very similar, and the correlation between them was significant. Our survey did not cover all areas deeper than 70 m after 1987, however we believe that our survey covered the areas of abundance, as discussed above. Thus the low correlation coefficient was possibly caused by some change around 1987. For example, the fisheries environment has changed in Russian areas around the South Kuril Islands since 1987; hence VPA may have been problematic in recent years. In this case, VPA would have underestimated the number of age-0 walleye pollock.

In summary, our results will be useful in assessing future recruitment not only of shishamo smelt but also walleye pollock. Further knowledge will be gained by extending the survey area to east of Kushiro and to 100 m depth.

Acknowledgments

Many scientists at Hokkaido Kushiro Fisheries Experimental Station (F.E.S.) took part in this survey, but we particularly want to thank Koji Abe, now the director of Hakodate F.E.S., and Mikio Koike, now a manager of Hokkaido Central F.E.S., for starting this work at Hokkaido Kushiro F.E.S. We also thank Isamu Nahira, the captain of the *No.5 Tensho-maru*, for his assistance. We thank Richard D. Brodeur, Alaska Fisheries Science Center, and Hitoshi Uto, Hokkaido Wakkanai F.E.S., for reading and making suggestions on this manuscript, and Tokio Wada and Kazutoshi Watanabe, Hokkaido National Fisheries Research Institute, for making valuable comments on an earlier draft.

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Distribution and Abundance of Age-0 Walleye Pollock, *Theragra chalcogramma*, in the Western Gulf of Alaska during September 1990

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ABSTRACT

A midwater trawl survey was conducted during September 1990 to examine the distribution patterns and to estimate the relative abundance of age-0 walleye pollock in the western Gulf of Alaska. We first examined the effect that fishing strategy and gear type had on age-0 pollock catches. Oblique tows appeared to be more efficient than stepped tows in catching age-0 pollock; however, these methods did not differ with regard to the length of fish caught (54–102 mm fork length). Gear type (anchovy trawl or shrimp trawl) did not affect the catch per unit of effort or size composition of age-0 pollock caught.

A subset of 67 hauls was used to examine the distribution and abundance of age-0 pollock. Numerically, age-0 pollock dominated the catch, but older age groups of pollock and gelatinous zooplankton were substantially more important by weight. The highest mean densities of age-0 pollock occurred inshore of approximately the middle of the continental shelf and were associated with temperatures ≥7°C at 50 m. There was an alongshore trend of decreasing density toward the southwest. The average catch per unit of effort in September—50,998 fish per km^2 (133 kg/km^2)—suggests that the 1990 year class was weak compared with previous years.

Overall, the fork length (FL) distribution of age-0 pollock was unimodal, with an average of 70.5 mm (range 44–102 mm). No significant differences in FL were found among the six survey strata. The length–weight relationship for individuals 50–100 mm FL is described.

Introduction

The juvenile stage of commercially important marine fishes has become increasingly significant to those studying recruitment. The longer duration of the juvenile stage relative to the egg and larval stages (Hjort, 1914; Houde, 1987) has led some researchers to predict that mortality during the juvenile stage can significantly affect year-class strength (e.g., Sissenwine, 1984; Peterman et al., 1988; Bradford, 1992). Bailey and Spring (1992) used periodic estimates of abundance to suggest that walleye pollock, *Theragra chalcogramma,* mortality during the postlarval first year of life (age-0) may significantly reduce year-class strength.

Estimating the abundance of age-0 pollock in the Gulf of Alaska is difficult because their distribution is widespread and complex. Ocean advection and diffusion expands what was once a fairly localized egg and larval distribution and spreads it over much of the shelf region in the western gulf (Kendall and Picquelle, 1990; Hinckley et al., 1991). As nekton, age-0 pollock have been found at various depths from near-bottom to near-surface. They exhibit diel vertical migration and aggregation behavior that may affect catchability (Traynor and Williamson, 1983; Bailey, 1989), and have been found at varying distances from shore in several surveys (Smith et al., 1984; Walters et al., 1985; Hinckley et al., 1991; Brodeur et al., 1995). This diversity of distribution and behavior patterns makes it much more difficult to estimate the abundance of age-0 pollock than the abundance of larvae. An effective survey of these fish requires that basic distribution patterns be determined (Koehler et al., 1986) and appropriate sampling strategies be developed.

As part of the Fisheries-Oceanography Coordinated Investigations (FOCI) program (see Schumacher and Kendall, 1991), we are studying the recruitment dynamics of walleye pollock, including the juvenile stage up to the end of the first year of life. Since estimating the abundance of age-0 pollock is important to understanding recruitment mechanisms, an acoustic/trawl survey was conducted during September 1990 to determine suitable sampling strategies and to examine the large-scale abundance and distribution patterns of these fish in the western Gulf of Alaska. We present an analysis of the trawl catches from this survey.

Study Area

Sampling was conducted on the continental shelf along the Alaska Peninsula in water from 30 to 200 m deep (Fig. 1). Most walleye pollock in the Gulf of Alaska spawn in Shelikof Strait, and the prevailing currents, principally the Alaska Coastal Current (ACC), carry the larvae either along the Alaska Peninsula or into the offshore waters of the Gulf of Alaska (Kim and Nunnallee, 1990; Hinckley et al., 1991). Historically, high densities of age-0 juvenile pollock have been observed along the continental shelf and in nearshore areas and bays along the Alaska Peninsula and around Kodiak Island (Smith et al., 1984; Walters et al., 1985). Surveys conducted in late summer from 1984 to 1988 (Spring and Bailey[1]) were used to establish the offshore boundary of our study area.

Currents in the survey area are complex because they flow over diverse topography punctuated by numerous islands, reefs, and gullies. The most prominent topographic features are the Shumagin Islands, located in the center of the study area, and, just to the northeast, the Shumagin Gully, which appears as an indentation of the 100-m isobath (Fig. 1). The ACC flows through the study area with mean speeds of 10–20 cm/s, but flow and salinity vary seasonally with changes in freshwater input and winds driving the current (Reed and Schumacher, 1986). The oceanic Alaska Stream also flows to the southwest offshore of the shelf break at speeds as high as 100 cm/s (Reed and Schumacher, 1986).

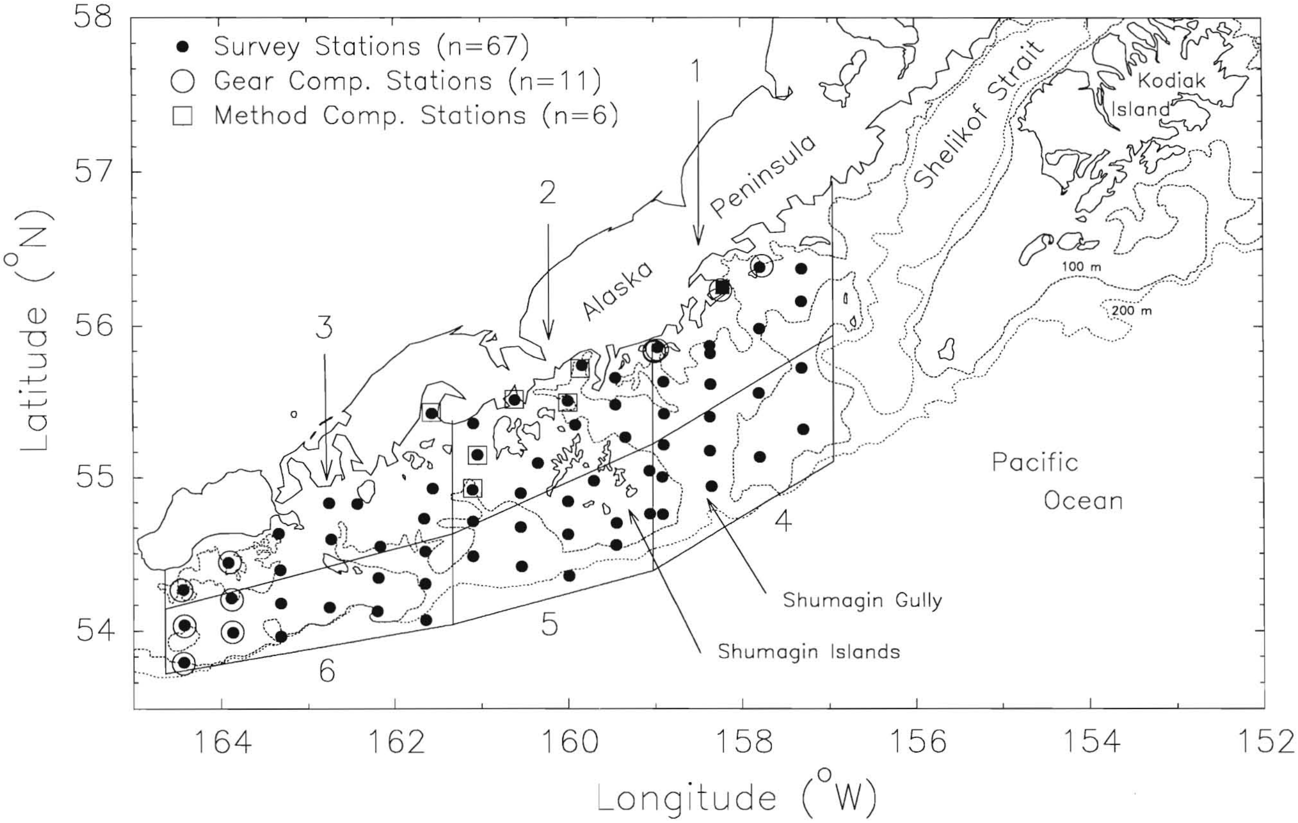

Figure 1

Bathymetry and location of stations during the September 1990 survey in the Gulf of Alaska. Symbols indicate the survey stations and where the paired-tow experiments were conducted. The strata boundaries are also shown.

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[1] Spring, S., and K. Bailey. 1991. Distribution and abundance of juvenile pollock from historical shrimp trawl surveys in the western Gulf of Alaska. AFSC Proc. Rep. 91-18, 66 p. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.

Methods

Survey Design and Methodology

A sampling grid of 67 stations was designed along the southern coast of the Alaska Peninsula on longitude lines approximately 36 km apart (Fig. 1). Stations were located 22 km apart along these lines from nearshore out to the 200-m depth contour. The NOAA vessel *Miller Freeman* trawled during all hours of the day between 6 and 23 September 1990. A total of 136 hauls were made during this survey.

The standard sampling gear was an 18.6-m (footrope and headrope lengths), high-opening shrimp trawl that was fished with 1.5 × 2.1-m doors. This trawl is designed to fish on bottom but was used in midwater as in the 1984–88 surveys (Bailey and Spring, 1992). When the trawl was fished this way, the height regulator and tickler chain were removed. The stretched-net mesh in the body of this trawl was 3.2 cm, and the 3.8-cm-mesh codend was equipped with a 3-mm knotless mesh liner. For the first half of our survey, the shrimp trawl was deployed in a stepped manner, with an average ship speed of 6 km/h. The total number of steps per tow was determined by water depth, with 10-min. steps made at each 50-m depth interval.

We initially used the stepped method because we thought that the net might not perform well when towed obliquely and that concentrating on predetermined depth layers would not impair the quality of the data. However, distinct layered patterns of sign at various depths were observed in acoustic transects between stations (Brodeur and Wilson[2]), indicating that a stepped net path at fixed depth layers was probably not sampling the water column adequately. Therefore, to achieve a representative sample, the trawl was fished along an oblique path for the rest of the survey.

A paired-tow experiment was conducted to examine the relative efficiency of the oblique method of fishing versus the stepped net path. This experiment consisted of sampling with each method at six stations where age-0 pollock were caught. The sequence of methods used at each station was random. Both hauls of a pair were done either during day, night, or twilight.[3]

We also compared the catch efficiency from the shrimp trawl with a midwater anchovy trawl to evaluate how well the shrimp trawl performed when fished midwater. Unlike the shrimp trawl, the anchovy trawl was designed to catch small pelagic fishes (Wyllie-Echeverria et al., 1990). The anchovy trawl is a modified Cobb trawl with an overall length of about 47 m and a square mouth (26.2 m on a side). The mesh size (stretched) decreased from 15.2 cm in the body to 3.8 cm in the codend. The codend was also equipped with a 3-mm knotless liner.

To examine the relative efficiencies of the shrimp and anchovy trawls, we used both gear types in alternate order at each of the last 11 stations of the survey. Both hauls at each station were oblique and were done either during day, night, or twilight.

At each trawl station, the catch was sorted, and the taxonomic composition (by numbers and weight) was determined. Walleye pollock were separated into nonoverlapping length intervals to reflect age: age 0, age 1, age 2, and 3 years and older (age 3+). Length ranges in each age category are based on historical data (Smith et al., 1984) and were easily discernable in the length distributions during this survey. A random length sample (fork length [FL] to the nearest millimeter) was taken of at least 100 age-0 juvenile pollock. All older pollock were measured, as were other selected species. Individual wet weights (to the nearest gram) were taken on whole age-0 juvenile pollock at sea to examine variation in condition. Expendable bathythermograph (XBT) casts were done at all trawl stations. A complete listing of biological and physical sampling localities and sequence is given in DeWitt and Clark (1992).

Data Analysis

Catch and length data were standardized to number or weight per square kilometer of sea surface, or per 100,000 cubic meters filtered, with methods similar to the area-swept method (Alverson and Pereyra, 1969). For each tow, we estimated the volume filtered by multiplying mean net mouth area by distance fished (distance fished is the maximum wire out plus distance travelled by the ship over the seafloor). We estimated net mouth area by using a Scanmar net mensuration system during several tows to measure height (distance between headrope and footrope centers) or width (distance between wing tips) while the net was retrieved at a constant rate (9 m/min). Least-squares linear and nonlinear regressions were fit to the data so that the net mouth area at a given length of wire out could be estimated for all other tows (Fig. 2). An average mouth area was then calculated for each tow. When fished in steps, the mouth area was assumed to change instantaneously between steps. Catch per square kilometer of sea surface was calculated as catch per volume multiplied by maximum net depth. Catch per unit area was used to estimate abundance indices and to compare geographic subareas, whereas density, or catch per unit volume, was used to evaluate variations in survey strategy (e.g., paired-tow experiments). When catch is ex-

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[2] R. D. Brodeur and M. T. Wilson. Mesoscale acoustic patterns of age-0 walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci., in press, 1996.

[3] Twilight was defined as the period 1 hour before to 1 hour after sunrise or sunset at Sand Point, Shumagin Islands, Alaska, between 6 and 23 September 1990.

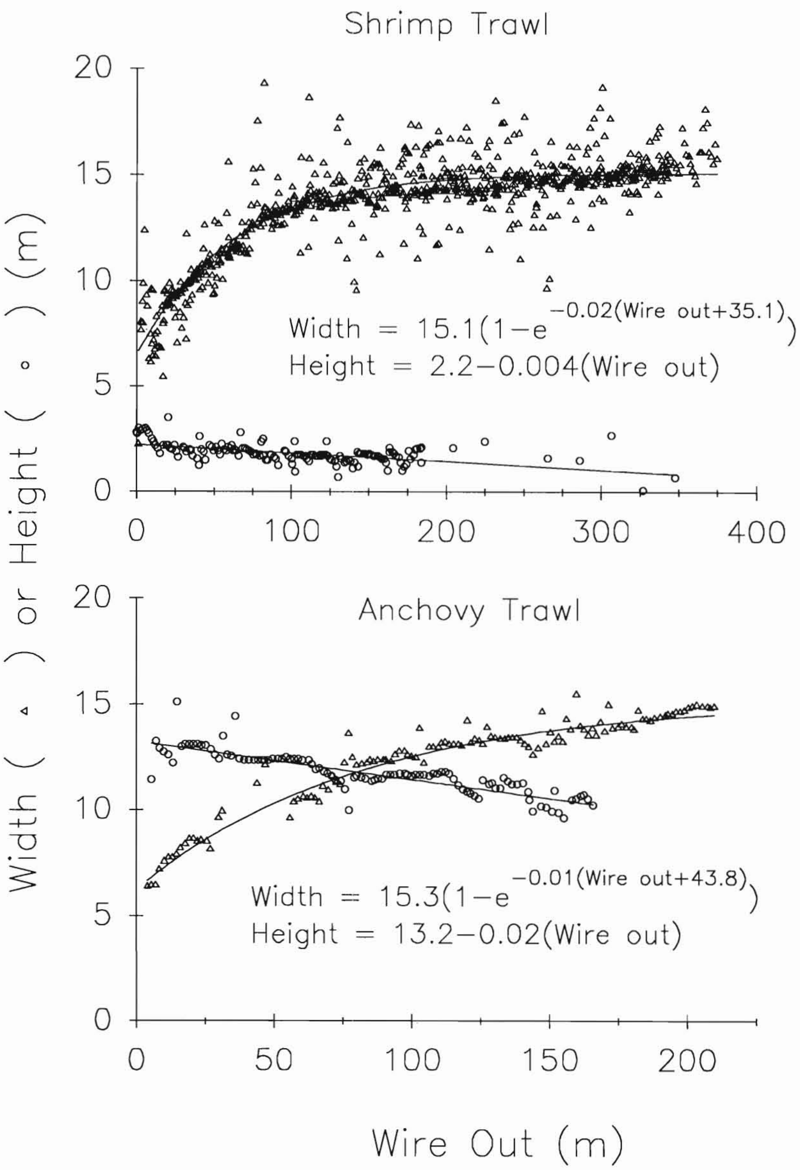

Figure 2

Net mensuration data showing trawl geometry (height or spread of net) with wire out for the shrimp trawl and the anchovy trawl (oblique tows only). The best-fit equation describing the relation between the variables is also given.

pressed per unit volume filtered, effort does not vary with maximum depth fished; thus any confounding effects of depth are not obscured.

Age-0 pollock density estimates from the paired trawl hauls were examined for differences between shrimp and anchovy trawls or fishing methods (stepped vs. oblique tows). Standardized catches of age-0 pollock were compared by means of two-tailed paired-sample *t*-tests. We also applied the nonparametric Wilcoxon paired-sample test because the sample sizes were small and we were uncertain whether the distribution of pairwise differences was normal (Zar, 1984).

We compared length distributions from the paired comparison hauls of age-0 pollock between gears or methods by using a multivariate analysis of variance (MANOVA) similar to that used by Bailey and Spring (1992) and Shima and Bailey (1994). The dependent variable was standardized catches within each 10-mm length interval, and the sampling pair was used as a blocking factor. Pillai's trace and its *F*-distribution approximation were used as the test statistics because they have been shown to have the best characteristics in terms of power and robustness of the available MANOVA statistics (Olson, 1974).

A single shrimp trawl haul at each of 67 stations was used to estimate the abundance and distribution of age-0 walleye pollock and other taxa of interest (Table 1). Where multiple hauls were made at a station, the haul selected conformed to the northeast-to-southwest sequence of occupation and, where possible, was fished on an oblique net path. A limited number of hauls targeting echo sign during this survey were not included because standardized catches from these hauls were significantly greater than hauls fished at predetermined locations ($P< 0.01$, Kruskal-Wallis nonparametric ANOVA).

For complete spatial coverage of the survey area, we included data collected during day and night; however, among the 67 tows, the hypothesis of independence between age-0 pollock presence or absence and diel period was rejected ($\chi^2=8.53$, $P=0.01$). Applying a presence/absence correction to catch data is problematic, and therefore we looked for a diel effect on catch or length. A Kruskal-Wallis mean rank test using all 67 hauls ($\chi^2=4.10$, $P=0.10$), and an ANOVA using the natural logs of the 35 hauls where age-0 pollock were caught ($F_{2,32}=1.72$, $P=0.20$) indicated that the diel effect on catch was not significant. Nor was the diel effect significantly related to mean FL, based upon an ANOVA where haul ($n=35$) was nested within the diel effect ($F_{2,32}=0.009$, $P=0.99$). Therefore, we did not apply a correction for diel variability in our catch or length data.

We examined alongshore and cross-shelf trends in abundance (fish per km^2) of age-0 pollock by using stratified means and geographic mapping. The survey area was divided into six strata (three inshore and three offshore) based on the expectation that alongshore and cross-shelf trends in abundance exist (Fig. 1, Table 1) and on our desire to equate sample sizes between each stratum. We also report stratified frequencies of occurrence and means of log-transformed catches because these parameters describe distribution characteristics.

We obtained length–frequency composition for each stratum by using a stratified estimator for age-0 pollock at 1-mm intervals and for older pollock at 1-cm intervals. When catch was subsampled, the observed length frequencies were expanded to total catch. All frequencies were standardized by effort before we combined data from multiple hauls.

Wet weight was measured individually on 401 age-0 pollock and Fulton's condition factor (K) ($K = [W/L^3 * 10^5]$, where W = wet weight in grams and L = FL in millimeters) was calculated. These data were collected from 28 tows in the survey area during 1990, but not all were from the 67 gridded survey hauls. We compared differences of age-0 pollock mean length or mean condition among strata by analyzing the observed frequencies (not standardized) using a nested ANOVA design where haul was nested within stratum.

Table 1

Characteristics of sampling effort, by stratum, expended during the 1990 juvenile walleye pollock survey aboard the R/V *Miller Freeman.*

Stratum	Area[2] (km^2)	September sampling date		Hauls[1]									Mean					
					Stepped				Oblique				Km per haul	Hour per haul	Wire out (m)	Depth		Surface temp. (°C)
		First	Last	Total	Sum	D	N	T	Sum	D	N	T				Net	Bot.	
Onshore																		
NE (1)	12,526	9	12	10	10	7	1	2	0	0	0	0	2.2	0.40	204	120	144	11.7
Mid (2)	10,835	12	14	13	4	1	1	2	9	2	3	4	1.8	0.32	162	91	103	11.5
SW (3)	12,550	14	22	11	0	0	0	0	11	6	3	2	1.4	0.22	132	70	79	10.6
Combined	35,911	9	22	34	14	8	2	4	20	8	6	6	1.8	0.31	165	93	107	11.2
Offshore																		
NE (4)	12,210	10	11	10	10	1	6	3	0	0	0	0	1.7	0.32	156	89	124	11.8
Mid (5)	11,548	12	14	11	8	4	3	1	3	2	0	1	1.7	0.29	143	80	102	11.5
SW (6)	11,864	15	22	12	0	0	0	0	12	5	5	2	1.8	0.30	168	96	155	10.9
Combined	35,623	10	22	33	18	5	9	4	15	7	5	3	1.7	0.30	156	89	128	11.4
All Areas combined	**71,531**	**9**	**22**	**67**	**32**	**13**	**11**	**8**	**35**	**15**	**11**	**9**	**1.7**	**0.31**	**160**	**91**	**117**	**11.3**

[1] The terms stepped and oblique refer to net path through the water column. D = day, N = night, T = twilight.

[2] Figures for combined areas may differ from column sums due to rounding error.

Results

Paired-Tow Experiments

Comparison of Net Paths—Catch data from the 1990 survey were not adjusted to account for differences in net path (stepped versus oblique). Six pairs of tows indicated that the oblique-path method, which adds net-retrieval rates to towing speed, was more efficient than stepped tows (Table 2). But because of the variability in catch, six pairs were too few to enable a suitably powerful statistical comparison or to allow for the calculation of a reasonably precise correction algorithm (Munro and Hoff[4]).

Distributions of age-0 pollock length frequency did not differ significantly (MANOVA; $F_{1,6}$=1.56, P=0.55) between the oblique ($\bar{x}$=71.5 mm FL) and stepped ($\bar{x}$=73.4 mm FL) methods (Fig. 3), thus a correction for size selection due to net path was not necessary.

Comparison of Gear—In terms of estimating age-0 pollock density, the data collected by the shrimp trawl were similar to the data from the anchovy trawl. The mean CPUE from the 11 tows made with the shrimp trawl was 72.43 × 10^5 fish per m^3 (SE=40.25), and the mean from the anchovy trawl was 82.46 × 10^5 fish per m^3 (SE=54.98). Differences in age-0 pollock CPUE between the two trawls were not significant when examined parametrically (t=0.50, P=0.628) or nonparametrically (Wilcoxon Z=−0.25, P=0.799). Incidentally, the anchovy net collected many taxa more frequently than did the shrimp trawl; this probably reflects the anchovy net's larger mouth area.

Distributions of age-0 pollock length frequency did not significantly differ between the anchovy trawl ($\bar{x}$=81.37 mm) and the shrimp trawl ($\bar{x}$=79.23 mm) (MANOVA; $F_{1,9}$=29.43, P=0.14; Fig. 3). Thus the shrimp trawl seemed comparable to the anchovy trawl in terms of age-0 pollock catch efficiency and size composition.

Table 2

Catch per unit of effort (CPUE; no. per 100,000 m^3 of age-0 pollock) for each haul from each of 6 pairs where the shrimp trawl was fished obliquely and at stepped depths. The difference in CPUE (stepped – oblique) is given.

	CPUE		
Pair	Stepped	Oblique	Difference
1	3.49	18.48	−14.99
2	7.55	224.44	−216.89
3	14.05	83.39	−69.34
4	68.13	147.70	−79.57
5	105.98	226.82	−120.83
6	197.20	184.02	13.18
x	66.07	147.48	−81.41
SE	31.00	33.81	33.38

Abundance and Distribution

Numerically, walleye pollock was the dominant finfish species collected over all six strata (Table 3). Age-0 individuals were taken at 35 of the 67 trawl stations and had a mean CPUE of 50,998/km^2. They ranked fourth among finfish in terms of biomass because of their low mean weight per individual (0.003 kg; Table 3). It is noteworthy that the jellyfish biomass was greater than that of all finfish combined.

The geographic distribution of age-0 pollock abundance varied throughout the survey area (Fig. 4). Despite considerable small-scale patchiness, age-0 pollock appeared to be more closely associated with the coast than with the shelf–slope break (200 m). Both the frequency of occurrence and the number of fish caught tended to be lower offshore (Table 4). These data also suggest that age-0 pollock were more prevalent upstream, rather than downstream, of the Shumagin Islands.

Temperature contours at 50 m, which roughly parallel the coastline, coincided with the overall geographic pattern of age-0 pollock abundance (Fig. 4). We used temperature at 50 m as an index of midwater temperature and found that most large catches of age-0 pollock were in areas inshore of the 7°C isotherm. Incidentally, ocean temperature at the surface and at the bottom did not visually correspond as well with age-0 catches; surface temperatures showed an alongshore gradient (Table 1), whereas bottom temperatures largely reflected water depth. Thus, relatively warm water at mid-depths may be one feature that makes the nearshore a good nursery area for age-0 pollock.

Length and Condition Characteristics

The standardized length distributions of all pollock from the 67 survey hauls showed several distinct modes that could be attributed to different age groups (Fig. 5). The smallest length group, associated with age-0 pollock, was distinct from all other groupings and ranged from 44 to 102 mm FL. Age-1 (~185 mm FL) and age-2 (~280 mm FL) modes were readily apparent, but length modes above 350 mm FL were not easily discernable.

We examined the length distributions by stratum

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[4] Munro, P. T., and R. Z. Hoff. 1994. Two demersal trawl surveys in the Gulf of Alaska: implications of survey design and methods. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. manuscr.

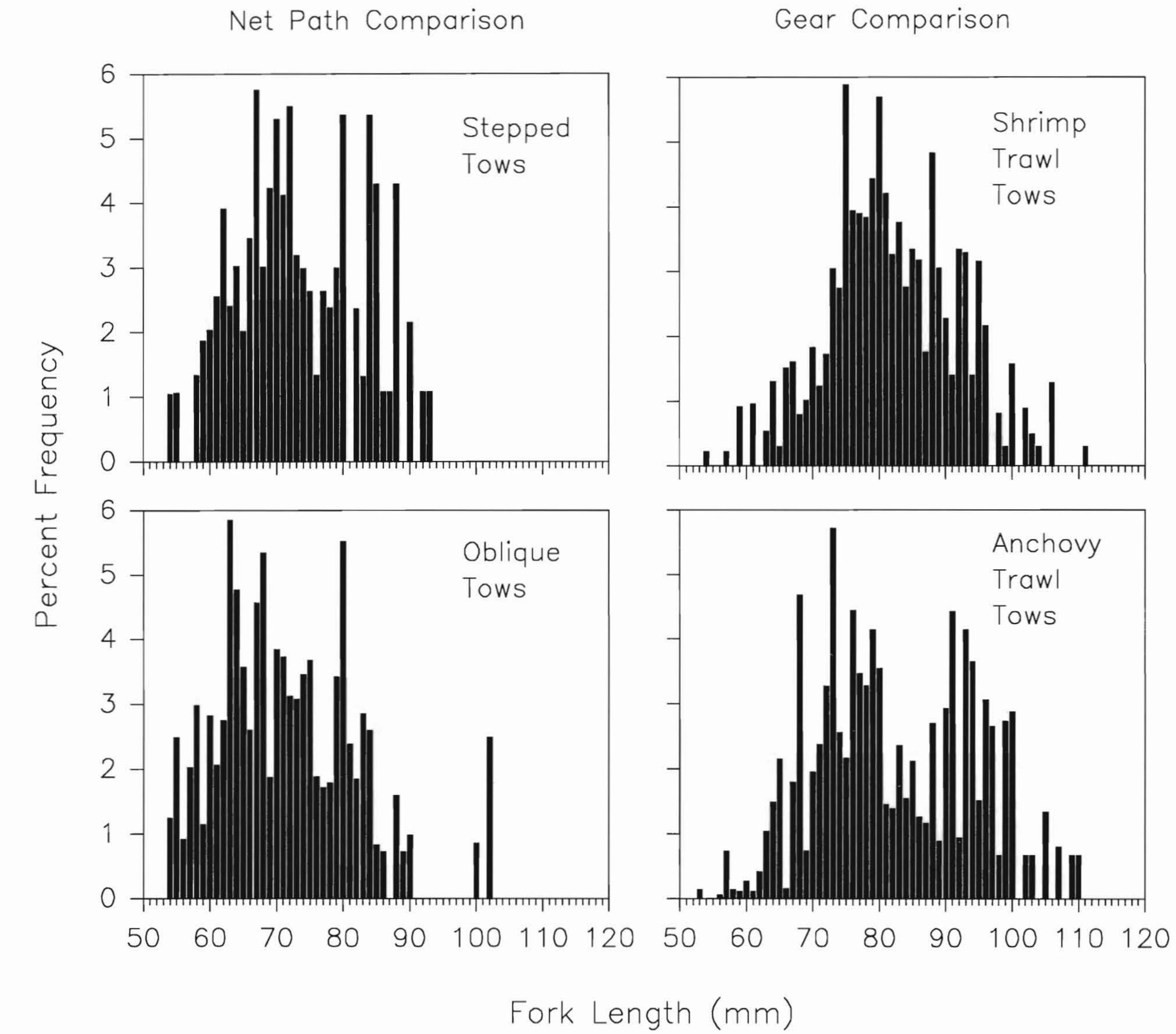

Figure 3

Fork-length distributions of age-0 walleye pollock from the net-path comparison (stepped vs. oblique net path) and the gear comparison (shrimp vs. anchovy trawl).

(Fig. 6) and found no significant differences in length among all strata (overall $\bar{x}=70.5$) (ANOVA; $F_{5,29}=0.39$; $P=0.85$). Tests on larger subsets of the data (i.e., inshore vs. offshore ($F_{1,33}=0.030$, $P=0.864$) and upstream vs. middle vs. downstream ($F_{2,32}=0.607$, $P=0.551$) were also not significant.

Age-0 pollock fork lengths accounted for 91% of the variation in weight (Fig. 7). The nonlinear equation fit to untransformed data gave an exponent of 3.101. Although this is close to 3.0, variation in weight for a given length makes it difficult to conclude whether the increase in body size is isometric or allometric.

Although condition factor (K) was not significantly related to stratum, some age-0 pollock had low values. All individuals with low condition factors were collected from the northeastern stations in strata 1 and 4. Nevertheless, no significant differences in K were observed among strata (nested ANOVA; $F_{5,22}=0.46$, $P=0.80$). Thus, K did not increase with fish size, nor was the variation of K associated with stratum (overall $\bar{x}=0.68$).

Table 3

Mean catch per unit of effort (CPUE) of fish and invertebrates from 67 stations sampled in the Gulf of Alaska along the Alaska Peninsula during September 1990 by the RV *Miller Freeman.*

Species	Number of hauls with: Catch data	Number of hauls with: Length data	CPUE per km² Number $\bar{x}$	CPUE per km² Number S^2	CPUE per km² Weight (kg) $\bar{x}$	CPUE per km² Weight (kg) S^2	Mean of individual weight (kg)
Fish	52		76,470	3.105E+08	8,138	3.920E+07	0.106
Age-0 *Theragra chalcogramma*	35	35	50,998	2.475E+08	133	1.748E+03	0.003
Age-1+ *Theragra chalcogramma*	13	12	10,906	8.420E+07	7,337	3.927E+07	0.673
Mesopelagic fishes	1	0	4,131	1.707E+07	23	5.277E+02	0.006
Mallotus villosus	17	4	2,956	8.359E+05	13	1.828E+01	0.004
Lumpenus maculatus	15	0	1,634	2.740E+05	4	2.744E+00	0.002
Atheresthes stomias	14	0	1,121	1.107E+05	278	1.161E+04	0.248
Thaleichthys pacificus	7	0	1,017	2.071E+05	19	7.280E+01	0.019
Cottidae	4	0	953	7.439E+05	2	2.182E+00	0.002
Hippoglossoides elassodon	7	0	499	4.963E+04	1	3.117E-01	0.003
Salmonidae	8	0	306	1.306E+04	31	2.061E+02	0.103
Zaprora silenus	7	0	263	1.196E+04	7	1.735E+01	0.028
Scorpaenidae	5	0	125	3.014E+03	1	6.198E-02	0.005
Cyclopteridae	3	0	112	4.202E+03	1	8.600E-02	0.005
Gadus macrocephalus	1	0	41	1.669E+03	287	8.251E+04	7.032
Agonidae	1	0	25	6.460E+02	<1	1.344E-02	0.005
Invertebrates	67		66,842	7.675E+07	8,815	8.323E+05	0.132
Gelatinous zooplankton	67		54,407[1]	2.662E+07	8,777	8.243E+05	0.161
Decapoda (shrimps)	15		11,679[1]	3.265E+07	26	1.851E+02	0.002
Cephalopoda (squids)	4		653	1.220E+05	3	3.324E+00	0.004
Other invertebrates[2]	3		104	3.643E+03	9	6.781E+01	0.082

[1] Estimated as biomass × mean weight.

[2] Includes a very small catch of benthic organisms.

Table 4

Abundance index (mean catch per unit of effort [CPUE]; no. per km²) of age-0 walleye pollock for the six geographic strata surveyed during September 1990. Frequency of occurrence and the average natural logarithm of positive CPUE values are also given.

Stratum	Number (per km²) n	Number (per km²) $\bar{x}$	Number (per km²) SE	Occurrence: Frequency n	Occurrence: Frequency (%)	Occurrence: Mean ln (CPUE)	Occurrence: SE
Nearshore							
1. Northeast	10	146,808	87,680	7	(70)	10.7	0.875
2. Middle	13	47,283	24,033	8	(62)	10.1	0.703
3. Southwest	11	54,439	35,545	6	(55)	10.8	0.610
Offshore							
4. Northeast	10	37,682	29,659	7	(70)	10.0	0.503
5. Middle	11	2,177	657	3	(27)	9.0	0.168
6. Southwest	12	10,826	15,342	4	(33)	9.1	0.936

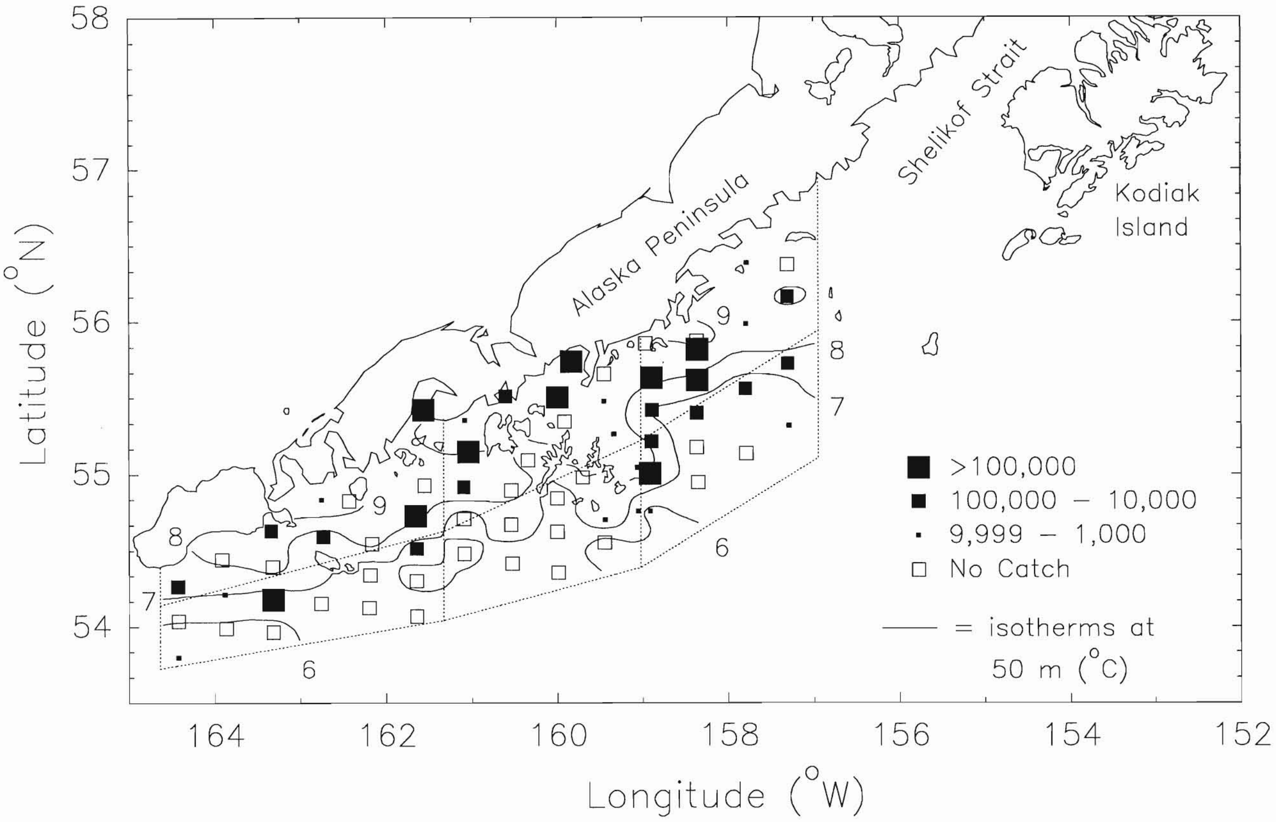

Figure 4

Geographic distribution of 0-age pollock abundance (no./km^2) superimposed on stratum boundaries (dotted lines) and on isotherms measured at 50 m with an expendable bathythermograph (XBT).

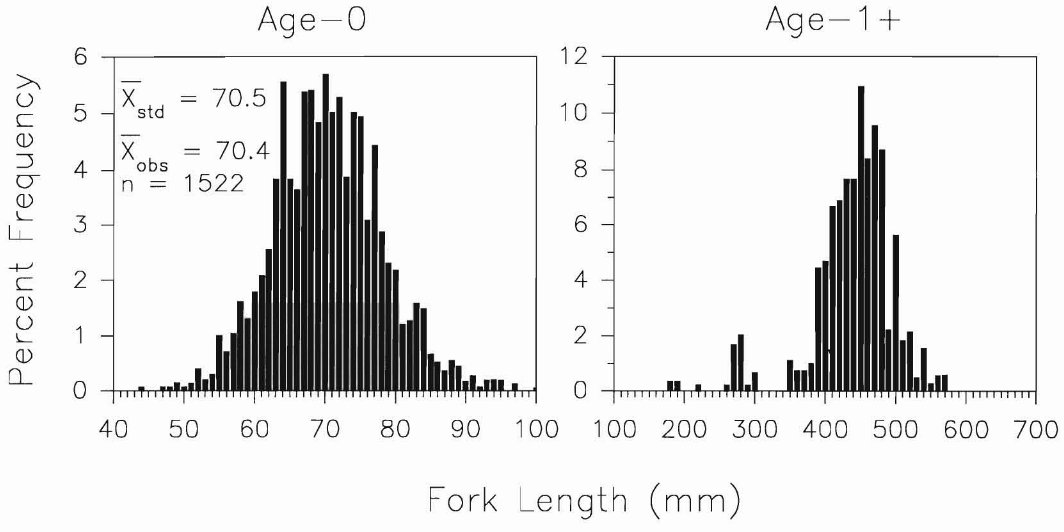

Figure 5

Length distribution, standardized to 1 km^2, of 0-age and older age classes of pollock from the stratified survey sampling. For age-0 pollock, the numbers of fish measured and their observed mean length (nonstandardized) are given.

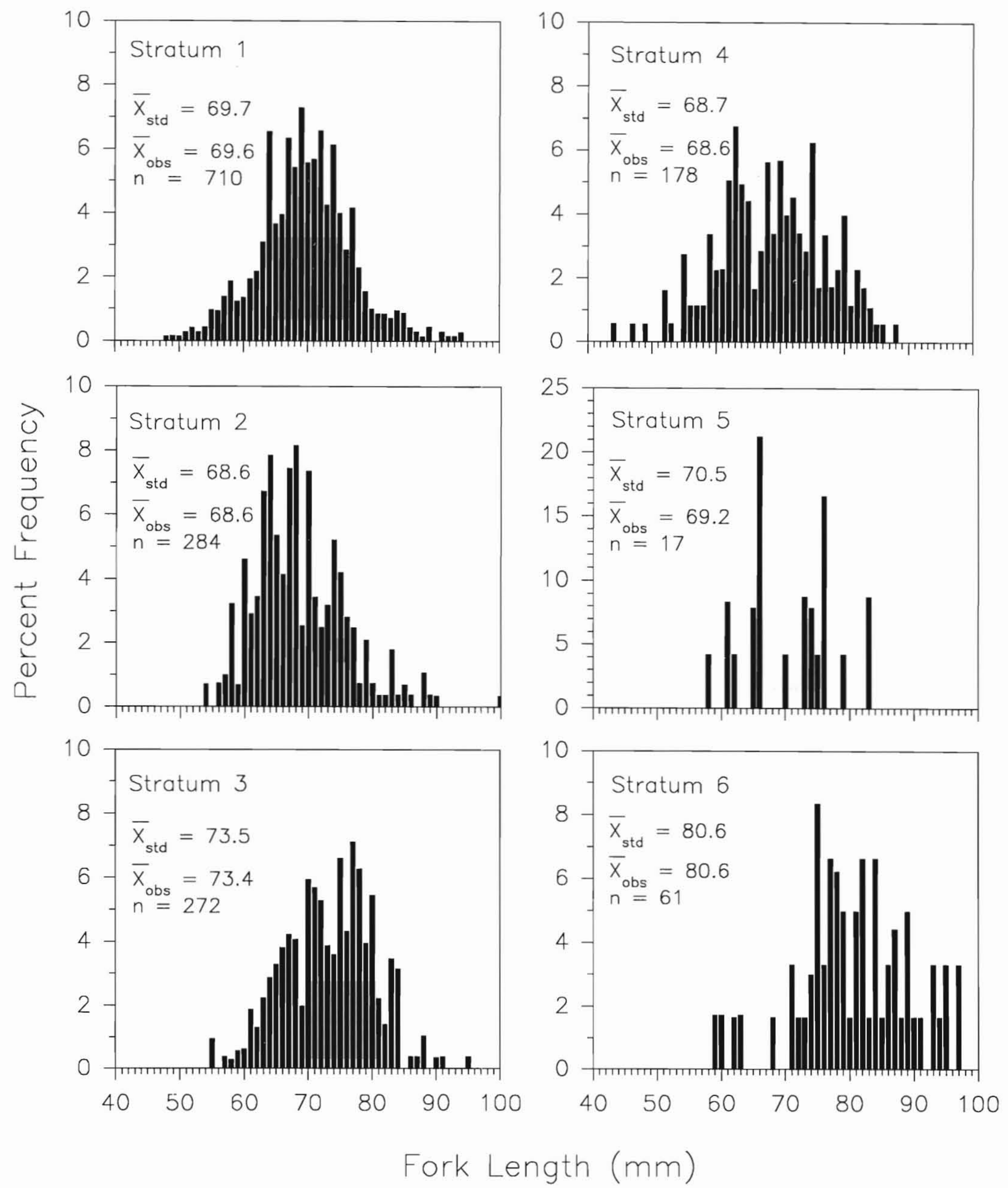

Figure 6

Length distribution of age-0 pollock by stratum, standardized to 1 km^2. The numbers of fish measured and their observed mean lengths (nonstandardized) are given.

Discussion

Paired-tow Experiments

Available information indicates that variation in the vertical distribution of age-0 pollock is best handled by choosing a survey strategy that distributes sampling effort equally among all depths. Walleye pollock are most abundant in the upper layers (<50 m) during the larval stage (Kendall et al., 1987) and move deeper as their size increases (Nakatani and Maeda, 1987). Postlarval age-0 fish have been found in large numbers near bottom over a broad range of water depths (40–120 m; Smith et al., 1984), and in midwater (Bailey and Spring,

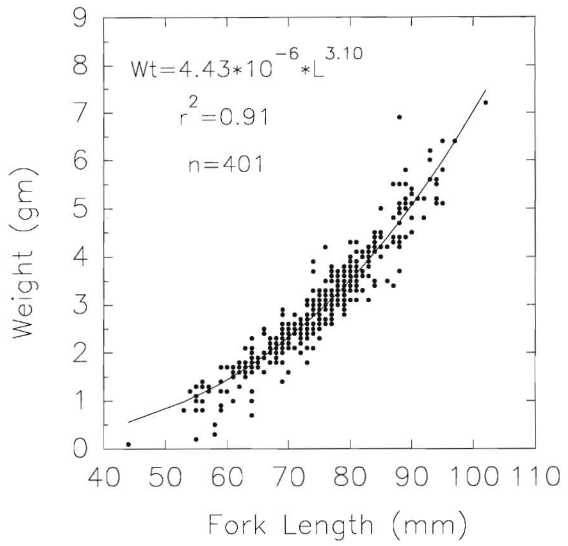

Figure 7
Length–weight relationship for age-0 walleye pollock.

1992; Brodeur and Wilson[2]). In the Bering Sea, age-0 fish were most abundant in the upper 40 m over the continental shelf (Lynde, 1984). Acoustic data indicate that age-0 pollock may be found at a substantial depth range from near surface to within a few meters of the bottom (Brodeur and Wilson[2]). Thus the depths for age-0 pollock are subject to substantial ontogenetic and spatial variability.

Variation in environmental conditions has been associated with differences in the depth distribution of age-0 pollock. Laboratory studies (Olla and Davis, 1990; Sogard and Olla, 1993) indicate that the vertical distribution of age-0 pollock in midwater results from an interplay of many factors (e.g., temperature, light, food, and predators). Unravelling the importance of these factors in the field is difficult. Evidence suggests that diel period and thermoclines in the Bering Sea may affect the depth distribution of age-0 pollock (Traynor, 1986; Bailey, 1989). Undoubtedly, age-0 pollock occur at a broad range of depths, and vertical positioning at any specific time and place may depend on a suite of environmental variables. Thus, targeting specific depths to survey the abundance of age-0 pollock would not be an advisable sampling strategy, based on what we know of the dynamics of their vertical distribution.

Performance of the sampling gear is another important consideration when choosing sampling strategies. For instance, we initially assumed that the shrimp trawl would perform best if fished stepwise, but we switched to an oblique path for biological reasons, after finding out that the performance of the trawl (as measured by age-0 pollock CPUE) was not compromised (Table 2). In fact, this change in net path appeared to improve trawl performance, perhaps because adding the wire retrieval rate to the towing speed increased the speed of the net through the water by 9 m/min (0.5 km/h).

If we had applied a correction factor to equate stepped-tow and oblique-tow catches, the age-0 abundance estimates, but not the distributional patterns, would have changed substantially. The overall abundance estimates of age-0 pollock would have substantially increased, since oblique tows generally caught more fish (Table 2). Also, in areas of high abundance all stations (strata 1 and 4), or some stations (stratum 2) were fished with the stepped method. When integrating the numbers and species composition of oceanic micronekton over discrete depth layers, Pearcy et al. (1977) used oblique rather than stepped net paths on the basis that the former provide a more representative sample because all depths within each stratum are fished. The shrimp trawl performed well when fished obliquely, and this should be the preferred method for estimating age-0 pollock abundance unless biological information about the vertical distribution of these fish, perhaps from echo sounders, suggests otherwise.

Although the shrimp trawl is designed to fish on the bottom, it was as effective as the anchovy trawl at sampling the age-0 pollock that we collected in midwater. But the anchovy trawl was designed to catch small pelagic fish, and samples collected with it are probably more representative of the overall midwater nekton community. The anchovy trawl's high vertical opening and large forward mesh allows more water to be filtered per distance towed, thereby boosting sampling effort and catches of rarer or more evasive species. Nevertheless, for estimating the distribution and size composition of age-0 pollock of the size range that we observed (53–110 mm), the two trawls appear to be equivalent.

Abundance and Distribution

Although some walleye pollock seem to spawn in the Shumagin Islands area and other areas of the western Gulf of Alaska (Kendall and Picquelle, 1990), we assume that most of the age-0 pollock caught were spawned in Shelikof Strait, where large numbers of pollock historically spawn during early April and are transported by southwesterly flow (Reed and Schumacher, 1986; Kendall and Picquelle, 1990; Kim and Nunnallee, 1990). The distribution center of young pollock in 1987 moved from the Shelikof spawning area in early April to downstream of the Shumagin Islands by September (Hinckley et al., 1991). In 1990, satellite-tracked buoys deployed into concentrations of larval pollock in Shelikof Strait all passed the Shumagin Islands by mid-September (Schumacher et al., 1993; Stabeno[5]). As pollock mature they become more active in determining their distribution, which probably relates to the distribution of prey or to areas of suitable temperature and other environmental variables. It is likely that most of the age-0 pollock collected had drifted from Shelikof Strait, and that their broad distribution reflects both physical transport and behavioral responses to their environment.

Given that most pollock in the western Gulf of Alaska spawn in Shelikof Strait and that their offspring pass each year through our survey area as age-0 fish, our abundance estimates should reflect large-scale regional abundance. Bailey and Spring (1992) estimated the abundance of age-0 pollock in this area for most years from 1975 to 1988 (1975–84: random bottom trawls during the day; 1985–88: midwater and bottom trawls targeted on echo sign during the day). Because the geographic extent of the data varied among years, we converted the overall abundance index for each year to number of fish per square kilometer of sea surface and found that our abundance index for 1990 (50,998 fish/km^2) ranked ninth out of 12 years. Bailey and Spring (1992) included results from around Kodiak Island, which we did not survey extensively. Excluding the results from this region did not change the conclusion that 1990 is a fairly weak cohort (ranked 10 out of 12). Assuming that these numbers are comparable and that they indicate regionwide trends, the 1990 year class of pollock in the western Gulf of Alaska appears to be weak (similar to 1987), but not the weakest on record. However, it is important to underscore that the sampling conducted in 1990 differed from earlier years (effort not allocated based on acoustic sign), and this may significantly affect age-0 abundance estimates.

When combined with previous survey work, our findings indicate that a variety of areas are used by age-0 pollock as nursery habitat and that some interannual variability may occur. Our survey indicated that most of these fish were found throughout the middle and inner continental shelf, and few fish were found near the 200-m isobath. However, Hinckley et al. (1991) show that during August and September of 1987, high abundances of age-0 pollock (>1,000/10 min) were found offshore near the 200-m isobath. In fact, the distribution patterns that we observed in September 1990 are more similar to those observed by Hinckley et al. (1991) during June and July for late larval and early juvenile pollock, than to those for late juveniles. Thus it appears that movement of age-0 pollock through the shelf waters off the Alaska Peninsula varies from year to year and may be an important factor affecting survival. Perhaps this variation relates to conditions in the nursery area, such as water temperature and prey availability, which might influence age-0 pollock distribution. Because these fish have recently become nektonic, variations in oceanic conditions during their planktonic larval stage, such as patterns of advection (Kendall and Picquelle, 1990), may also have important effects on their distribution as juveniles.

Neither our study nor that of Hinckley et al. (1991) effectively sampled the full range of potential age-0 habitat, because little sampling was done in enclosed bays. Smith et al. (1984) reported that mean catches of age-0 pollock in each of several bays located in our survey area ranged as high as 555×10^4 fish per m^2 (55,500 fish per km^2). This upper range of mean abundance is similar to mean abundances found in our stratum 3 (54,439 fish/km^2; Table 4). The highest mean abundance of age-0 pollock found by Smith et al. (1984) was $4{,}083 \times 10^4$ fish per m^2 (408,300 fish per km^2) for Alitak Bay at the south end of Kodiak Island, which was almost three times the highest mean abundance of any stratum in our study. Sampling during September in bays around Kodiak Island (M. Wilson, unpubl. data) also indicated that age-0 pollock occur, at all times of the day, throughout the water column both inside and outside of bays. Thus, while it is evident that substantial numbers of age-0 pollock inhabit much of the continental shelf along the Alaska Peninsula and Kodiak Island, the importance of semienclosed areas as habitats still needs to be determined.

The association between high age-0 pollock density and warm water at intermediate depths over the inner and middle shelf suggests that these habitats may be more suitable for juveniles than colder offshore waters. Brown and Bailey (1992) report an association between growth rate, inferred from otolith microstructure, and water temperature for age-0 pollock collected from the western Gulf of Alaska during August and September of 1987. Smith et al. (1986) show in laboratory experiments that water temperature differences similar to those observed in this study (6°–9°C) affected pollock growth rates. The increased growth rates could translate into increased survival if size-selective mortality occurs.

Bottom topography may be another physical characteristic important to age-0 pollock, because the alongshore distribution of these fish may relate to topographical differences along the continental shelf. In particular, the high abundances of age-0 pollock over the Shumagin Gully may be associated with warm nearshore water in close proximity to the greater depths of the gully. This may facilitate an ontogenetic movement into deeper water, perhaps to satisfy changing dietary requirements (Kamba, 1977; Nakatani and Maeda, 1987). High densities of age-0 pollock have

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[5] P. Stabeno. Pac. Mar. Environ. Lab., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. data.

been found in other gullies in the Gulf of Alaska, which extend from the continental slope (200 m) into bays (Wilson, unpubl. data).

Although our sampling was conducted at all hours of the day, future sampling of age-0 pollock should consider diel differences in distribution as a means to reduce the variation associated with abundance estimates. Diel variation in aggregation patterns has been observed among juvenile pollock (Traynor and Williamson, 1983; Traynor, 1986) and may explain our observation that the presence or absence of these fish in the catch is not independent of photoperiod. It is likely that these fish disperse at night to feed (Merati and Brodeur, 1996) and are aggregated in schools during the day, which could account for the day–night differences that we observed. Age-0 pollock were less frequently caught during the day than at night, but when the fish were caught, daytime catches were larger than nighttime catches. We might have expected daytime catches to be low and to contain mostly small individuals, since Bailey (1989) found that large individuals sometimes move close to the bottom during this time. This factor would be particularly problematic in shallow water, where the fish could move close to the bottom, below the depth sampled by our midwater trawl. Thus, diel sampling may have introduced variation into our mean age-0 pollock CPUE estimates; its effect on large-scale distribution patterns, however, is probably negligible, because photoperiod was randomized with regard to abundance and area.

We did not attempt to correct our length data for growth despite a collection interval of 17 d. Using otoliths, Bailey et al.[6] estimated a mean growth rate of 1.01 mm SL/d for these fish. Therefore, we were not surprised to find large mean sizes for fish collected in the downstream strata, which were sampled last. Nevertheless, the lack of statistical differences among strata suggests that, over the duration of our survey, increases in fish size were small relative to other sources of variability. We tried to compare the results of our length analysis to those of Walters et al. (1985), but differences in mesh size weaken the biological significance of this comparison.

Some uncertainties encountered during this study stemmed from a lack of understanding of the vertical distribution of age-0 pollock, catchability throughout the photoperiod, schooling dynamics, and the time that they spend in the nursery area. Resolving these questions is fundamental to understanding age-0 pollock ecology at a level sufficient for population-scale assessments of their abundance and distribution, and, ultimately, the source and magnitude of their mortality during their first summer.

Acknowledgments

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Juvenile Walleye Pollock, *Theragra chalcogramma*, Distribution and Abundance in Shelikof Strait— What Can We Learn from Acoustic Survey Results?

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ABSTRACT

Since 1980, winter and spring echo-integration trawl surveys have been conducted by the Alaska Fisheries Science Center annually (except in 1982) in the Gulf of Alaska to assess the distribution and abundance of walleye pollock, *Theragra chalcogramma.* Survey data are used to describe vertical and geographical distribution of age-1 walleye pollock in Shelikof Strait, as well as relationships between age-1 abundance and distribution. Age-1 pollock were consistently found in the southern region of Shelikof Strait, and relatively strong year classes formed a distinct scattering layer extending from the central part of Shelikof Strait south to near the Semidi Islands. A significant correlation was found between the abundance of age-1 pollock in Shelikof Strait and estimates for the same year class 2 and 3 years later in the Gulf of Alaska. This finding supports the use of acoustic estimates to forecast year-class strength of walleye pollock for management purposes.

Introduction

Fishery managers and biologists focus considerable effort on understanding the population dynamics of Gulf of Alaska walleye pollock, *Theragra chalcogramma* (Megrey, 1991; Schumacher and Kendall, 1991). Research on recruitment variability is motivated by its effect on pollock stock biomass (Alton et al. 1987; Megrey, 1989; Hollowed and Megrey[1]) and in estimating resource productivity for fisheries management purposes (Sissenwine, 1984). Further motivation is provided by the desire to predict properties of the upcoming year classes (Rothschild, 1986; Wooster and Bailey, 1989).

Since 1980, the Alaska Fisheries Science Center (AFSC) has annually (except 1982) conducted an echo-integration trawl survey in the Shelikof Strait region of the Gulf of Alaska to assess the distribution and abundance of walleye pollock. These surveys were conducted between late February and early April, when the abundance of spawners was believed to be at its peak (Nelson and Nunnallee, 1985a). Although the primary goals and design of the surveys focused on the adult spawning population, the surveys also provide data on juvenile (age-1) pollock. The goals of this paper are to describe the juvenile pollock data that are available from these historical acoustic surveys (1981, 1983–93) and to evaluate the time series of abundance estimates for age-1 pollock as an index of year-class strength.

Materials and Methods

Vessel, Acoustic Equipment, and Trawl Gear

All survey data were collected aboard the National Oceanic and Atmospheric Administration (NOAA) research vessel *Miller Freeman,* a 66-m stern trawler. In 1983, the NOAA research vessel *Chapman,* a 39-m stern trawler, also participated in the survey.

In all surveys, acoustic data were collected with a 38-kHz echo-sounder system interfaced to computer systems designed to implement echo-integration data analyses. The acoustic systems were improved over the study

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[1] Hollowed, A. B., and B. A. Megrey. 1990. Gulf of Alaska walleye pollock: population assessment and status of the resource in 1991. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115. Sect. 1, 68 p. Unpubl. manuscr.

period; acoustic data were collected with a Biosonics[2] dual beam system during 1981–85 (Nelson and Nunnallee, 1985a, b), a Biosonics split beam/dual beam system during 1986–90 (Traynor and Ehrenberg, 1990), and a split beam Simrad EK500 system during 1991–93 (Bodholt et al. 1989). From 1981 to 1990, the transducer was housed in a towed body deployed behind the vessel approximately 17 m deep. From 1991 to 1993 the transducer was mounted on the bottom of the vessel's centerboard, about 9 m below the water surface (Ona and Traynor, 1990).

The acoustic equipment was calibrated to estimate the transmitting and receiving characteristics of the system. From 1981 to 1987 a standard hydrophone was used to measure the acoustic parameters (Blue, 1984) before and after each survey. Since 1988, the more accurate standard sphere calibration procedure (Foote et al. 1987) was used, allowing calibrations to be made anytime during or after a survey.

Three different midwater trawls and three different bottom trawls were used between 1981 and 1993 (Table 1). Midwater echo sign was primarily sampled with a Diamond 1000 midwater trawl in 1981 and 1983–87, and with modified Northern Gold 1200 midwater rope trawls in 1988–93. Demersal echo sign was sampled with an Eastern 83/112 bottom trawl except in 1990, when a Poly-Nor'eastern bottom trawl was used, and in 1992, when a Nor'eastern bottom trawl was used. A codend liner with 3.2-cm (1.25-in.) mesh was used for all trawls. Vertical net dimensions were determined for all surveys with a netsounder mounted on the headrope; horizontal net measurements were made on some surveys with a SCANMAR net mensuration system.

Survey Methods

Survey operations were conducted 24 hours per day and consisted of two or more passes through Shelikof Strait along zigzag (1981–87) or parallel (1988–93) tracklines. Generally these tracklines traversed the strait between the 91-m isobaths and extended from near the Semidi Islands, around 56°00'N latitude, northward to about 58°30'N, depending on the extent of echo sign (Fig. 1). Tracklines were uniformly spaced at intervals of 3.5–10 n.mi., depending on the survey pass and year. Often additional passes were made to sample the densest pollock aggregations observed on previous passes. Vessel speed varied between 5 and 12 knots, depending on weather conditions.

Trawl hauls were made in an opportunistic manner during each survey to identify echo sign and to gather data on its biological composition. The duration of each haul varied, depending on the estimated time needed to provide an adequate sample size as indicated by the netsounder echo trace. Average trawling speed was about 3 knots. Standard AFSC catch-sorting and biological sampling procedures (Hughes, 1976) were used to determine weight and number by species for each haul. Pollock were further sampled to determine the fork length (FL), weight, sex, age, and maturity composition of the haul. Catch data were not used to generate abundance estimates.

Table 1

Trawl gear used during the winter and spring echo-integration trawl surveys in Shelikof Strait, 1981 and 1983–1993.

Trawl type	Years used	Head-rope (m)	Foot-rope (m)	Mesh size[1] (cm)	Spread (m)	Height (m)	Approximate opening (m^2)
Midwater							
Diamond 1000	1981, 1983–87, 1993	54	54	40.6, 81.2, 8.9	No data	16	
Northern Gold 1200							
rope with bridle	1988	91	85	163, 8.9	45	27.5	1237.5
with no bridle	1989—93	95	50	163, 8.9	No data	19	
3/4 scale Norse	1984	63	58	81.2, 8.9	No data	7.5	
Bottom							
Eastern 83/112	1981, 1983, 1986, 1991, 1993	26	34	10.2, 8.9	18	2	36
Poly-Nor'eastern	1990	27	37	12.7, 8.9	14	7.6	108
Nor'eastern	1992	27	32	12.7, 8.9	18	6	106

[1] First number is mesh size at wings. Last number is mesh size at codend. Where three numbers are given, second is size of a section of mesh between wings and codend. Codend liner was of same mesh size in all cases (see text).

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[2] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

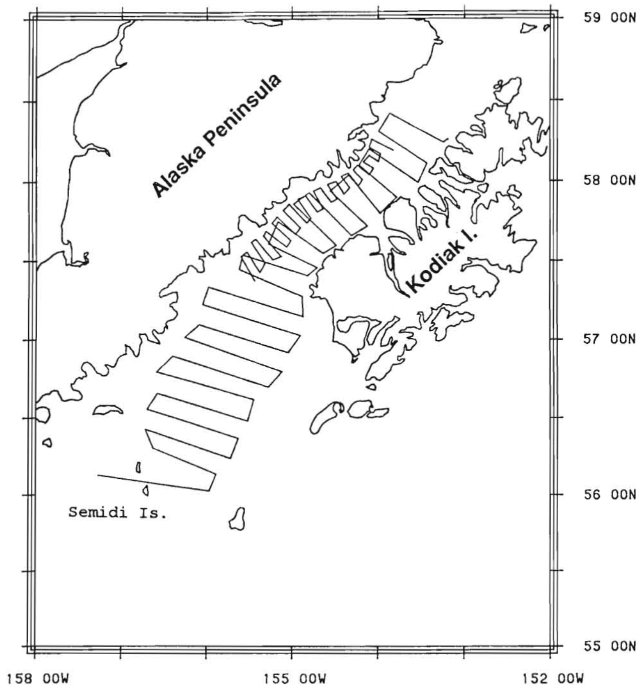

Figure 1
Survey trackline for the winter/spring 1992 pollock echo-integration trawl survey of Shelikof Strait, showing one pass through the strait area and a second pass of more closely spaced transects through the region of high spawner densities.

Echo-integration data were used to obtain estimates of fish abundance along each transect. Transects were partitioned into strata by depth and time/distance intervals. Strata where echo sign was determined to represent pollock were then selected, and the echo integration values within each stratum were summed over all chosen depth strata to provide estimates of biomass per unit area. Surface echo-integration values were scaled to estimates of absolute density (kg/m^2) by means of weighted pollock size compositions, a length-weight relationship derived from the trawl catches, and a previously-derived relationship between target strength and fish length (TS = 20 log(FL) – 66; Foote and Traynor, 1988). Biomass was calculated as the product of the average surface density and the area surveyed. Length- and age-specific biomass and population estimates were calculated with the biomass estimate, length-composition data, a length-weight relationship, and an age-length key. Because of equipment difficulties, pollock abundance was not estimated in 1987.

Analytical Approach

Age-1 pollock were selected from length-frequency records as the size range 9–16 cm FL in all years except 1986, when they were selected as 9–15 cm. Fish from this size range formed a clearly discernible size mode and were believed to have hatched 11–12 months before the survey. The proportion of age-1 pollock in each catch was determined from the length-frequency sample and extrapolated to the total catch.

Trawl hauls where age-1 pollock dominated the catch by number were identified. The corresponding extent and depth of the scattering layers for those fish were determined. Geographic and vertical distribution plots of age-1 pollock were created for each survey. Hauls with unsatisfactory gear performance were not included. Catch rates (no/h) were used to describe age-1 pollock relative abundance (e.g., high, medium, low) throughout the strait but were not used to determine actual abundance estimates. The difference in gear types probably affected catch rates (e.g., mouth area of the largest midwater net is 11–34 times larger than the mouth area of the bottom trawl; Table 1). Although no corrections were made to account for these differences, catch rates from the midwater trawls should be roughly comparable to those from other midwater trawls, and rates from the bottom trawls should be comparable to those from other bottom trawls.

Results

Juvenile Pollock Indices

Estimates of age-1 pollock abundance are presented in Table 2. Age-1 juvenile pollock were most abundant during the survey years 1985, 1986, and 1989, corresponding to the relatively strong 1984, 1985, and 1988 year classes.

The Shelikof Strait age-1 acoustic estimates were compared to the Gulf of Alaska age-3 and age-4 model estimates to see if Shelikof Strait age-1 abundance can be used to indicate year-class strength of Gulf of Alaska pollock. The Gulf of Alaska estimates were derived from an age-structured stock synthesis model described by Hollowed et al,[3] which incorporated fisheries, survey, and egg production data to generate a pollock abundance estimate that represents the entire Gulf of Alaska. Age-1 acoustic data were not included in this model. There was a significant relation (R^2=0.61; Fisher's *z*-transformation, p=0.01) between acoustic estimates of age-1 abundance and model estimates of recruited age-3 pollock (Fig. 2), particularly for the stronger year

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[3] Hollowed, A. B., C. Wilson, E. Brown, and B. A. Megrey. 1994. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1995. N. Pac. Fish. Manage. Council, P.O. Box 103136, Anchorage, AK 99510. Sect. 1, 66 p.

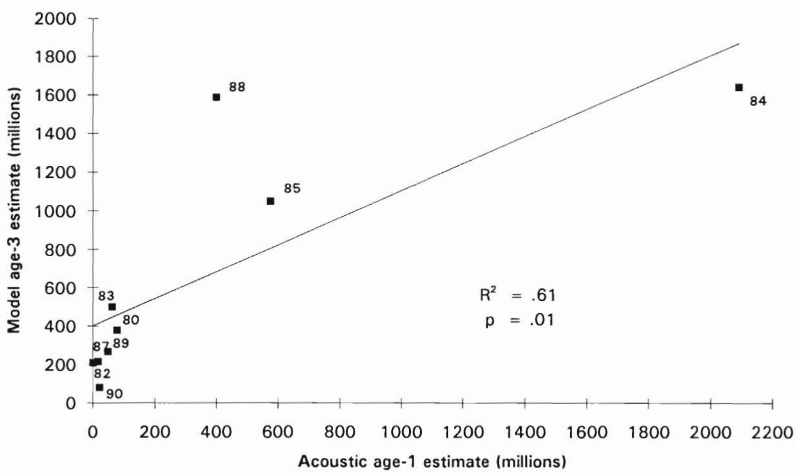

Figure 2

Scatterplot of Gulf of Alaska stock synthesis model age-3 pollock estimates and Shelikof Strait winter acoustic age-1 pollock estimates for year classes 1980–90. The fitted linear regression line indicates a positive relationship and is not intended for predictive purposes.

classes (Fig. 3). The same relation was found between acoustic age-1 and the model age-4 pollock. It would seem that the 1984 year-class data point drives this correlation, but when it was removed, the relationship remained strong (R^2=0.74; p<0.01).

Age-1 abundance estimates were also compared to acoustic estimates of ages 2–4 from the same year class. All comparisons showed a significant relationship. However, the strongest relationship was between the age-1 and age-3 acoustic estimates (R^2=0.89; p<0.01).

The Shelikof Strait age-2 acoustic abundance estimates were then compared to the Gulf of Alaska age-3 model estimates to see if the age-2 acoustic estimates could be used to indicate year-class strength. This relationship was also significant (R^2=0.77; p<0.01).

Juvenile Pollock Distribution

Age-1 pollock were present in the southern strait region (south of 57°00'N) in all survey years; in several years they were also found in the northern strait (Fig. 4). In "low" abundance years (Table 2), age-1 pollock were found dispersed throughout the strait and mixed together in scattering layers of predominately larger pollock, usually over a depth range of 225–250 m, within 50 m of bottom. However, patches of predominately age-1 pollock echo sign were observed in 1984 at the southern end of the strait and in 1990 at the northeastern end. In contrast, during the "medium" and "high" abundance years, age-1 pollock formed a discrete scattering layer in the southern region of Shelikof Strait; in 1985 and 1989, the layers extended up to the central part of the strait.

Age-1 pollock scattering layers were observed at various depths (Table 2). In 1985, 1987, and 1989, layers were generally at 140–215 m, above a deeper scattering layer of older pollock. In 1985 and 1989 there were also occurrences of a "sandwich" effect, where the age-1 scattering layer was observed between two layers of older pollock. On two occasions the 1985 scattering layer was observed by itself within 15 m of bottom. In contrast, the 1986 age-1 pollock layer was found at 195–245 m, within 15 m of bottom, without the deeper or shallower layers of older pollock (Fig. 5). Although abundance and distribution information for age-1 pollock in 1992 is not mentioned in Table 2, Figure 4 indicates relatively high bottom trawl catches of age-1 pollock. Further investigation of how vertical distribution has changed over the years is warranted.

Discussion

Echo integration has become a well-established technique for measuring fish abundance and can provide quick information about pelagic fish distribution (MacLennan and Simmonds, 1992). The annual Shelikof Strait acoustic surveys provide information that describes the winter distribution and relative abundance of age-1 pollock.

For walleye pollock and many other marine fish species, the magnitude of recruitment may be established

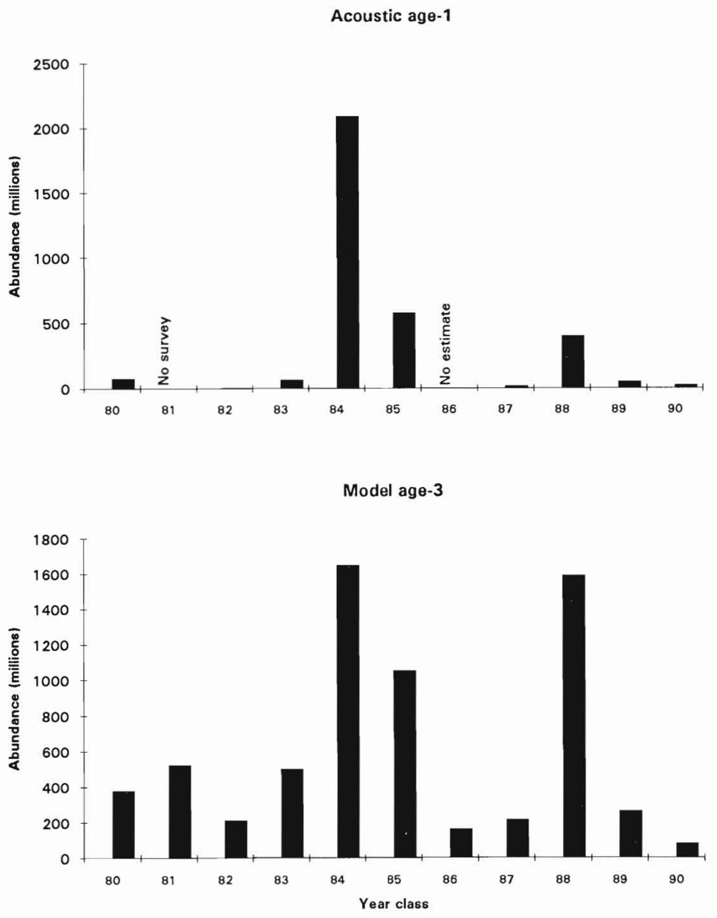

Figure 3
Shelikof Strait winter acoustic age-1 pollock estimates and Gulf of Alaska stock synthesis model age-3 pollock estimates.

Table 2
Echo-integration trawl survey abundance estimates (millions) and echo sign distribution of age-1 pollock from Shelikof Strait, Alaska, for the years 1981, 1983–86, and 1988–91.

Survey Year	Abundance (millions)	Relative abundance category[1]	Age-1 pollock echo sign	Depth of juvenile layer (m)
1981	77.7	Low	None	
1982	No survey			
1983	1.2	Low	None	
1984	61.7	Low	Light patch in south	180–200
1985	2,091.7	High	Moderate, south to central	140–215
1986	575.4	Medium	Moderate in south	195–245
1987	No estimate		Light in south	175–205
1988	17.4	Low	No echograms available	
1989	399.5	Medium	Moderate, south to central	175–215
1990	49.1	Low	Light patch in north	223–228
1991	22.0	Low	None	

[1] Abundance <250 million was considered "low." Abundance ≥250 and <1250 million was considered "medium." Abundance ≥1,250 million was considered "high."

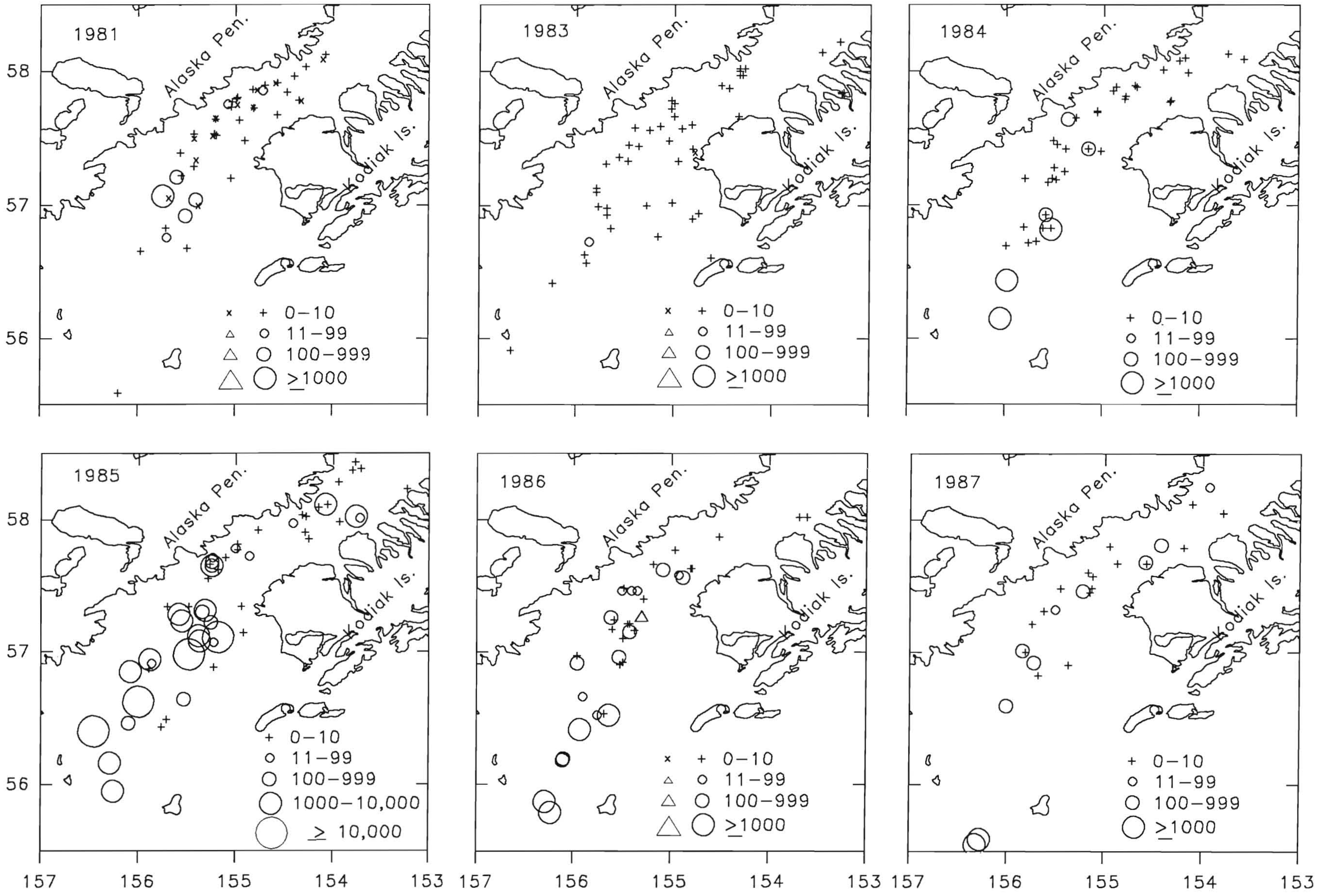

Figure 4

Shelikof Strait winter age-1 pollock distribution plots for survey years 1981, 1983–87. Catch rates (no/h) are indicated for midwater trawls (+, ○) and bottom trawls (×, △).

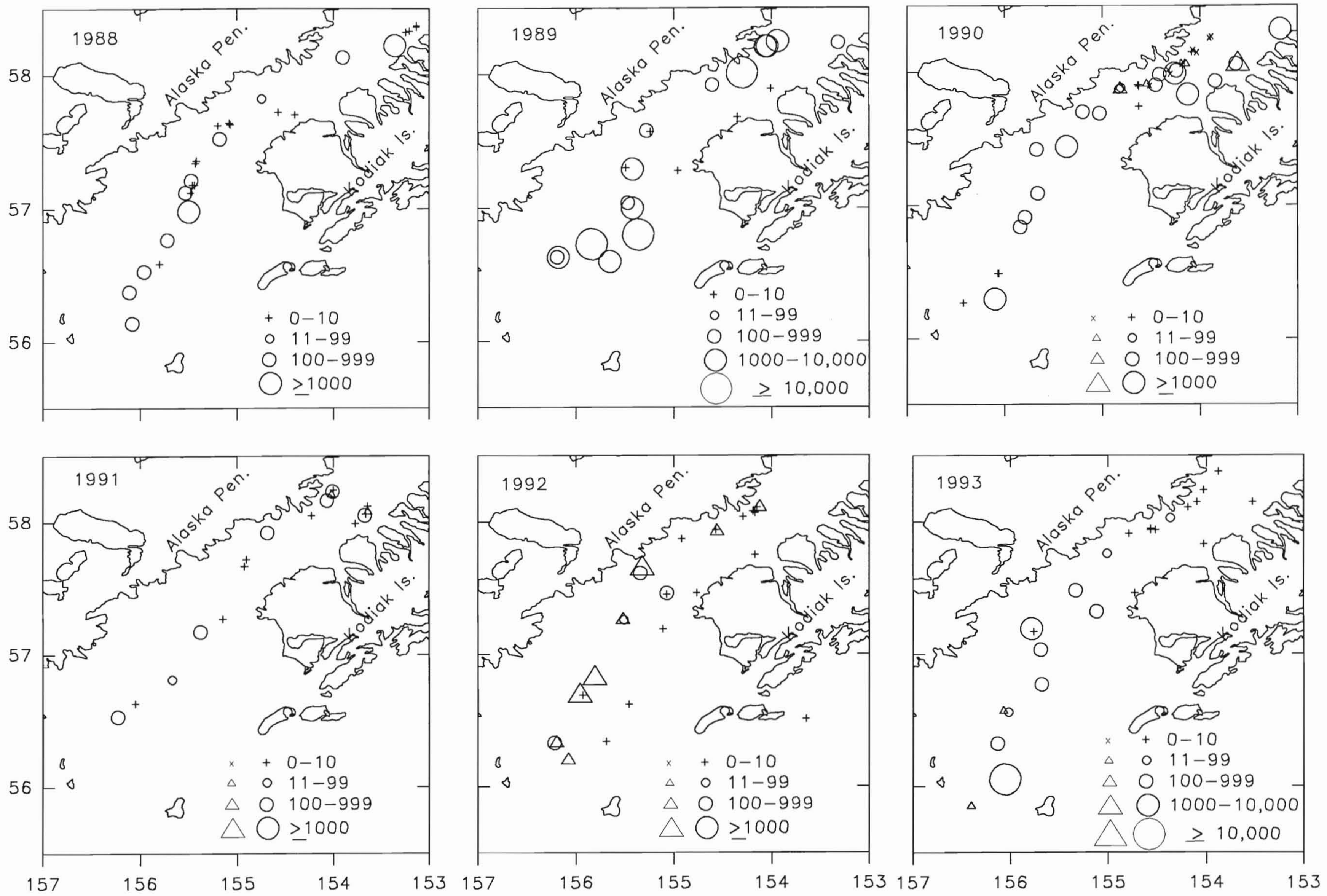

Figure 4 (continued)
Shelikof Strait winter age-1 pollock distribution plots for survey years 1988–93. Catch rates (no/h) are indicated for midwater trawls (+, ○) and bottom trawls (×, △).

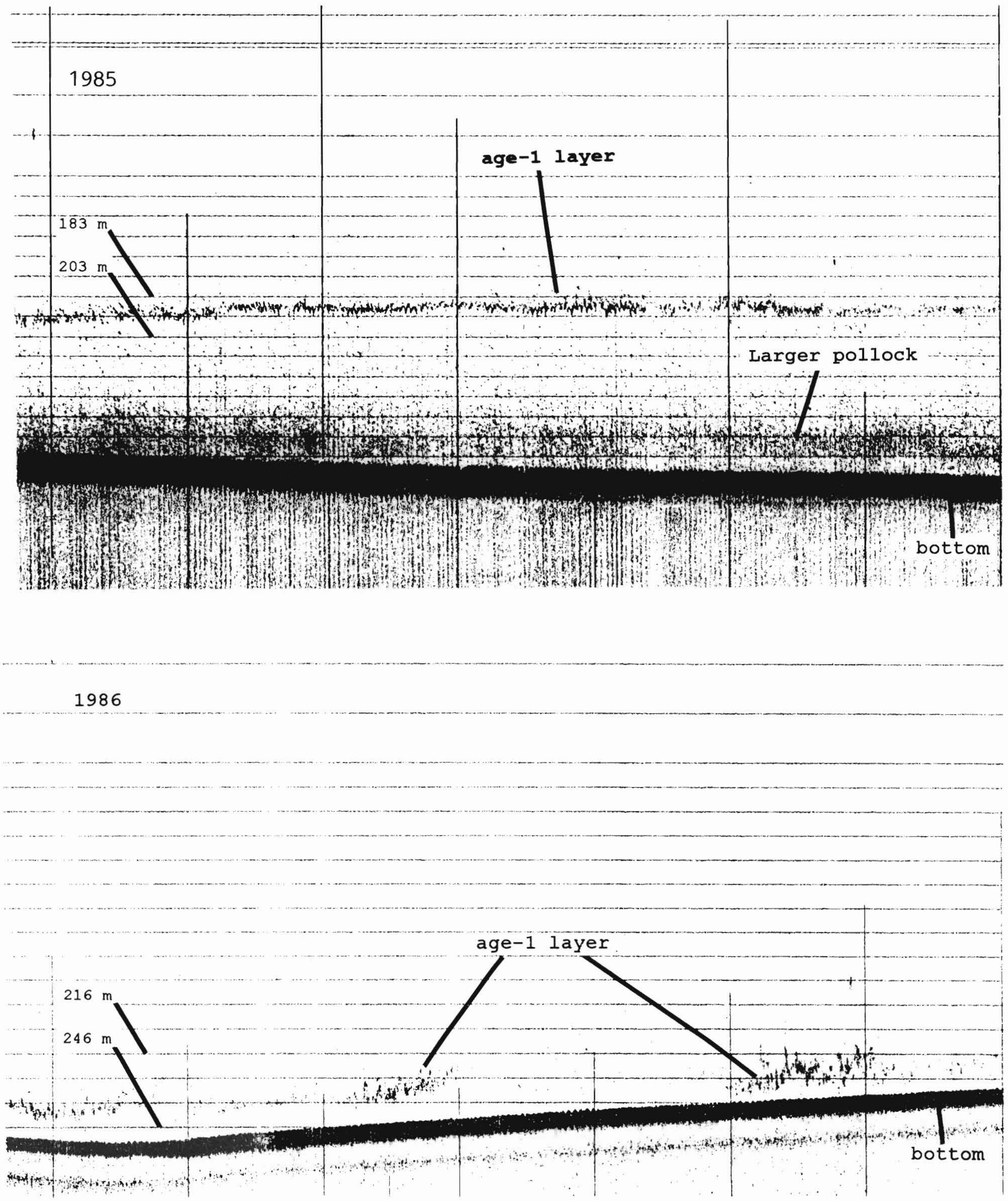

Figure 5
Echograms of age-1 pollock layers found during the 1985 and 1986 winter acoustic surveys. In 1985, the upper layer was predominately age-1 pollock and the lower layer was primarily older pollock.

in the early life stages, suggesting that prerecruit surveys may be a valuable tool for previewing the upcoming year class (Wooster, 1983; Bailey and Spring, 1992; Hinckley et al., 1993). Although the primary objective of the Shelikof Strait acoustic surveys was to assess the distribution and abundance of the adult spawning population, results suggest that Shelikof Strait age-1 acoustic estimates can be used to indicate relative year-class strength for the Gulf of Alaska, particularly as an indicator of high recruitment. Results also showed a strong relationship between age-2 acoustic and model estimates. Since, however, the goal was to find an indicator of year-class strength as early in the life history of pollock as possible, age-1 acoustic estimates are emphasized. To use the abundance estimates as a relative index of recruitment, one must be willing to assume that the same percentage of the Gulf of Alaska age-1 pollock inhabit Shelikof Strait each year.

Sources of Bias

Accuracy of an index depends on the errors incurred. Various sources of error are discussed by Traynor et al. (1990) and MacLennan and Simmonds (1992) regarding abundance estimates derived from echo-integration surveys.

Target strength is a particularly difficult parameter to estimate but is necessary for converting echo-integration values to fish density. The TS-length function (TS = 20 log(FL) – 66) was used to estimate mean target strengths. However, this function was derived primarily from larger pollock.

Another important source of error affecting acoustic estimates of age-1 pollock abundance is thresholding. The noise threshold setting on the echo integrator must be low enough to accept signals from valid fish targets but high enough that the integration of noise (unwanted signals) does not contribute significantly to echo integration. The scientist may also introduce error during post-processing of the echo-integrator data by incorrectly excluding data from analysis. If age-1 pollock are lightly dispersed, it is possible that they will be excluded from the echo-integration values by either the mechanical or judgement-based thresholding process. If, on the other hand, age-1 pollock are in a dense aggregation, as in a layer, their likelihood of contributing to echo integration will be much higher and they will have a greater chance of being sampled. Thus the index will be more accurate in "high" abundance years.

Other possible sources of bias include differences in vulnerability to the trawls and net selectivity (MacLennan and Simmonds, 1992; Gunderson, 1993). These sources of bias would hamper obtaining a biological sample representative of the corresponding echo trace. This would affect the size-composition (and therefore age-composition) estimates as well as the target strength estimates for those years when target strength was estimated by means of size composition and a TS–length relationship.

The index described in this paper could be improved by more intensive sampling in the southern strait (known area for age-1 abundance) to better define the southern extent of juvenile echo sign and to sample in low-density situations. Also, the survey design did not necessarily include areas where juvenile pollock were found in the past (e.g., inside bays) (Hinckley et al. 1991; Bailey and Spring, 1992). A survey designed to cover these areas could be used to develop a more accurate index.

Future Work

Future work should address the "selection" and maintenance of a particular depth stratum by age-1 pollock as well as how vertical distribution has changed over the years. Several possible hypotheses explaining habitat choice are related to predator avoidance, prey availability, density-dependent habitat selection (MacCall, 1990), and environmental cues.

Acknowledgments

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Summer Distribution and Abundance of Age-0 Walleye Pollock, *Theragra chalcogramma*, in the Aleutian Basin

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ABSTRACT

An echo-integration and midwater trawl survey of the Bering Sea for walleye pollock, *Theragra chalcogramma*, was conducted from June to August 1993. Large concentrations of age-0 walleye pollock were observed in the Aleutian Basin. Age-0 juveniles were mainly distributed in the northeastern part of the basin, extending from northwest to southeast, with the highest concentrations between the eastern continental slope and the international waters of the central Bering Sea. For the most part, age-0 juveniles inhabited waters 80–120 m deep, but a distinct diurnal vertical migration was observed. During July, age-0 pollock in the northeastern part of the Aleutian Basin ranged from 29 to 47 mm fork length (FL), while juveniles in the Bogoslof Island area ranged from 11 to 17 mm FL. This difference may indicate two separate spawning stocks. The temperature of the water inhabited by juveniles was 3°–5°C; the salinity was about 33‰. A relationship exists between concentrations of age-0 pollock and the continental slope environment.

Introduction

Walleye pollock, *Theragra chalcogramma*, is one of the most biologically and economically important species in the Bering Sea. Many recent studies have investigated the biology and the juvenile stages of this species to gain a better understanding of Bering Sea pollock population dynamics (Traynor, 1986; Bulatov, 1989; Mulligan et al., 1989; Traynor and Smith, 1996; NRIFSF[1, 2, 3]; Yoshimura[4]). This paper presents new information on geographic distribution, vertical migration, growth, and relative density of age-0 walleye pollock, and on how these juveniles relate to the environment and juveniles of other species in the Aleutian Basin. This information was gathered by an echo-integration and midwater trawl survey conducted by the Yellow Sea Fisheries Research Institute during the summer of 1993.

Materials and Methods

Survey Design

An acoustic/midwater trawl survey of the abundance of walleye pollock in the Aleutian Basin during the period of 28 June–2 August 1993 was conducted by the Chinese R/V *Bei Dou*, a 56.2-m ship with fisheries and oceanographic capabilities. The transects and stations occupied for pelagic trawling and environmental observations are shown in Figure 1. The distance between transects was 22 n.mi. near Bogoslof Island, and 44 n.mi. in other areas.

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[1] National Research Institute of Far Seas Fisheries (NRIFSF). 1994. Preliminary report of biological information obtained from 1990 summer pollock stock research in the Bering Sea by *Daian Maru* No. 128. Document for Bering Sea pollock survey working group. January 1994, Tokyo, Japan.

[2] National Institute of Far Seas Fisheries (NRIFSF). 1994. Preliminary report of biological information obtained from 1991 summer pollock research in the Bering Sea by *Shoyo Maru*. Document for Bering Sea pollock survey working group. January 1994, Tokyo, Japan.

[3] National Institute of Far Seas Fisheries (NRIFSF). 1994. Preliminary results of larval pollock survey conducted by the *Kaiyo Maru* in 1993. Document for Bering Sea pollock survey working group. January 1994, Tokyo, Japan.

[4] Yoshimura, T. 1990. Biological information on pelagic pollock in the Aleutian Basin during the summer of 1988. Compilation of papers presented at the International Symposium on Bering Sea Fisheries, April 2–5, 1990, Khabarovsk, USSR, p. 261–275.

The acoustic data were collected with a scientific echo sounding–integrating system (SIMRAD[5] EK400/38 KHz echo sounder with a hull-mounted SIMRAD ES38 transducer and a SIMRAD QD digital echo integrator). All data were logged onto a personal computer. The SIMRAD EK400 (120 kHz) echo sounder was also used to help identify different echo signs in the

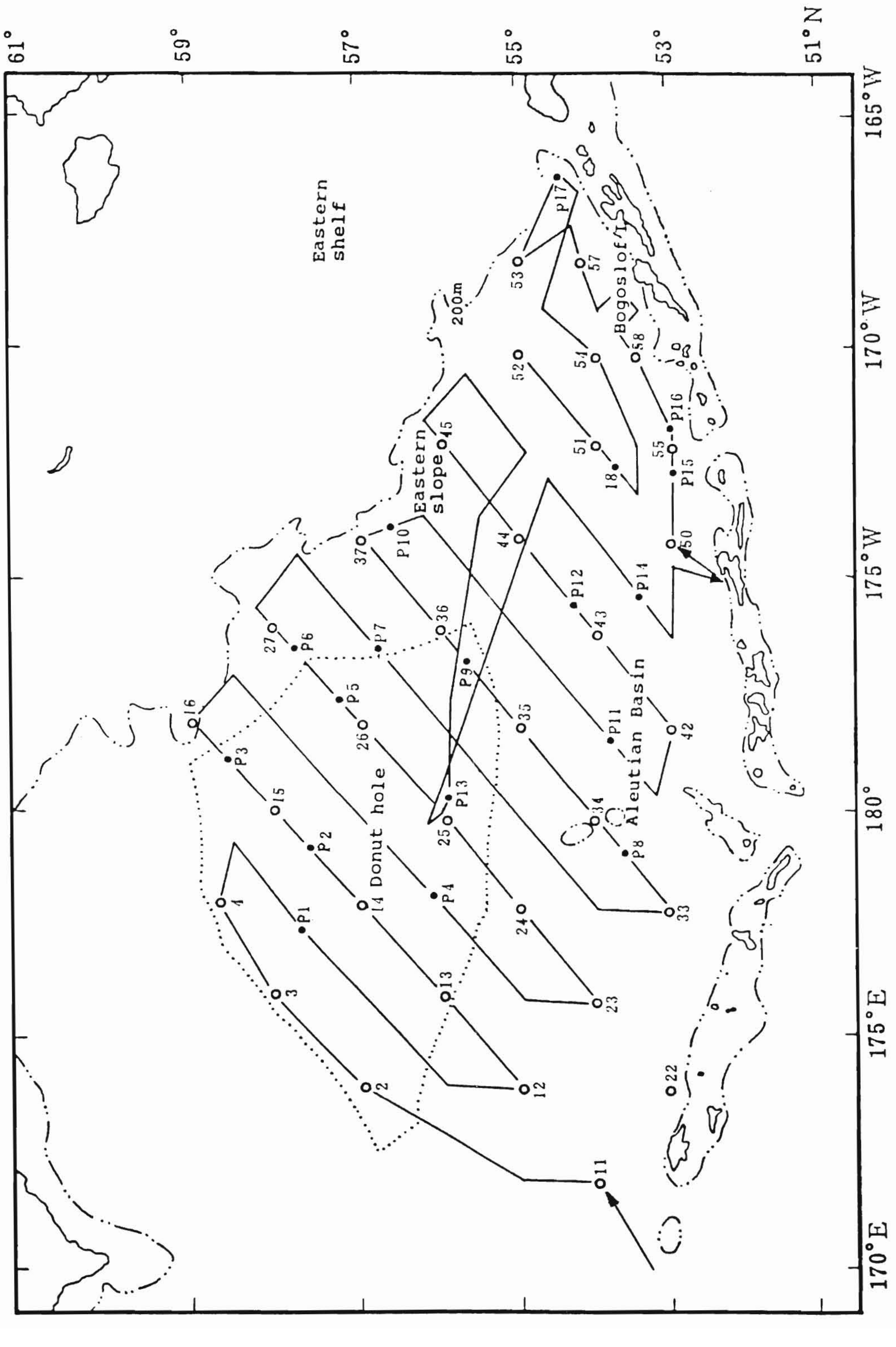

Figure 1
Trackline and positions of midwater trawl (dot) and hydrographical (circle) operations in the acoustic/midwater trawl survey for walleye pollock in the Aleutian Basin, June 28–July 24, 1993.

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[5] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

upper 100-m layer. The integration value (S_A, area backscattering strength) was given for each 5-n.mi. section of the transect for a set of successive depth intervals and was regarded as a relative abundance index for the detected fish. The overall acoustic system was calibrated with a standard target (60-mm-diameter copper sphere with known target strength of −33.6 dB) at a frequency of 38 kHz (Foote et al., 1987; Zhu and Iversen, 1990) at the beginning and end of the cruise while anchored outside Qingdao Harbor. No significant differences in the system performance were observed between the calibrations. The main instrumental parameters are shown in Table 1.

Biological Sampling and Environmental Observations

The acoustic survey covered about 710 × 10^3 km^2 of the Aleutian Basin of the eastern Bering Sea (Fig. 1). A pelagic trawl with 400-cm wing mesh and 4-cm-mesh codend was used to collect juvenile specimens. The trawl was towed from the stern of the vessel and had a vertical opening of 38–40 m; the distance between two otter boards was 121–123 m. Thirty-minute trawls provided adequate catches of age-0 juveniles. Other species caught in the trawls helped us identify the various acoustic targets. Some juvenile specimens were also collected with an 80-cm surface plankton net.

Water temperatures, salinity, and dissolved oxygen (DO) at the surface and at 25, 50, 100, 150, 200, 300, and 500 m were measured at predetermined stations. In addition, water temperature at 5-m depth was continuously monitored with a CHINO EA2P00 temperature recorder.

Results

Geographic Distribution

Large numbers of age-0 pollock were discovered in the northern and eastern parts of the Aleutian Basin (Fig. 2),

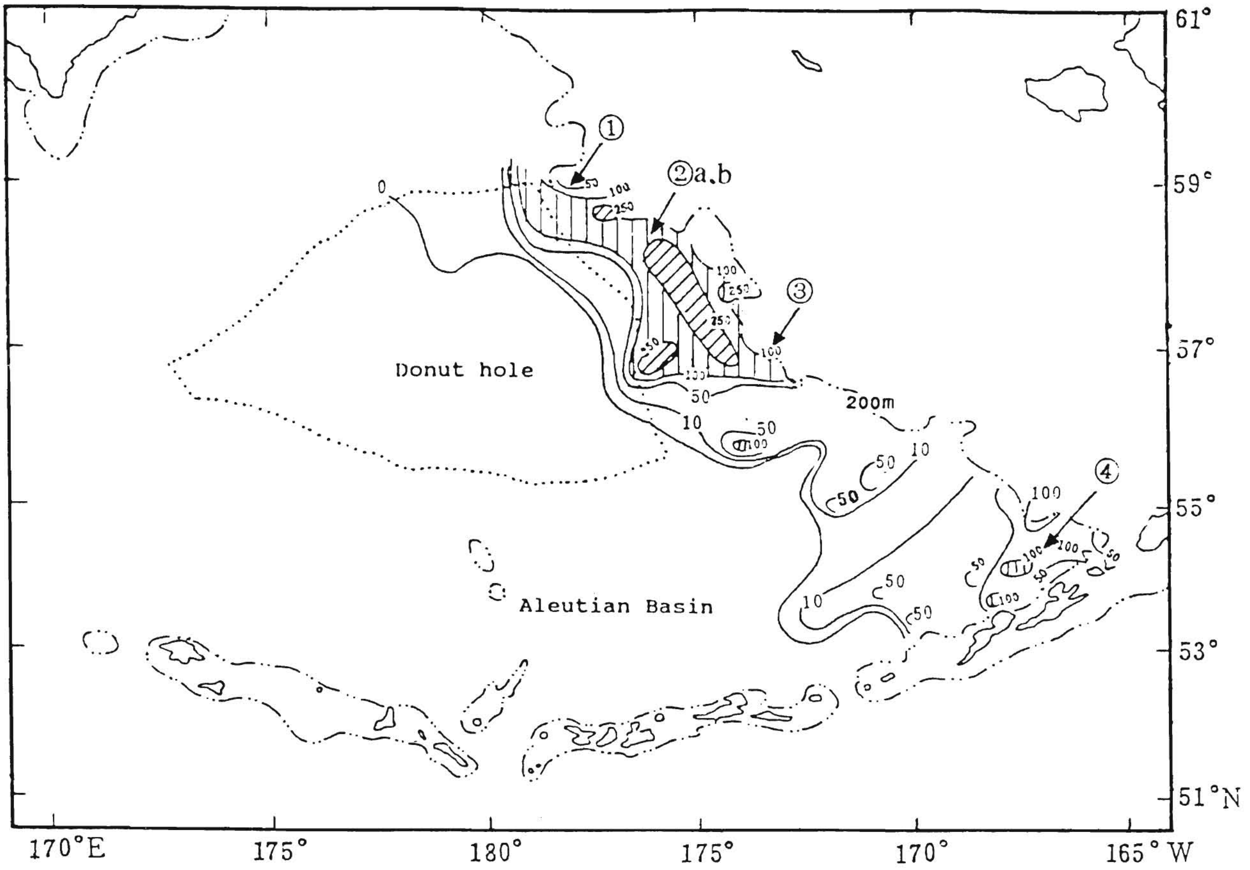

Figure 2

Distribution and relative density (integration value) of juvenile walleye pollock in the Aleutian Basin (June 28–July 24, 1993). Circled numbers indicate sampling stations for juvenile pollock.

Table 1
Technical specifications and main settings of acoustic equipment during R/V *Bei Dou* survey from June 28 to July 24, 1993.

Echo sounders	**SIMRAD EK 400**	**SIMRAD EK 400**
Frequency	38 kHz	120 kHz
Recorder gain	9	5
TVG and gain	20 log R–20	20 log R
Pulse duration	1.0 ms	1.0 ms
Bandwidth	3.3 kHz	3.3 kHz
Transmitting power (dummy 60 ohm)	3500 W	500 W
Basic range	0–300 m	0–300 m
Receiver gain	84.5 dB	84.0 dB
Transducer	**SIMRAD ES38**	**SIMRAD 68BA**
Beamwidth (–3 dB) LP/TP	7.9° × 8.4°	10° × 10°
Equivalent beam angle (10 log)	–20.1 dB	–17.6 dB
Source level + voltage response	139.8 dB	113.2 dB
Calculated instrument constant C_I (ref. –20 dB)	1.77 $m^2/nm^2 \cdot mm$	1.20 $m^2/nm^2 \cdot mm$
Integrator	**SIMRAD QD/38 kHz**	
Integrator threshold	13.8 mV	
Integrator gain	–22.49 dB	
Integration intervals	5–100/100–150/150–175/175–200/200–225/225–250/250–300/300–581 m	

extending from the edge of the eastern Bering Sea shelf to the basin. The zero-distribution isoline was approximately parallel to the 200-m isobath, and about 100 n.mi. from the 200-m-depth contour line. Areas with densest concentrations were located at the northeastern part of the surveyed area (north of 56°30'N and east of 180°E); the highest integration value was 498. An area of approximately 30 × 10^3 km^2 had an integration value of more than 100. Low concentrations were observed in the southeastern corner of the basin (east of 168°W, around Bogoslof Island), where integration values were mostly below 100. No juvenile pollock were found within a broad area of the western Aleutian Basin (Fig. 2), where mainly adults (4–20 years old) were distributed (Fig. 3). Adult distributions were centered in the central to northern parts of the international waters and the southeastern basin. Thus there was some overlap between the distributional areas of juveniles and adults, but no overlap between the areas with the densest juvenile and adult concentrations. No immature (1–3 years old) pollock were found in the Aleutian Basin.

Vertical Migration

Although juvenile pollock were centered around the 100-m water layer in summer, a distinct diurnal vertical migration was observed (Fig. 4, 5). During daytime hours (0800–1400), juvenile pollock were mainly distributed from 80 to 120 m deep. From 1600 to 2000, they gradually migrated to 20–60 m. Around midnight (2200–0200), juvenile pollock were concentrated in the upper 10 m, where they could be caught by surface plankton nets. At dawn (0300–0400), juveniles descended rapidly to the 60–90-m depth layer and gradually stabilized at about 100 m. Throughout all depths, age-0 pollock exhibited a strong schooling behavior, remaining in a layer 10–20-m thick (Fig. 5).

Biological Status

Age-0 walleye pollock caught in the northeastern part of the international water zone had a fork length that ranged from 29 to 47 mm, with a mean of 40.2 mm, and a mean body weight of 0.43 g. The dominant length was in the range of 36–44 mm (Fig. 6A). Slight differences in individual sizes were observed in fishes collected from three different locations (Table 2, Fig. 2). Juvenile pollock caught near Bogoslof Island were noticeably smaller; fork lengths ranged from 11 to 17 mm, with a mean of 13.8 mm, and the mean body weight was 0.03 g (Fig. 6B). The relation between fish length and age in days was used to back-calculate the age of juvenile pollock (Nishimura et al., 1996). Spawning was estimated to have occurred in late March in the northern part of the basin, and in late May in the southern part (around Bogoslof Island).

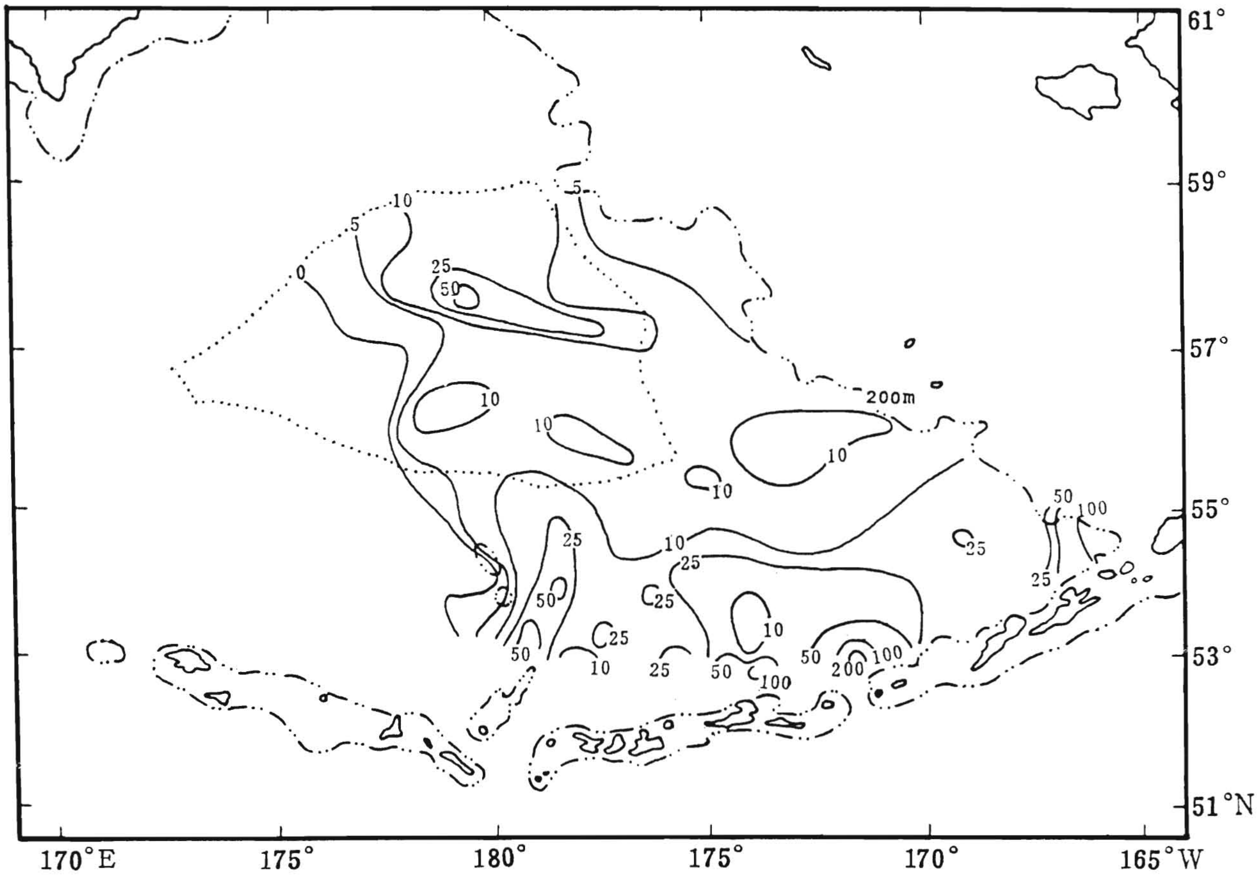

Figure 3
Distribution and relative density (integration value) of adult walleye pollock in the Aleutian Basin (June 28–July 24, 1993).

Relations with Other Juvenile Species

Additional juvenile fishes were collected in both the deepwater and surface samples. These specimens ranged from 2 to 6 cm in length and included Greenland halibut, *Reinhardtius hippoglossoides*; ronquil, *Bathymaster* spp.; sablefish, *Anoplopoma fimbria*, and squids (Table 3). Greenland halibut were relatively abundant over a large area, especially at the first sampling station (Fig. 2), where they contributed 11.3% of total juvenile catch by number. Their body lengths ranged from 26 to 42 mm, with a mean of 33 mm, and their mean body weight was 0.28 g. In addition, age-0 ronquil, possibly two species, were also abundant there. At the first sampling station, ronquil accounted for 6.1% of the total juvenile catch by number. They ranged from 40 to 51 mm FL ($\bar{x}$=45 mm), and had a mean body weight of 0.77 g. At the fourth sampling station (near Bogoslof Island), 72.1% of the juveniles by number were ronquil. Their body size was smaller, 6–13 mm FL ($\bar{x}$=11 mm), and their mean body weight was 0.017 g. Overall, the distributional area and density of juveniles of other species were less than those of juvenile pollock.

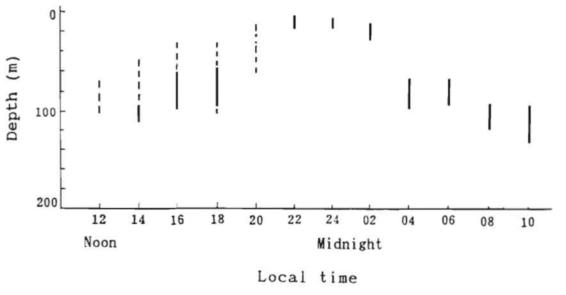

Figure 4
Day and night variation in distribution of juvenile walleye pollock in the northern part of the Aleutian Basin (July 7, 1993). Solid lines represent high concentrations; broken lines represent low concentrations.

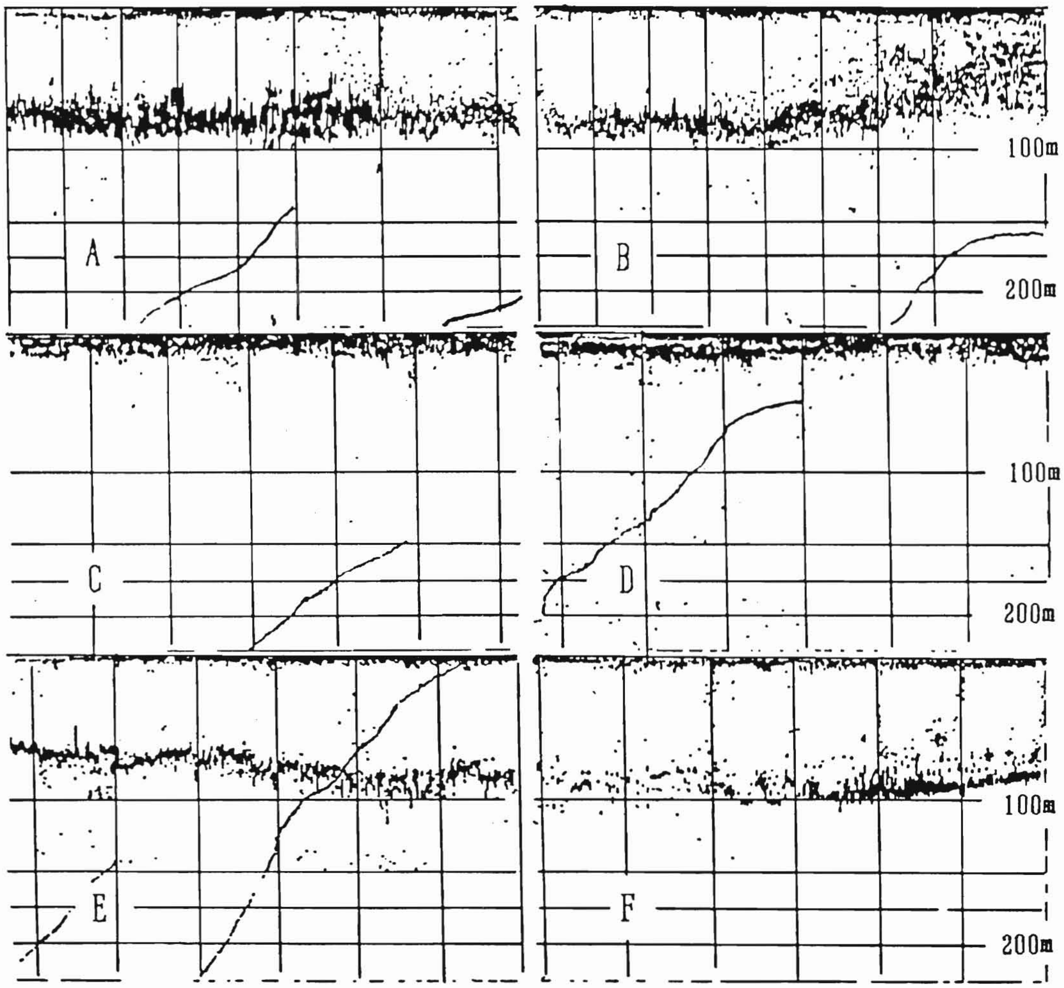

Figure 5

Echograms of vertical distribution of juvenile walleye pollock in the northern part of the Aleutian Basin. Local time: A, 1510–1535; B, 1650–1720; C, 2105–2125; D, 0140–0205; E, 0615–0640; F, 1050–1115.

Relations with Environmental Factors

At the surface, age-0 walleye pollock were generally distributed at temperatures of 7°–9°C, salinities of 32.5‰–33.0‰, and a DO level of 10 mg/l. At 50 m they were concentrated at temperatures of 3°–6°, salinities of 32.6‰–33.0‰, and DO levels of 8–10 mg/l. Finally, at 100 m, highest numbers were seen at a temperature range of 2°–5°, salinities of 32.9‰–33.2‰, and DO levels of 7–10 mg/l. Overall, the highest concentrations of juveniles were observed at about 100-m depth, at temperatures of 3°–5°, salinities of 32.9‰–33.1‰, and DO of 8–9 mg/l.

Distributions indicate that juvenile pollock mainly inhabit the waters between the sharpest thermocline (25–50 m) and a cold-water pocket at 100–200 m (Fig. 7). However, the vertical migration did not appear to be affected by the temperature gradient. For example, dense concentrations could rapidly pass through the thermocline during the diel migration to the surface

Table 2

Mean length (FL) and weight (W) of juvenile pollock collected from the survey in July 1993. Stations are the same as in Figure 2.

Date	Station	FL (mm)	W (g)
4	1	36	0.28
7	2a	40	0.38
8	2b	41	0.49
11	3	43	0.54
23	4	13.8	0.03

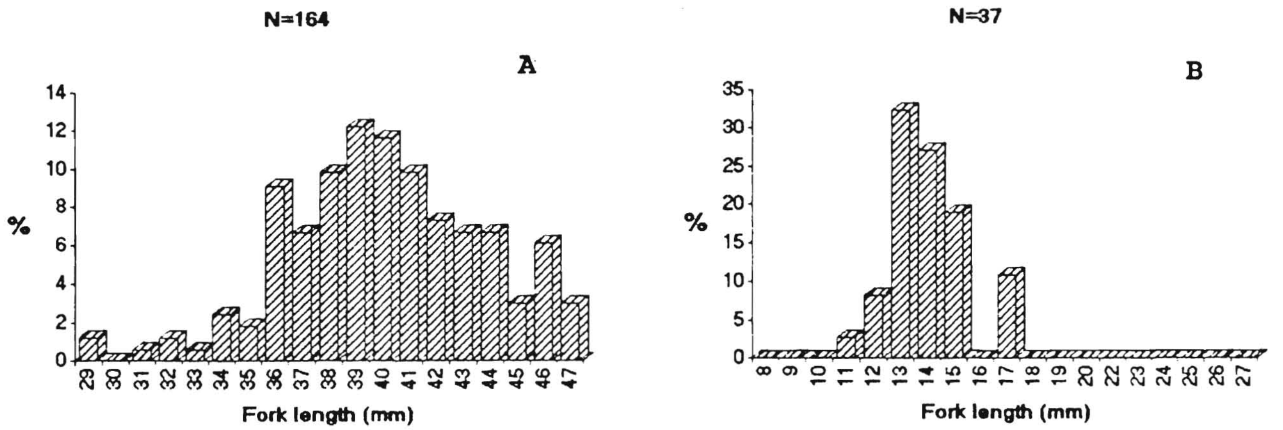

Figure 6
Length distribution of juvenile walleye pollock in (A) the northeastern part of the Aleutian Basin and (B) the area north of Bogoslof Island.

layer, where temperatures were 7°–9°C. Water temperatures decreased from east to west in the Aleutian Basin (Fig. 8). The highest juvenile distributions were located in the northeastern basin, and no juveniles were observed to the west along the same 3°C isotherm. When age-0 pollock distribution is compared with the horizontal distribution of salinity, the juvenile pollock were concentrated in areas of low salinity with relatively dense isohalines (Fig. 9).

Discussion

The Source of Age-0 Pollock

If the most current relationship between target strength and length of pollock (Foote and Traynor, 1988; Traynor[6]) and relevant data (integration values) are used to expand our acoustic data to estimate the total population of age-0 pollock in the northeastern part of the Aleutian Basin, we arrive at a biomass of about 20,000 t, corresponding to 58.2 billion fish. Although this estimate is crude and possibly low because the acoustic assessment did not include fish located shallower than the transducer, it implies a large concentration of age-0 pollock in the northeastern part of the Aleutian Basin in an area of 150 × 10^3 km^2. Thus the northeastern part of the Aleutian Basin appears to be an important nursery area for age-0 pollock. In light of the present understanding of the population structure and spawning of Bering Sea pollock (Hinckley, 1987; Bulatov, 1989; Mulligan et al., 1989), these juveniles might have originated from the areas around Bogoslof Island, the Pribilof Islands, or the Aleutian Basin.

The area near Bogoslof Island is one of the most important spawning grounds for pollock. But the individual sizes around Bogoslof Island are small, and the distribution of this population shows a discontinuity at 55°N, 170°W (Fig. 2, Table 2), which implies that it is unlikely that they moved directly northwest but instead might have arrived by way of the northeastern shelf.

The main spawning period of pollock on the shelf of the eastern Bering Sea, around the Pribilof Islands, is from April to June; only part of the shelf pollock population spawns in early spring (Hinckley, 1987). The survey data of the Japanese R/V *Kaiyo Maru* in 1993 showed that the dominant length group was 10 mm in June, indicating a spawning time of May.[3] Thus, on the basis of the larger individual size of juveniles in the northeastern part of the basin, it is likely that only a small number of age-0 pollock on the shelf come into the basin.

Because the major spawning period of pollock in the southeastern part of the Aleutian Basin is earlier than that of other spawning stocks (Hinckley, 1987; Sasaki, 1989), and because individual juvenile size decreased from sampling stations 3 to 1 (Fig. 2, Table 2), we conclude that most of the age-0 pollock collected in our study came from the southeastern part of the Aleutian Basin. If this is true, our data suggest that there is not only a nursery area but also a spawning ground for pollock within the Aleutian Basin.

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[6] Traynor, J. J. 1994. Target strength measurements of walleye pollock and Pacific whiting. Paper for Bering Sea Pollock Cooperative Survey Working Group Meeting. January 1994, Tokyo, Japan.

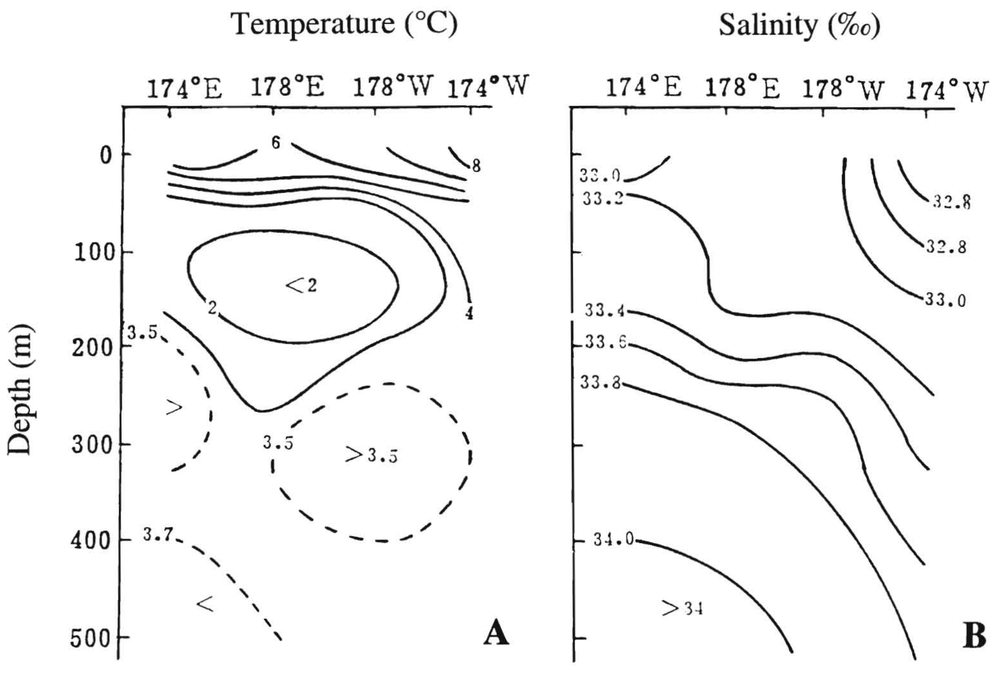

Figure 7
Vertical distributions of (A) temperature and (B) salinity along the 57°N section.

Table 3
Species composition (%) of juvenile fish in the Aleutian Basin during the survey June 28–July 24, 1993. The locations are the same as in Figure 2. Stations 1–3 were sampled by pelagic trawl and were located in the northeastern part of the Aleutian Basin; station 4 was sampled by surface plankton net and was located north of Bogoslof Island. N = number, W = weight.

	Sampling station									
	1		2a		2b		3		4	
Species	*N* (%)	*W* (%)	*N* (%)	*W* (%)	*N* (%)	*W* (%)	*N* (%)	*W* (%)	*N* (%)	*W* (%)
Walleye pollock										
Theragra chalcogramma	78.8	69.4	97.6	98.3	98.7	99.0	100	100	27.2	61.6
Greenland halibut										
Reinhardtius hippoglossoides	11.3	9.9	2.4	1.7	1.3	1.0				
Ronquils										
Bathymaster sp. A	6.1	14.8								
Bathymaster sp. B									72.1	28.6
Sablefish										
Anoplopoma fimbria									0.7	9.8
Squid										
Teuthoidea	3.8	5.9								

Survey Methodology

Many surveys on age-0 Bering Sea pollock have been conducted by the United States, Japan, and Russia. The general conclusion is that age-0 pollock are mainly distributed on the eastern Bering Sea shelf, and that only a small part of the population is found on the eastern Bering Sea slope and in the Aleutian Basin (Haryu, 1980; Lynde, 1984; Haryu et al., 1985; Traynor, 1986; Bulatov, 1989; Mulligan et al., 1989; Bakkala et al.;[7]

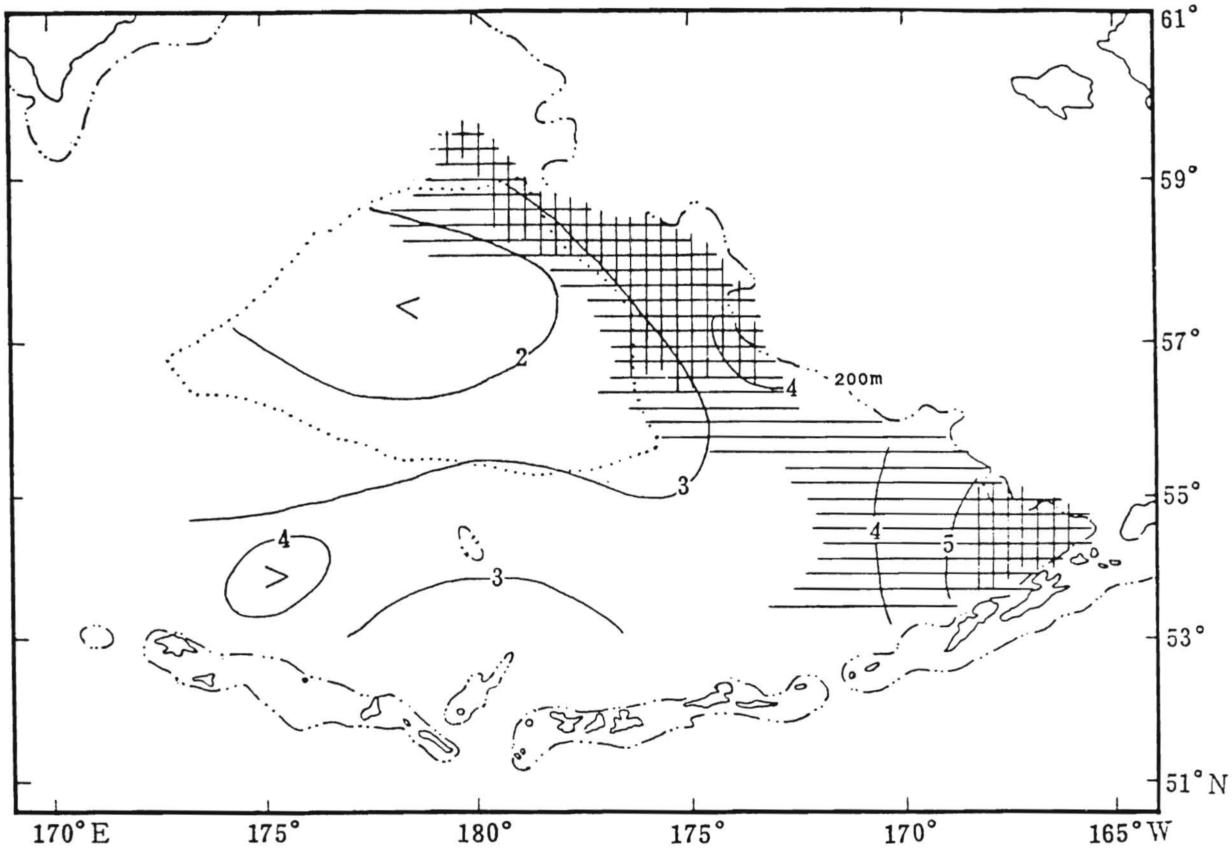

Figure 8

Relation between the distribution area of juvenile walleye pollock and temperature (°C) at 100 m depth. Single hatching represents the overall juvenile distribution; crosshatching represents the highest-density distribution.

NRIFS;[1, 2, 3] Yoshimura[4]). This may be due to an incomplete understanding of the distribution of age-0 pollock and a survey effort largely limited to the shelf. This conclusion may also be related to the survey methodology. Mulligan et al. (1989) pointed out that valid sampling for any fish species at any stage of development depends upon the proper use of appropriate gear; abundance of juvenile pollock in the Aleutian Basin may be higher than previously reported because of the use of inappropriate gear. The sampling gears they used have a relatively small mouth opening (e.g., Methot trawl with a mouth of 5 m^2) for vertical or oblique sampling, and net avoidance may have biased the results.

When dense scattering was observed during the acoustic survey in the Aleutian Basin, what was believed to be dense aggregations of some fish at about 100-m depth was determined by sampling with the pelagic trawl to be mainly age-0 pollock with a few other species. When the survey was extended over a large area, a relatively complete picture of the distribution and abundance of age-0 pollock in the Aleutian Basin was obtained from only one week of sampling. This indicated that a combination acoustic and trawl survey may be necessary to survey age-0 pollock. This method may be especially suitable for surveying juvenile fish over a large area of relatively deep water. If the target strength of juvenile pollock can be more accurately measured, and the codend mesh size of our net adjusted for sampling smaller juveniles, more accurate abundance estimates of age-0 fish may be obtained.

Acknowledgments

The support of the Bureau of Aquatic Products, Ministry of Agriculture of China, Chinese Academy of Fishery Sciences, China National Fisheries Corp. (NFC), Dalian, Yantai, Qingdao, Shanghai and Zhoushan Deep Sea Fisheries Corp., as well as the U.S. office of NFC, is

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[7] Bakkala, R., K. Wakabayashi, J. J. Traynor, H. Yamaguchi, K. Okada, M. Nelson, T. Sample and M. Alton. 1983. Results of cooperative U.S.–Japan groundfish investigations in the Bering Sea during May–August 1979. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N. E., Seattle, WA. Unpubl. manuscr.

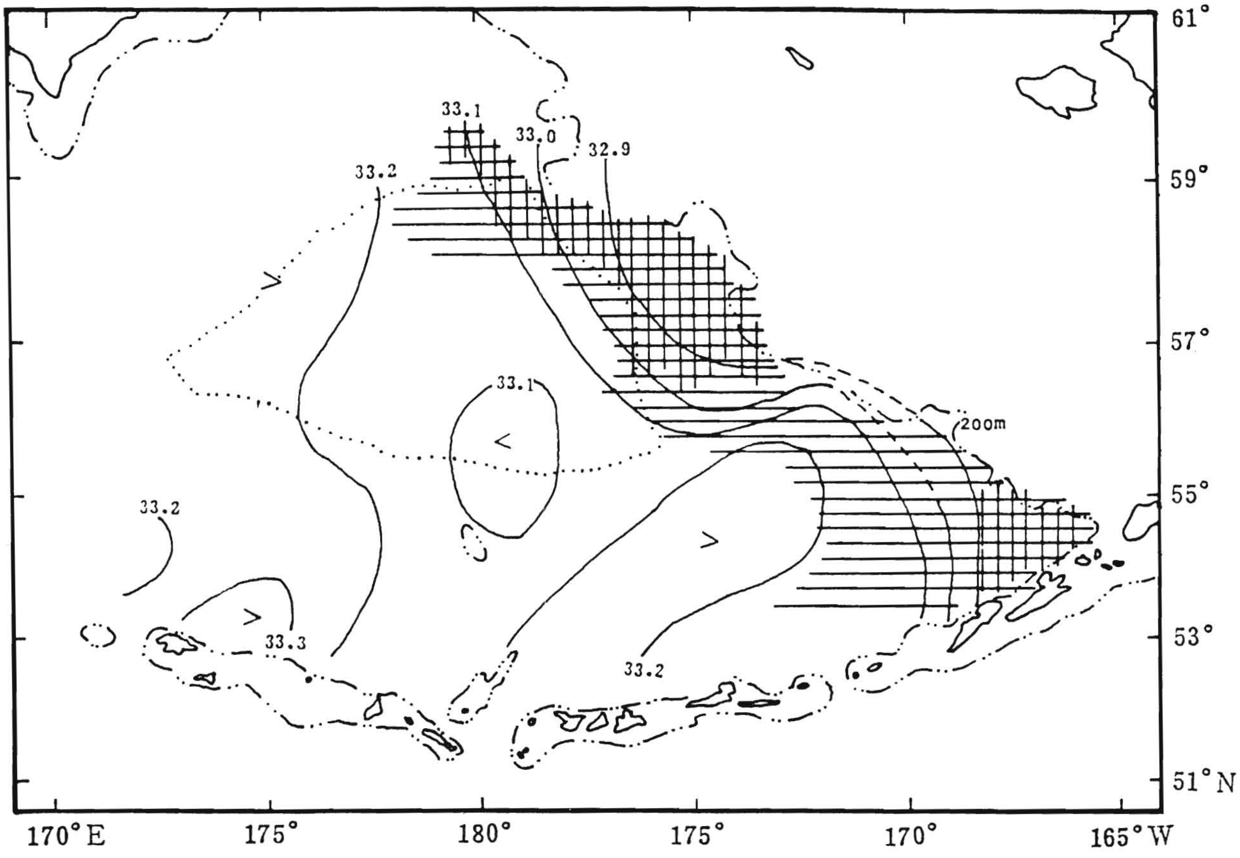

Figure 9
Relation between the distribution area of juvenile walleye pollock and salinity (‰) at 100 m depth. Single hatching represents the overall juvenile distribution; crosshatching represents the highest-density distribution.

greatly appreciated. We thank the captain, chief engineer, and other crew of the R/V *Bei Dou,* and A. Kendall and A. Matarese of the NMFS Alaska Fisheries Science Center, who helped us identify some juvenile specimens.

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The Relationship between the Distribution of One-Year-Old Walleye Pollock, *Theragra chalcogramma*, and Sea-Ice Characteristics

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ABSTRACT

Distributions of one-year-old walleye pollock, *Theragra chalcogramma*, were obtained from bottom trawl surveys conducted on the southeastern Bering Sea shelf between 1972 and 1992. Coincidentally, seasonal sea-ice characteristics during this period were available from satellite imagery. These two data sets provided a time series for exploring the relationship between sea ice and fish. Years characterized by heavy ice conditions occurred in 1972–78, coincident with the highest abundance of walleye pollock in the outer domain. Years of light ice conditions occurred in 1979–87, when walleye pollock were most numerous over the middle domain. Intermediate ice conditions occurred in 1988–92, when walleye pollock were most numerous over the middle and inner domains. The link between walleye pollock distribution and ice cover lies in the relationship of ice and bottom-water temperatures. One-year-old walleye pollock do not concentrate in waters colder than 2°C. Thus the condition of seasonal sea ice on the eastern Bering shelf during winter forecasts the distribution of one-year-old walleye pollock on the shelf the following summer. This shift can be predicted from the duration of ice cover over the middle domain, ΔT_M. When ice remains over the middle domain (south of 59°N) less than 20 weeks, most of the one-year-old walleye pollock will be found in the middle domain. When ΔT_M is longer than 24 weeks, a higher proportion of fish will be located in the outer domain.

Introduction

One-year-old walleye pollock, *Theragra chalcogramma*, occur throughout the eastern Bering Sea shelf, northward to Kotzebue Sound, and into the southeastern Chukchi Sea (Wolotira et al.[2]). Sampling of one-year-old walleye pollock from the northeastern Chukchi Sea in 1990 (Wyllie-Echeverria, 1995), a year of reduced ice cover (ice extended to 75°N, the farthest north in 30 years), suggests that sea ice might influence walleye pollock distribution. It has been observed that survival of tanner crab, *Chionoecetes opilio*, seems related to the maximum extent of sea ice in April (Somerton, 1982). In addition, during years of heavy ice cover and more cold bottom water in the middle domain of the southeastern Bering shelf, distribution of young walleye pollock changed in relation to the 2°C isotherm (Bakkala and Alton, 1986). Changes in the distribution of walleye pollock are probably a function of systemwide changes linked to seasonal sea-ice cover.

A dominant characteristic of the Bering Sea shelf in winter is seasonal ice cover, the extent of which varies interannually (Overland and Pease, 1982). The amount of ice cover extending over the shelf affects the biological and physical environment in a number of ways. Ice affects shelf hydrography through melting and freezing that locally redistributes salt and heat in the water column, changes vertical stratification, and directly influences shelfwide heat and salt budgets (Schumacher et

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[1] Present address: JISAO, PMEL, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.

[2] Wolotira, R. J., Jr., T. M. Sample, and M. Morin Jr. 1977. Demersal fish and shellfish resources of Norton Sound, the southeastern Chukchi Sea, and adjacent waters in the baseline year 1976. Northwest Alaska Fish. Cent. Proc. Rep., U.S. Dept. Commer., NOAA, Natl. Mar. Fish. Serv., Seattle, WA. 292 p.

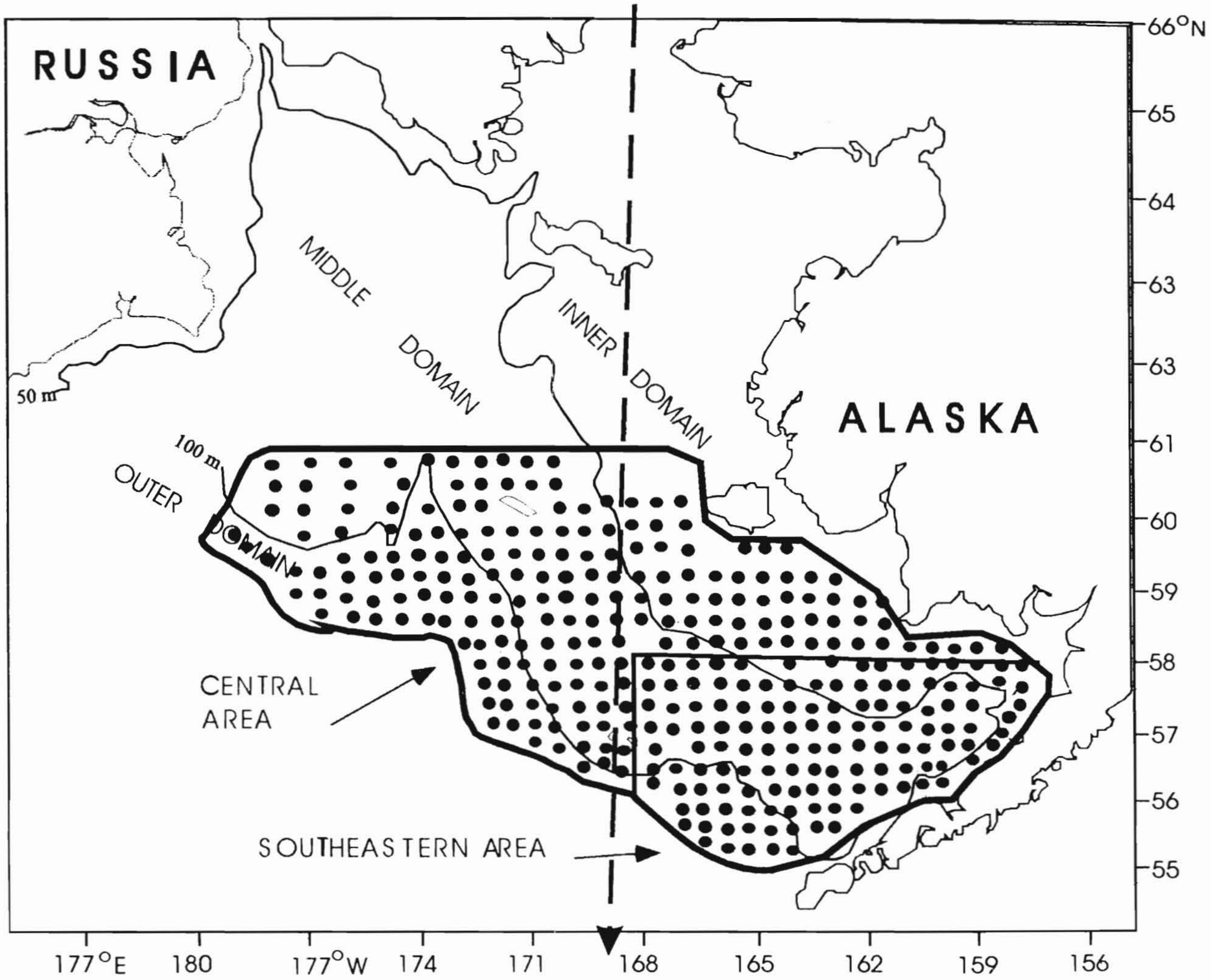

Figure 1

Study area on the Bering Sea shelf. Station locations from the bottom trawl surveys are indicated by dots. Inner, middle, and outer domains are bounded by the 50-, 100-, and 200-m isobaths. The core area used in the analysis is the southeastern area, with comparisons to the central area. Seasonal sea-ice characteristics are represented by ice position along longitude 169°W (dashed line with arrow).

al., 1979). The extent of cold bottom water in the middle domain may be directly affected by the amount of ice cover the previous winter (Takenouti and Ohtani, 1974). Additionally, ice melt generates a relatively strong current in the marginal ice zone (Muench and Schumacher, 1985). The timing of the ice-edge phytoplankton bloom, as well as the subsequent spring bloom, is affected by the ice cover and by the date of its retreat (Niebauer et al., 1995).

The walleye pollock–sea ice interaction is examined within three hydrographic domains on the southeastern Bering Sea shelf (Kinder and Schumacher, 1982; Fig. 1). The inner domain, with depths 50 m or less ($Z \leq 50$ m), is vertically mixed by tidal action throughout the year. The middle domain ($50 < Z \leq 100$ m) is mixed by heat loss in winter, except at the ice edge, where continuous melting produces a surface layer of low-salinity water. In summer the buoyancy flux from ice melt and heating stratifies the water column so that a less-saline surface layer extends down 20–50 meters, depending on wind conditions. The more saline bottom layer is colder and results from the previous winter's ice cover and mixing by tidal currents (Barnes and Thompson, 1938; Takenouti and Ohtani, 1974; Coachman and Charnell, 1979). The outer domain (>100 m) is a stratified system in summer and winter, influenced by water intruding onto the shelf from the Bering slope in the bottom layer, and mixed by winds in the surface layer.

In this paper, I examine interannual variation in the distribution of one-year-old walleye pollock for the period 1972–92. Discernible distribution patterns emerge over interannual and longer time periods. The amount and characteristics of seasonal sea ice also vary over such time periods and may affect the distribution of walleye pollock. I discuss the relation between summer variability in one-year-old walleye pollock distribution on the shelf and seasonal sea-ice during the preceding winter, with the intent of developing a method to predict distribution of pollock from sea-ice characteristics.

Methods

One-Year-Old Walleye Pollock

I generated distribution maps for one-year-old walleye pollock from the data base compiled by the National Marine Fisheries Service, Resource Assessment and Conservation Engineering Division, Sand Point Way N.E., Seattle, Washington. This data base (RACEBASE) contains biological data gathered from bottom trawl surveys on the Bering Sea shelf conducted by Japan, Russia, Canada, and the United States during summer months between 1972 and 1992 (Mintel and Smith, 1981). Two areas were investigated, the southeastern and the central shelves (Fig. 1). In order to maximize the time frame of the data set, I chose a core area of southeastern shelf stations that were sampled each year, beginning in 1972, for my initial data analysis. I compared a reduced data set from the central shelf area with the southeastern area to investigate intra-annual patterns in areal distribution. One-year-olds were considered to be fish with a fork length ≤20 cm.

Three domains, based on the boundaries of the inner, middle, and outer fronts, were analyzed in each area. The number of stations varied in the early years and between domains (Tables 1 and 2). Although abundance data exist for this data set, limitations arise because of the variety of ships and gear employed. As a consequence, a difference in CPUE can be a function of gear rather than a real change in abundance (Walters and McPhail, 1982; Hoff, 1989) and was not used in this study. In order to standardize the effort between areas and domains, I divided the number of stations with one-year-old walleye pollock by the total number of stations sampled each year. The resulting calculation is the percentage of stations with one-year-old walleye pollock by area and domain (Table 1, 2). The domain with the highest percentage of stations with walleye pollock was designated the domain of principal distribution for that year. If the difference between domains was <10%, both or all were considered the principal domain (Fig. 2).

Sea Ice

Data for the position of the ice edge were extracted from products of the Navy/NOAA Joint Ice Center (JIC), Suiteland, Maryland. The JIC produces a digitized data set (SIGRID) that presents the weekly concentration (areal coverage) and position of sea-ice cover. These data begin 1 January 1972. I extracted data for the position of ice with concentration of at least 30% along meridian 169°W from the SIGRID database for the period 1972–92, and verified them with the weekly ice charts for the western Arctic (Naval Polar Oceanography Center, 1986). I chose meridian 169°W to represent shelfwide ice conditions because it provides a mechanism for updating the analysis with a single data point (latitude of 30% ice cover); it lies over open water for the entire extent of the Bering and Chukchi shelves; it intersects the shelf break at the southernmost reaches of the shelf; and it borders the area sampled by the bottom trawl surveys analyzed in this study (Walters and McPhail, 1982; Walters, 1983; Fig. 1).

During a given year the seasonal pattern of ice growth and retreat can be characterized by several features. For the Bering shelf, these include (a) the number of weeks ice extended over the middle domain (ΔT_M) and (b) the outer domain (ΔT_O); (c) the southern latitude of ice extent (P_S); (d) how long ice was at this southern latitude (ΔT_S); and (e) the date of ice retreat (T_R) (Fig. 3).

Table 1

Distribution of demersal one-year-old pollock on the central Bering Sea shelf. Percentage of stations in the inner, middle, and outer domains with pollock in 1972–1992. Numbers of stations sampled in parentheses.

	Domains of the central Bering Sea shelf		
Year	Inner % (*N*)	Middle % (*N*)	Outer % (*N*)
1972	Not sampled	Not sampled	66 (3)
1973	Not sampled	64 (11)	71 (7)
1974	0 (9)	33 (18)	70 (10)
1975	46 (54)	14 (71)	18 (61)
1976	14 (21)	41 (34)	68 (28)
1977	Not sampled	73 (26)	95 (20)
1978	Not sampled	64 (53)	98 (51)
1979	37 (54)	94 (80)	98 (61)
1980	55 (53)	79 (71)	79 (48)
1981	45 (20)	77 (66)	69 (55)
1982	60 (55)	78 (80)	75 (61)
1983	69 (55)	84 (80)	76 (58)
1984	64 (55)	84 (80)	64 (61)
1985	64 (55)	38 (80)	15 (61)
1986	42 (55)	36 (80)	8 (61)
1987	11 (55)	21 (80)	10 (61)
1988	67 (55)	78 (80)	51 (61)
1989	35 (55)	88 (80)	48 (61)
1990	85 (54)	94 (80)	61 (61)
1991	82 (55)	83 (80)	72 (61)
1992	36 (39)	52 (75)	23 (60)

Table 2

Seasonal sea-ice characteristics along longitude 169°W, and the distribution of walleye pollock on the southeastern Bering Sea shelf: the number of weeks seasonal ice extended into the middle domain, the date and week when seasonal ice began to retreat northward, the southernmost extent of the winter ice, and the percentage of stations with one year-old-walleye pollock in each domain.

	Seasonal sea-ice characteristics				One-year-old walleye pollock distribution		
Year	Middle domain (weeks)	Date of retreat	Week of retreat	Southern latitude	Inner domain % (*n*)	Middle domain % (*n*)	Outer domain % (*n*)
1972	22	May 1	17	56°15'	43 (21)	82 (56)	75 (16)
1973	27	May 8	18	57°15'	4 (24)	14 (49)	70 (23)
1974	28	Apr 16	15	56°00'	21 (28)	31 (70)	41 (27)
1975	28	May 6	18	56°30'	25 (28)	44 (70)	52 (27)
1976	21	May 26	21	56°00'	21 (28)	41 (70)	44 (27)
1977	27	Apr 19	15	57°15'	0 (28)	25 (61)	0 (27)
1978	19	Mar 28	12	58°00'	11 (28)	41 (70)	19 (27)
1979	3	Mar 20	11	58°45'	82 (28)	73 (70)	85 (27)
1980	21	Mar 18	11	56°45'	61 (28)	49 (70)	13 (23)
1981	17	Mar 17	11	57°45'	29 (28)	63 (70)	15 (27)
1982	23	Mar 23	12	56°15'	43 (28)	66 (70)	56 (27)
1983	20	Mar 15	11	57°30'	36 (28)	69 (70)	22 (27)
1984	21	Apr 3	13	56°30'	46 (28)	61 (70)	19 (27)
1985	19	Apr 30	17	57°15'	75 (28)	59 (70)	11 (27)
1986	20	Apr 8	14	56°45'	43 (28)	46 (70)	19 (27)
1987	20	Apr 21	16	58°30'	29 (28)	30 (70)	0 (27)
1988	4	Apr 19	16	57°00'	43 (28)	54 (70)	19 (27)
1989	17	Apr 4	13	58°00	18 (28)	56 (70)	7 (27)
1990	14	Apr 24	16	57°15'	75 (28)	77 (70)	41 (27)
1991	14	Apr 23	16	57°00'	86 (28)	69 (70)	26 (27)
1992	16	May 13	19	56°45'	29 (28)	53 (70)	0 (27)

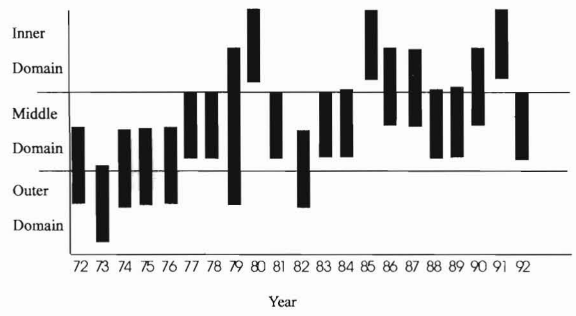

Figure 2

Principal domain(s) of distribution of one-year-old walleye pollock in the southeastern Bering shelf annually, between 1972 and 1990. When percentages of stations with pollock were within 10% in two (or all three) domains, both (or all) domains were considered to be principal domains.

The relation between ice extent and the cold bottom water in the middle domain was explored using data collected with XBT (expendable bathythermograph) probes during the groundfish surveys (Goddard and Zimmermann[3]). The southernmost position of the seasonal ice extent along 169°W was compared to the average bottom temperature (T_B) on the shelf during summer. The availability of ice data before the summer sampling season could be used to evaluate future hydrographic conditions.

Results

Sea Ice

The use of sea-ice characteristics along 169°W as an index is based on the assumption that they are representative of ice conditions over the Bering shelf. Comparison with areal ice coverage between 160°W and 180°W (Chapman and Walsh, 1993) revealed that the southernmost latitude reached by ice along 169°W is significantly correlated with ice-covered shelf area ($r = 0.91$;

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[3] Goddard, P., and M. Zimmermann. 1993. Distribution, abundance, and biological characteristics of groundfish in the eastern Bering Sea based on results of the U.S. bottom trawl survey during June–September 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent. Proc. Rep. 93-15, 324 p.

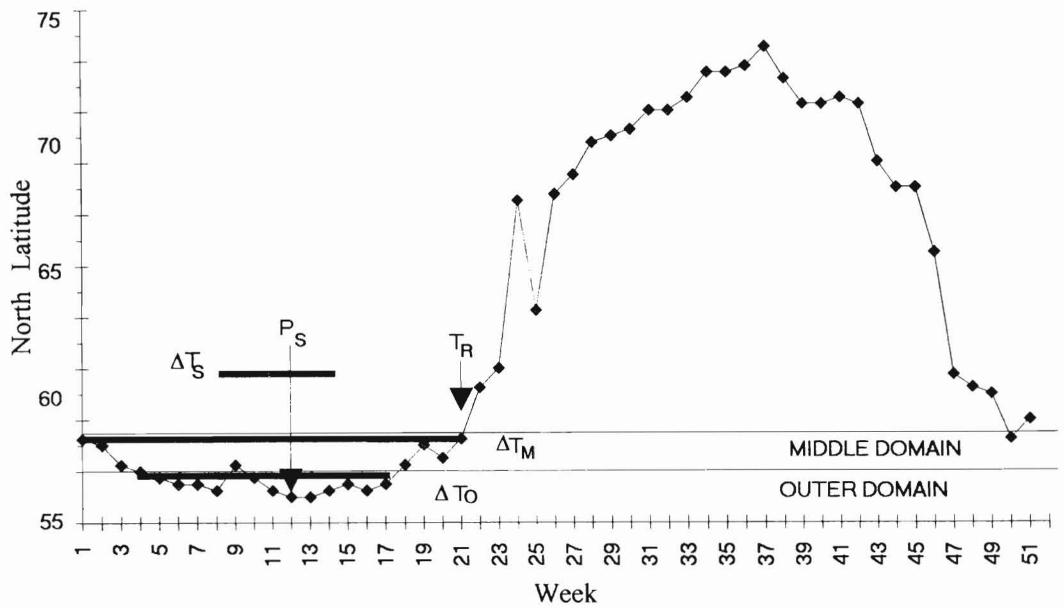

Figure 3

Weekly ice-edge positions (diamonds) along meridian 169°W in 1976. Characteristics of position and time used to describe interannual variability in seasonal sea ice in the Bering Sea are noted. ΔT_M = duration of ice extent over the middle shelf domain; ΔT_O = duration over the outer domain; P_S = the position of ice edge at the southern extent; ΔT_S = duration at the southern extent; T_R = time of ice retreat. The boundary of the middle domain is latitude 58°50'; the boundary of the outer domain is 57°00'.

$p = 0.01$). A measurement of the advance and retreat of the ice edge along one degree of longitude has the added advantage of permitting the timely updating and evaluation of sea-ice conditions from the weekly sea-ice maps. Areal calculations, in contrast, must await the release of the SIGRID data base, which is usually delayed by 2–3 years.

Juvenile Walleye Pollock

The distribution of one-year-old walleye pollock changes interannually and over longer time periods (Tables 1 and 2; Fig. 2). I investigated intra-annual relationships in the distribution of pollock to explore the possibility that the populations may shift between the southeastern and central areas. The percent distributions of one-year-old pollock, between areas and domains, for the years 1979–92 were positively correlated. I did not use the complete data set for this analysis because some areas were not sampled early in the period. Significant correlation between the southeastern and central areas and the inner, middle, and outer domains indicates that pollock are not switching domains or areas within years but rather that a shelfwide shift happens between years.

The distribution of one-year-old walleye pollock did not exhibit extreme shifts each year, but rather displayed sequences of years in which one domain had higher values (Fig. 2). Higher percentages of stations with walleye pollock occurred in the outer domain between 1972 and 1976 than in the middle or inner domains. Percentages increased in the middle domain between 1977 and 1984, and in the inner domain between 1985 and 1991. The middle shelf of the southeastern Bering shelf had the highest concentrations of one-year-olds in 81% of the years sampled.

Sea Ice and Cold Bottom Water

Sea-ice growth over the shelf is an easily observed, remotely sensed feature that offers insights into some of the physical conditions in the water column. In each year, seasonal ice extended beyond 58°30'N and covered the inner domain. In addition, ice occurred over the middle domain for as long as 28 weeks, and over the outer domain for up to 13 weeks. The beginning of its retreat varied from mid-March to the end of May (Table 2). The southern extent of sea ice ranged over two degrees of latitude, between 58°40', in 1979, to the shelf break at 56°00', in 1976.

Several trends exist in seasonal sea-ice characteristics. A marked shift in the number of weeks that ice extended over the middle domain occurred in 1979 and 1988. Ice extended over the middle shelf domain for an average of 24 weeks between 1972 and 1978, 20 weeks between 1980 and 1987, and 15 weeks between 1989 and 1992 (Table 2). Thus, periods of increasingly reduced ice cover occurred over this period, punctuated by two years of extremely light ice cover. A late ice retreat (in May) dominated the early period, followed by an early retreat (in March), and ending with an intermediate time of retreat (in April). The transitions occurred in 1978 and 1984.

The southernmost extent of ice, P_S, was significantly correlated with average bottom temperatures (r=0.74; p=0.05). The duration of ice over the middle domain and the timing of its retreat were also significantly correlated with bottom temperatures (r=–0.52 and –0.42, respectively).

The linear model

$$°\text{C (bottom water)} = P_S\,(0.76) - (40.2),$$

where °C is the average bottom temperature for the southeastern Bering shelf in summer, and P_S is the southernmost latitude reached by seasonal sea ice along longitude 169°W during the previous winter, can be used to predict average bottom-water temperatures on the southeastern Bering shelf for the following summer. The farther south the seasonal ice advances, the longer it will remain over the middle domain; thus a later retreat will result in lower bottom temperatures on the southeastern Bering shelf.

Sea Ice/ Bottom Temperature/ Pollock Interactions

The distribution of one-year-old walleye pollock on the Bering shelf varies in concert with sea-ice conditions (Fig. 4).

The linear model

$$\%\text{ (pollock)} = 1.7\,(\Delta T_M) - 84.2,$$

where ΔT_M is in weeks, and % represents the percentage of stations in the middle domain where one-year-old walleye pollock were caught by bottom trawl surveys, can be used to predict the percent distribution of one-year-old walleye pollock (r=–0.65; p=0.01; Table 3). The less time ice remains over the middle domain (south of 59°) the more one-year-old pollock will be concentrated in the middle domain (Fig. 5). When ΔT_M is greater than 24 weeks, pollock are more concentrated in the outer domain (Table 2). The year 1979 is an exception to the model; fish were distributed throughout the shelf and reflected the record year class of 1978 rather than the extremely mild ice conditions.

The average bottom temperature (T_B) in the southeastern Bering Sea is significantly correlated with the

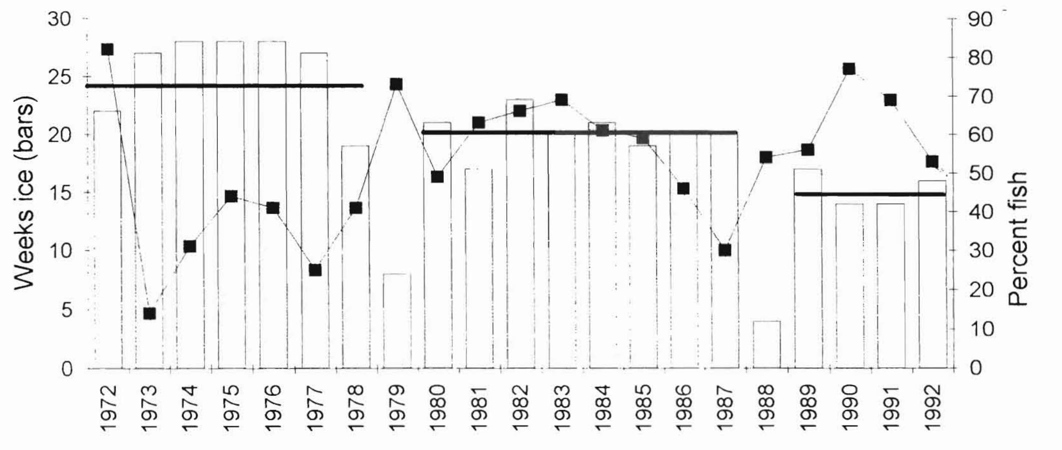

Figure 4

Number of weeks ice extended over the middle domain (ΔT_M) (bars) and the percentage of stations with one-year-old walleye pollock in the middle domain (squares). Three periods of fairly consistent ice cover (1972–78, 1980–87, and 1989–92), were punctuated by years of extremely limited ice cover.

percentage of stations with pollock in the middle domain of the central shelf area (r=0.43), but not in the southeastern area (r=0.14). About 40% of the variability of pollock distributions can be related to the variation in average bottom temperatures on the central shelf. Warmer overall bottom temperatures result in increased densities in the middle domain of the central shelf.

Seasonal sea-ice characteristics are useful indicators of conditions in the water column and of the distribution of walleye pollock the following summer. In particular, the duration of ice cover over the middle domain (between latitudes 56°45' and 59°N) is significantly correlated with bottom temperatures and with the concentration of one-year-old walleye pollock in the middle domain of the Bering shelf.

Discussion

Ebbesmeyer et al. (1991), using 40 environmental and biological variables, detected a general shift in the Pacific climate, beginning in 1977. This shift occurs in ice cover, air temperature, and sea-surface temperature in the Bering Sea (Niebauer, 1988). Another significant climatic feature occurred in 1983—one of the strongest El Niño events of this century (Hollowed and Wooster, 1992; Trenberth and Hurrell, 1994). A large shift in ground fish recruitment (including walleye pollock) has been observed in the North Pacific from the mid to late 1970s (Hollowed and Wooster, 1992), coincident with the shift in physical features that seems related to the position and intensity of the Aleutian low-pressure system (Beamish, 1993; Niebauer and Hollowed, 1993). Large-scale shifts in the North Pacific apparently extend into the Bering Sea, and the periodic variation in sea-ice characteristics and one-year-old walleye pollock distribution operates on the same time scale.

Bakkala and Alton (1986), using the same survey data as this paper for 1975 and 1979–82, observed a higher proportion of one-year-old walleye pollock in the outer shelf area in cold years (1975, 1982) and a higher proportion in the middle-inner shelf area in warm years (1979–81), indicating an interannual variation coincident with the bottom-temperature contour of 2°C. The results from the study reported here were similar for the same time period. Highest percentages of stations with walleye pollock occurred in the outer domain in 1975 (67%) and 1982 (67%), the middle domain in 1979 (96%) and 1981 (65%), and the inner domain in 1980 (68%; Table 1). Interannual variation, however, appears secondary to periods when walleye pollock are concentrated in the outer (1972–77), middle (1978–90), or inner (1983–88) domains if a longer time frame is investigated (Fig. 6).

Comparisons of year-class strength estimated from annual trawl surveys (1979–91; Wespestad and Dawson, 1993) and the distribution of walleye pollock show a significant correlation between year-class abundance and the distributional pattern of the corresponding year class in the outer (r=0.68) domain, but not the middle (r=0.16) or inner (r=0.16) domains. The outer domain is occupied when population levels are high, but the distributions on the middle and inner shelves apparently have no relation to density.

The fish examined in this paper are limited to the catches from the eastern Bering Sea bottom trawl surveys. One-year-old walleye pollock are not limited to the benthic habitat over the shelf (Bakkala and Alton, 1986), as evidenced by portions of the population lo-

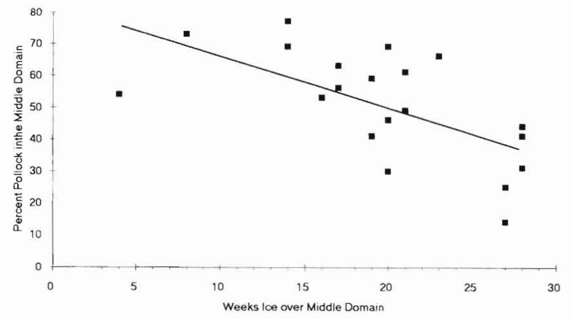

Figure 5

Linear regression between number of weeks ice extended over the middle domain and the percentage of stations with one-year-old walleye pollock in the middle domain. Correlation was significant with $r = -0.65$; $p = 0.01$.

Table 3

Prediction of population distribution based on the number of weeks ice remained over the middle domain, and the predicted percentage of walleye pollock in the middle domain of the Bering shelf. When ΔT_M is greater than 22 weeks the population increases in the outer domain.

ΔT_M (weeks)	Pollock in middle domain %
1	83
5	76
10	67
15	59
20	50
25	42
30	33

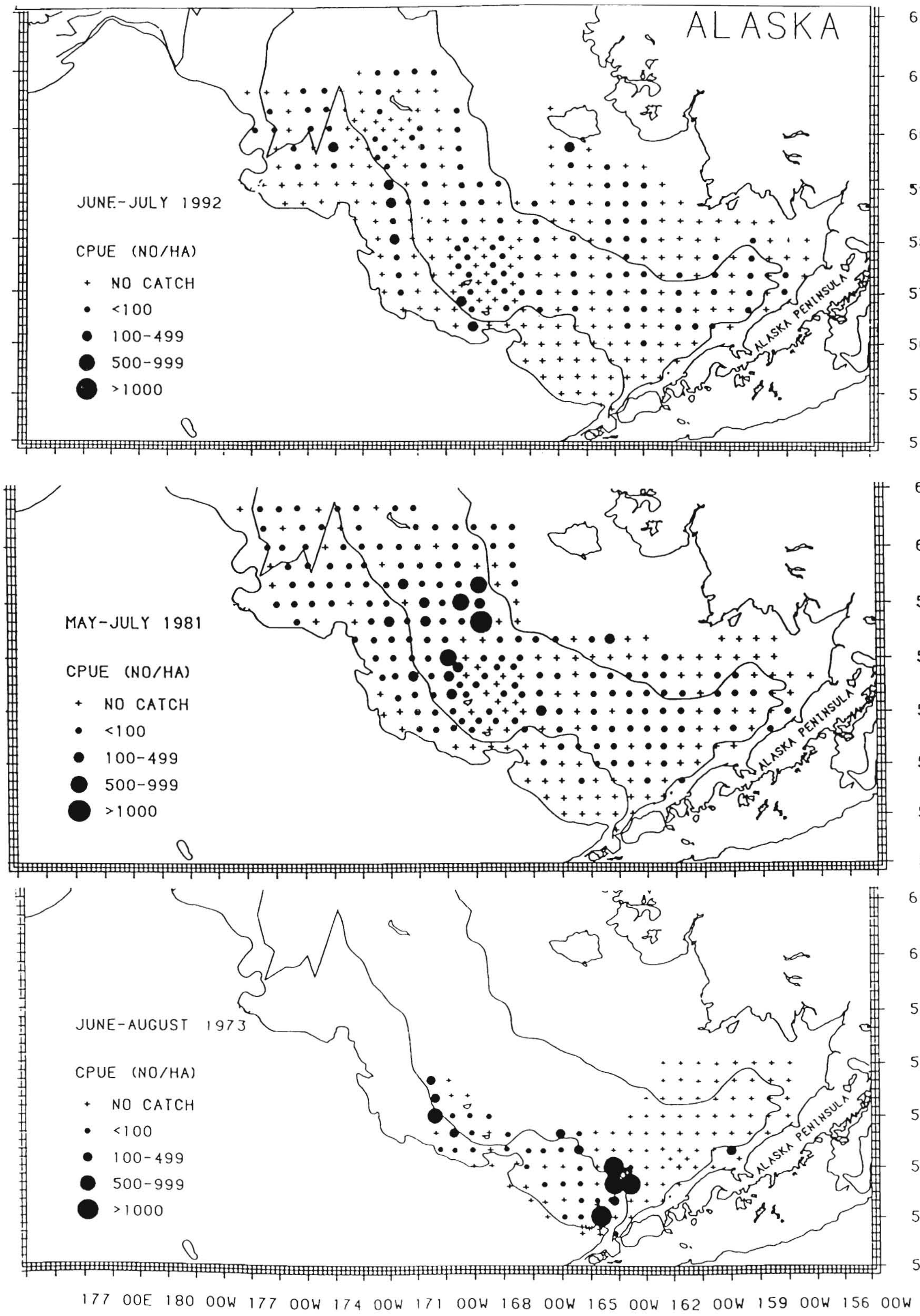

Figure 6

Distribution maps for one-year-old walleye pollock on the Bering shelf. Representative maps from the cold period (1972–78), the warm period (1979–87), and a warmer period (1988–92) are presented.

cated in midwater by acoustical surveys (Walters et al., 1988). The proportion of fish in the water column has been assessed for 1979, 1982, 1985, and 1988, and shows no consistent portion of the population in the pelagic versus the demersal habitats (Traynor et al. 1990).

In conclusion, longer periods of environmental conditions rather than interannual variability appear to affect the demersal distribution of one-year-old walleye pollock. Comparative analysis over a twenty-year period reveals a concurrent shift between areas of distribution and environmental conditions, related to warm and cool episodes. The time period examined spanned cool to warm to warmer conditions, so repeating conditions did not occur. If cool conditions reappear, as they often have in the past, one-year-old walleye pollock should shift their population to the outer domain. This shift can be predicted from the duration of ice cover over the middle domain. The outer domain appears to be a secondary habitat for one-year-olds, occupied when the middle domain is cold or crowded.

Acknowledgments

Many people contributed to this work, including those who collected and processed sea-ice data at the Joint Ice Center in Suitland, Maryland, and the species data in the RACE division at National Marine Fisheries Service in Seattle, Washington. People who directly aided in the analysis, discussion, or review of this work and whom I would like to thank are Tim Irwin, Gary Walters, Claire Armistead, Willard E. Barber, Sandy Wyllie Echeverria, Anne Hollowed, Warren Wooster, and Jim Schumacher. This work was partially funded by Mineral Management Service, U. S. Department of the Interior, Anchorage, Alaska, contract No. 14-35-0001-3-559; the Pacific Marine Environmental Laboratory, Department of Commerce, Seattle, Washington, of which it is contribution number 1552; and the Joint Institute for the Study of Atmosphere and Ocean, of which it is contribution number 268.

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Summer Distribution and Abundance of Age-0 Walleye Pollock, *Theragra chalcogramma*, in the Bering Sea

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Summer surveys of age-0 walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea were conducted in 1982, 1984, and 1985. Because of the limited spatial coverage and the paucity of trawl hauls, the survey in 1982 was viewed as a pilot survey, and few conclusions resulted. Conversely, the surveys in 1984 and 1985 covered the entire eastern Bering Sea shelf area and included enough hauls to describe the spatial distribution by size of age-0 pollock in the shelf region. The two primary objectives for the surveys were 1) to determine the feasibility of conducting acoustic abundance estimation surveys for age-0 pollock with a low-frequency echo-sounding system (38 kHz) and 2) to determine the biological characteristics and distribution of age-0 pollock on the eastern Bering Sea shelf.

In 1982, echo-integration data were collected with a Biosonics[1] Model 101 echo sounder operating at 38 kHz and a Model 120 digital echo integrator. The system's transducer was mounted in a 2-ft V fin towed behind the vessel. In 1984 and 1985, no quantitative echo-sounding system was used, but a Simrad EQ-38 echo sounder, interfaced with a JRC16 color echo-sounder recorder, was used to obtain relative abundance estimates during the surveys. Age-0 walleye pollock were sampled with a Marinovich trawl for all survey years. The codend was equipped with a 9.6-mm knotless web liner in 1982 and part of 1984, and with a 3.2-mm codend liner in 1985 and part of 1984. The vertical mouth opening of the trawl ranged from 4 to 6 m.

There was not a strong relation between numerical catch per unit of effort (CPUE) of age-0 walleye pollock and acoustic density determined by echo integration. Also, there was not a strong relation between the total weight of the catch and acoustic density. Both results are probably due to the small size of these organisms relative to the acoustic wavelength at 38 kHz (about 40 mm).

The CPUE indicated a center of abundance of age-0 pollock in the vicinity of the Pribilof Islands in each of the three surveys. In 1984 and especially in 1985, a second peak of abundance was observed in the inner Bristol Bay area (Fig. 1). Intermediate to high densities were observed in the Bristol Bay area at approximately 164°W. In general, CPUE's were higher in 1985 than in 1984; the highest was near the Pribilof Islands.

Distribution by size was similar between 1984 and 1985: age-0 pollock (>50 mm fork length, adjusted to size at August 1, assuming a growth of 0.5 mm/d) were found only in the vicinity of the Pribilof Islands, while smaller fish were found throughout the survey area. A closer examination of the size composition in 1985 reveals that the distribution of age-0 pollock by size is fairly complicated (Fig. 2). Up to three size modes were observed at trawl locations, and two modes were very common. The inner Bristol Bay area had modal fish lengths in the 20–30-mm or 30–40-mm size range. On the outer shelf area southeast of the Pribilof Islands, size modes were observed in two categories: 30–40 mm and 50–60 mm. In the vicinity of the Pribilof Islands, size modes ranged from 20 to 60 mm. In the extreme northern portion of the area, most fish were in the 20–40-mm modal size range.

Although it is not possible to determine the spawning date accurately, it is possible to approximate the spawning time with a number of assumptions. Assuming 1) approximately 20 days from egg release to hatching, 2) that the fish reach 20 mm after about 60 days, and 3) that the growth rate is approximately 0.5 mm/d after 60 d, the spawning period associated with each mode discussed above can be estimated as May 1 for 25-mm fish, April 10 for 35-mm fish, March 20 for 45-mm fish, and March 1 for 55-mm fish. The calculations assume that the growth rate of the age-0 pollock is constant and unaffected by environmental conditions (temperature) or food availability, which is almost certainly not true. However, the calculations provide an

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[1] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

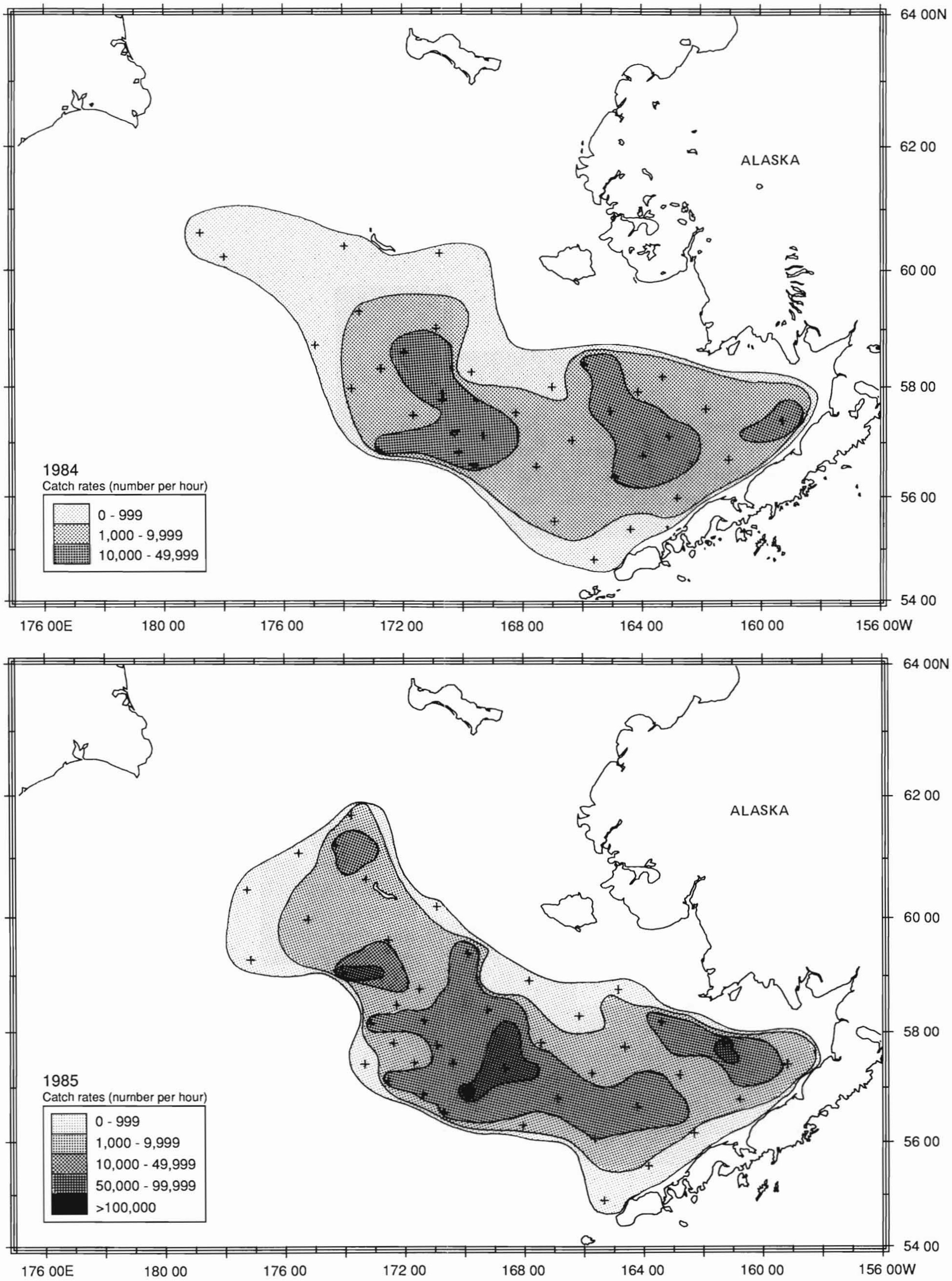

Figure 1

Catch-rate distributions for age-0 walleye pollock in the eastern Bering Sea during 1984 (upper) and 1985 (lower). Catch rates are in number per hour. The plus signs indicate Marinovich haul locations.

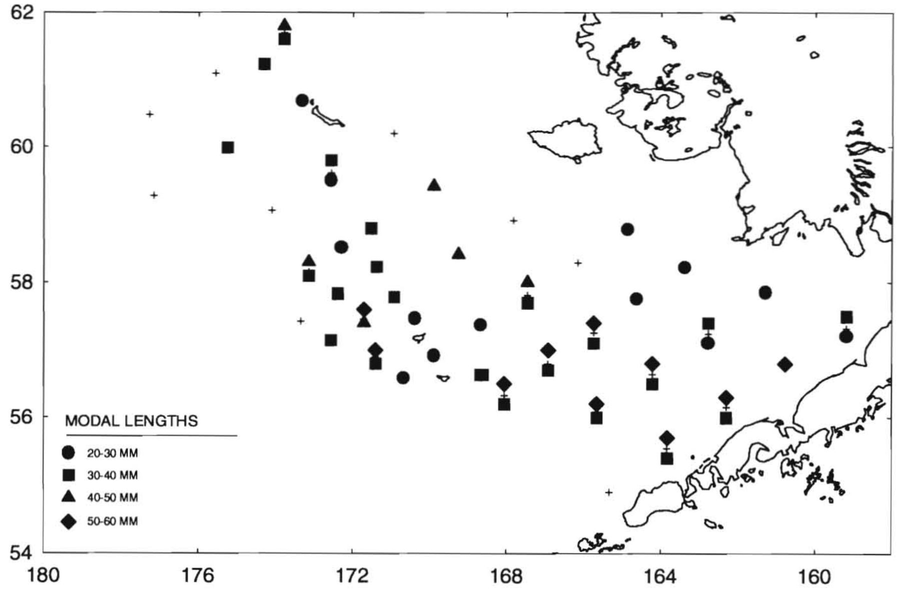

Figure 2

Modes of length frequency for age-0 walleye pollock in 1985. All length frequencies were adjusted to August 1, assuming a growth rate of 0.55 mm/d. The plus signs indicate Marinovich haul locations.

indication of the range of spawning periods probably represented by age-0 pollock on the eastern Bering Sea shelf.

The spawning time of pollock is known fairly accurately only for the Bogoslof population, where essentially all spawning occurs in very late February or early March. There are three areas of spawning in the eastern Bering Sea: near Bogoslof Island, near Unimak Island, and in the vicinity of the Pribilof Islands. Spawning appears to occur in April near Unimak Island and in April or somewhat later near the Pribilof Islands. The above scenario indicates that the larger size modes would come from the Bogoslof spawning group, whereas the smaller size groups would result from spawning on the shelf. The presence of the larger size modes near the shelf and in the vicinity of the Pribilof Islands is consistent with the known current pattern, based on drift-buoy trajectories, which would distribute pollock from near Bogoslof Island onto the eastern Bering Sea shelf in the vicinity and to the south of the Pribilof Islands.

Distribution of Early Juvenile Walleye Pollock, *Theragra chalcogramma*, and Associated Species in the Gulf of Alaska

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A midwater trawl survey was conducted in July 1991 to examine the large-scale distribution pattern of late larval and juvenile walleye pollock, *Theragra chalcogramma*, and associated fish taxa in the western Gulf of Alaska. Gear comparisons between the anchovy and Methot trawls were done to evaluate which sampling trawl was most efficient at capturing the size range of walleye pollock available during this time of the year. Both gears caught similar length distributions in the dominant size class of pollock caught, but the Methot trawl caught significantly more walleye pollock in the smallest (mostly larval) size classes and had higher standardized catches overall. Based on these results, a grid of 60 stations was sampled with the Methot trawl only.

Although 64 taxa of fishes were collected overall, most (84%) of the larval catch consisted of just five taxa (flathead sole, *Hippoglossoides elassodon*; walleye pollock; arrowtooth flounder, *Atheresthes stomias*; Pacific cod, *Gadus macrocephalus*; and sculpins, *Icelinus* spp.). Walleye pollock and Pacific cod were the dominant (>99%) juveniles collected in the survey. The highest catches of juvenile walleye pollock (26–52 mm standard length) were from midshelf waters along the Alaska Peninsula and near the Shumagin Islands. Recurrent group analysis and two-way indicator species analysis both showed that juvenile pollock were frequently associated with a large, heterogeneous grouping of larval and juvenile fishes, including Pacific cod, flathead sole, arrowtooth flounder, and other winter–spring spawning species. The abundance rankings of the dominant fishes from the Methot trawl survey were more similar to the abundance rankings of adults from trawl surveys the previous summer than were those of an ichthyoplankton survey that used bongo nets several months before the Methot survey.

Size-Related Depth Distribution of Juvenile Walleye Pollock, *Theragra chalcogramma*, in the Western Gulf of Alaska during 1984–1990

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Analysis of a subset of the juvenile walleye pollock, *Theragra chalcogramma*, length and abundance data collected by the Resource Assessment and Conservation Engineering (RACE) division of the National Marine Fisheries Service (NMFS) suggests that a size-related depth distribution exists within age groups. The bottom (n=97) and midwater (n=336) trawl hauls we examined were collected during daylight from August to early October from 1984 to 1990 in the western Gulf of Alaska. Our data indicate that hauls where the average size of age-0 pollock was about 60 mm fork length (FL) were made from 20 to 160 m. However, hauls with an average age-0 pollock size of 100 mm FL were made at deeper depths (80 to 240 m). High abundances of age-0 pollock were found at depths of 120 m or less both on bottom and in midwater, but individuals were found down to 250 m. No differences in size were found between age-0 pollock collected on bottom and those collected in midwater. Regardless of whether they are on bottom or in midwater, age-0 pollock tend to undergo an ontogenetic migration into deeper water. The influences of region and temperature on the size distribution of juvenile pollock were also explored.

Juvenile Walleye Pollock, *Theragra chalcogramma*, Distribution and Association with Other Dominant Species in the Gulf of Alaska

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The main purpose of our study was to identify areas of juvenile (ages 0 and 1) walleye pollock, *Theragra chalcogramma*, habitat and key species associated with juvenile pollock in the Gulf of Alaska as a preliminary step in modeling how environmental and fishing variability affects juvenile pollock distribution and, in consequence, foraging by Steller sea lions, *Eumetopias jubatus*.

We explored the vertical distribution of juvenile pollock collected on select NMFS cruises. Three years (1973, 1982, and 1986) of the NMFS groundfish and shrimp trawl surveys were selected because they spanned the late 1970's, when the North Pacific experienced a well-documented regime shift from cool to warm waters. Juvenile pollock were divided into two size classes that roughly represent age groups. Juveniles <150 mm (age 0) were caught at slightly greater bottom depths than pollock from 150 to 230 mm (age 1) in 1973, but this trend was reversed in 1982 and 1986. This finding could have been confounded by the fact that two different gear types were used between 1973 and the 1980's. In general, pollock were caught at greater depths in the Shumagin Islands than around Kodiak Island. When additional data from only one gear type (high-opening shrimp trawl) from 1984 to 1990 were examined, both age groups of pollock were distributed throughout the water column. Their widespread distribution could be related to the warm water temperatures measured at the surface (>9°C) and at bottom (>7°C).

Comparison of the NMFS bottom trawl surveys of the Chirikof region in 1975, 1984, 1987, and 1990 revealed that, although the dominant groundfish species remained the same, the relative abundance of each species changed from 1975 to 1990. In 1975, walleye pollock represented 69%, and arrowtooth flounder, *Atheresthes stomias*, represented only 10%, of the groundfish trawl biomass in the Chirikof region. By 1990, arrowtooth flounder represented 53% and walleye pollock represented only 10% of the groundfish trawl biomass in this region.

Interspecies associations were examined through a clustering technique (Bray-Curtis method) used on the shrimp-trawl data. Pollock <150 mm were often found in association with other nearshore species such as Pacific herring, *Clupea pallasi*, and capelin, *Mallotus villosus*, until the early 1980's. This smaller size class of juveniles was not found together with adult pollock until the mid-1980's. Pollock between 150 and 230 mm were found with adults from 1980 and were mostly associated with more benthic-oriented species. This transition in species associations could result from juvenile pollock moving to adult pollock habitat or from adults moving into the nearshore areas commonly inhabited by juveniles. The latter hypothesis is consistent with trends in the distribution of age-1 fish before and after the climate shift.

Distribution and Abundance of Juvenile Walleye Pollock, *Theragra chalcogramma*: Summary and Recommendations for Future Research

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Research to date provides a somewhat fragmented picture of juvenile walleye pollock distribution, largely because most existing information is based on incidental catches made during bottom trawl or acoustic/midwater trawl surveys for other species or age groups. The surveys described in this symposium by Wilson et al. and Traynor and Smith were the only ones designed with the principal objective of examining the distribution and abundance of juvenile pollock (age-0 in this case).

Nevertheless, the information presented during this symposium serves to demonstrate that juvenile pollock are found in significant concentrations in both the midwater pelagic zone (Tang et al., Wilson et al., McKelvey) and on the seabed (Wyllie-Echeverria, Miyake et al., Wilson et al.). The use of these habitats may vary within years, because of ontogenetic changes in preferred habitat (Miyake et al., Wilson and Shima), and between years, because of environmental variability (Wilson et al., Wyllie-Echeverria).

Miyake et al. reported that walleye pollock larvae and juveniles (4–38 mm long) were distributed mainly in the surface layer along the coast of southeastern Hokkaido. Juveniles migrate offshore as they grow, and move to the bottom layer. Off southeastern Hokkaido, juveniles 50–150 mm long are found in significant numbers in waters 40–100 m deep, where they can be captured with a demersal trawl.

Wyllie-Echeverria demonstrated that the spatial distribution of 1-year-old pollock in the eastern Bering Sea shifted significantly during 1972–90, partly because of interannual changes in ice coverage and its influence on environmental conditions (surface temperature, bottom temperature, salinity structure, timing of the phytoplankton bloom, etc.).

During their survey of the western Gulf of Alaska, Wilson et al. found that most age-0 fish (averaging 70 mm long) occurred in midwater over the middle and inner continental shelf, whereas previous investigators encountered high abundances offshore near the 200-m isobath, or near the seabed in embayments.

The papers presented at this symposium also indicated that juvenile surveys may eventually provide reliable forecasts of year-class strength. McKelvey found a significant correlation (r^2=0.58) between the abundance of age-1 pollock in Shelikof Strait and Gulf of Alaska stock assessment estimates from the same year class 2 years later. Miyake et al. were less successful (r^2=0.21) in predicting year-class strength from the abundance of age-0 juveniles in trawl surveys off southeastern Hokkaido, probably because the survey area (designed for smelt assessment) did not cover the entire range of this age group in some years.

The vertical and spatial distribution of juvenile pollock appears to be quite plastic, resulting from an interplay of many factors (e.g., temperature, light, food, and predation). Combined midwater trawl/acoustic and demersal trawl surveys are required to provide a holistic picture of the distribution of juvenile pollock, and—at least during the initial years of survey development—they must extend over a broad geographic area. Improved surveys of juvenile pollock are essential if we are to gain a significant understanding of their basic ecology (distribution, feeding, mortality processes, etc.) and the factors that determine year-class strength.

Feeding Habits and Daily Ration of Juvenile Walleye Pollock, *Theragra chalcogramma*, in the Western Gulf of Alaska

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ABSTRACT

The stomach contents of age-0 walleye pollock, *Theragra chalcogramma*, collected in the western Gulf of Alaska during September of 1990 were examined to determine diel feeding patterns and variations in feeding habits with respect to time of day, fish size, and geographic area. Most (90%) of the 549 fish examined (length range 49–113 mm standard length) had food in their stomachs, with an overall median fullness of 1.6% body weight (BW). Juvenile pollock fed mainly at night, with stomach fullness and prey condition declining throughout the daylight hours. Daily ration was estimated to range from 7.4% to 8.5% BW/d based on the diel trajectory of stomach content weight.

The dominant prey by number were larvaceans and copepods (copepodites and adults), whereas euphausiids were the dominant prey by weight, constituting >80% of the total biomass consumed. Despite some apparent trends in the diet with size of predator (i.e., copepods gradually decreased and larvaceans and euphausiids increased in importance with increasing size of pollock), there did not appear to be an abrupt ontogenetic shift in the diet of these juveniles. However, there were major changes in the diet depending on geographic area. Stomach samples collected near Kodiak Island contained mainly euphausiids, whereas those collected in the western part of the study area contained large numbers of larvaceans. There was no discernable pattern in the type of prey consumed at different times of day.

Introduction

In 1980 a large spawning population of walleye pollock, *Theragra chalcogramma*, was discovered in Shelikof Strait, Gulf of Alaska, and soon became the object of an intense multinational fishery (Megrey, 1991). Most Gulf of Alaska pollock migrate into the strait in late winter and spawn in deep water (Kendall and Picquelle, 1990; Kim and Nunnallee, 1990). The eggs hatch in mid-April, and larval patches are transported southwest to nursery grounds along the Alaska Peninsula (Hinckley et al., 1991; Wilson et al., 1996). To better understand the processes critical to the survival of pollock, investigators continue to study both the biotic and abiotic factors that may influence year-class success (Schumacher and Kendall, 1991).

If survival during the first summer and fall is crucial to recruitment of age-2 fish to the fishery, as shown for some years by Bailey and Spring (1992), then it is important to learn more about their early life history beyond the larval stage. Fish that survive to the juvenile stage have passed through critical larval stages where starvation is thought to be a major cause of mortality. Though juvenile fish do not appear to be as susceptible to starvation as larvae are, the amount and quality of food available may affect their growth rate and distribution, and ultimately their survival (Walline, 1983).

Owing to walleye pollock's considerable commercial and trophodynamic importance in the North Pacific Ocean (Springer, 1992), many studies have examined the predator–prey relationships of their early life stages. Although the feeding habits of young walleye pollock have been described in detail (Kamba, 1977; Walline, 1983; Clarke, 1984; Krieger, 1985; Lee, 1985; Kendall et al., 1987; Nakatani and Maeda, 1987; Grover, 1990, 1991; Takatsu et al., 1992), most of these studies have dealt with populations outside the Gulf of Alaska or

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have examined only early juvenile pollock (<30 mm standard length) collected over a small geographical area. At present, the only available studies on food habits of late juvenile age-0 pollock in the Gulf of Alaska ecosystem are those of Walline (1983), Krieger (1985), and Livingston[2] but these studies had a limited sampling size and in each case, the fish were taken over a relatively restricted area of the gulf. If feeding in the juvenile stage is linked to vertical and horizontal distribution patterns and ultimately to survival, then the knowledge gained from this study may prove useful in answering questions about juvenile pollock's migratory behavior and recruitment success.

The objectives of this study are fourfold: 1) to describe the diel feeding chronology of age-0 juvenile walleye pollock in the western Gulf of Alaska; 2) to estimate daily ration based on diel changes in stomach fullness; 3) to describe the prey of juvenile walleye pollock; and 4) to examine changes in prey with respect to time of day, fish size, and geographical area. These results are discussed in light of what is presently known about the trophodynamics of juvenile pollock in the Gulf of Alaska and elsewhere in the North Pacific Ocean.

Materials and Methods

Sample Collection and Processing

Age-0 pollock were collected during 6–23 September 1990 aboard the NOAA vessel *Miller Freeman* in the western Gulf of Alaska (Table 1; Fig. 1). Several different gear types and fishing strategies were employed to investigate the distribution and catchability of age-0 pollock (Wilson et al., 1996). Most hauls were made in midwater along a grid of stations set up along the Alaska Peninsula, but opportunistic midwater and near-bottom tows were also made in order to identify acoustic sign and to sample inlets around Kodiak Island and

Table 1

Summary of haul collections used for age-0 walleye pollock feeding study. Lengths are means and standard deviations (in parentheses) of fish whose stomachs were examined.

Haul number	Geographic region	No. of stomachs	Standard length (mm)	Collection date	Time (ADT)
6	I	26	80.58 (1.19)	8 September	1119
7	I	20	81.21 (1.72)	8 September	2142
8	I	20	90.86 (2.46)	8 September	2340
15	II	20	59.60 (1.28)	9 September	1710
25	II	20	74.90 (1.23)	10 September	1840
26	II	20	70.70 (1.97)	10 September	2025
31	II	20	73.81 (2.02)	11 September	0642
34	II	20	72.74 (1.58)	11 September	1143
35	II	20	70.40 (1.95)	11 September	1307
49	II	20	72.59 (1.12)	13 September	1917
50	II	20	70.24 (1.56)	13 September	2045
71	III	20	73.62 (1.66)	14 September	0959
73	III	20	72.68 (1.80)	14 September	1124
95	III	21	80.20 (1.74)	16 September	1129
98	III	20	75.24 (2.30)	16 September	1803
100	III	20	69.98 (1.51)	17 September	0152
111	II	20	76.63 (2.38)	18 September	0245
112	II	20	81.02 (2.15)	18 September	0432
113	II	20	79.26 (1.94)	18 September	1031
114	II	20	78.22 (1.79)	18 September	1137
117	II	21	76.88 (1.65)	18 September	1750
120	II	21	87.96 (2.96)	19 September	2046
121	II	20	78.93 (1.72)	19 September	2132
122	II	20	81.33 (1.65)	20 September	0013
123	II	20	94.86 (1.41)	20 September	0200
124	II	20	73.68 (1.44)	20 September	2318
136	III	20	76.21 (1.67)	22 September	0533

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[2] Livingston, P. A. 1985. Summer food habits of young-of-the-year walleye pollock, *Theragra chalcogramma*, in the Kodiak area of the Gulf of Alaska during 1985. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. manuscript.

other areas (see DeWitt and Clark[3] for station locations and sampling chronology). The primary midwater gears used were an 18.6-m high-opening shrimp trawl and a 24.4-m anchovy trawl, which both contained 3-mm mesh liners (Wilson et al., 1996). Tows were made throughout the water column in either an oblique or stepped-oblique fashion at an average ship speed of 5.9 km/h. Near-bottom juveniles were sampled with a 37-m Nor'eastern bottom trawl fitted with a 5-mm mesh liner. Collections at any particular station were not predetermined as to time of sampling, except for five repeat tows made at the same station over a span of 15 h (termed the semidiel study).

After retrieval of the nets, juvenile pollock were quickly sorted from the catch, counted, and measured. Age-0 fish were easily differentiated from older age classes by length distributions; a subsample (a minimum of 20) of these fish was placed in buffered 10% formalin or 90% ethanol. These fish were approximately 110-140 d old (Brown[4]).

Because we were interested in characterizing the feeding habits of the main component of the age-0 population and wished to maintain a minimum sample size

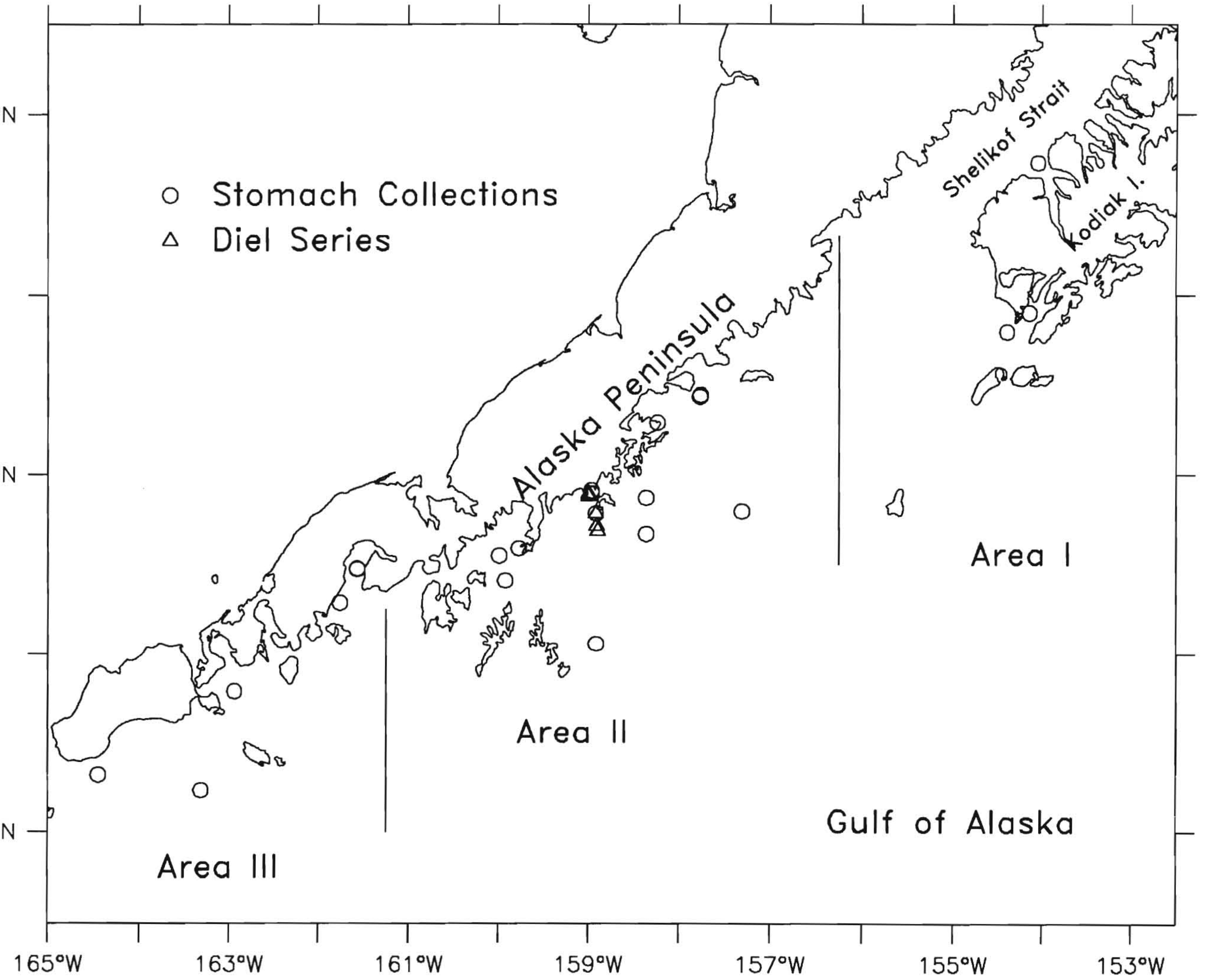

Figure 1

Locations where stomach collections were made in the western Gulf of Alaska during September 1990. The regular collections are shown as circles and the diel collections are shown as triangles. Also shown are the three areas examined for geographic variability in food habits.

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[3] DeWitt, C., and J. Clark. 1992. Fisheries-Oceanography Coordinated Investigations Shelikof Strait: 1990 field operations. NOAA Data Rep. ERL PMEL-39, 98 p.

[4] Brown, A. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. data.

per station ($n \geq 20$), we chose fish only from stations where large numbers of juveniles were caught. Age-0 pollock were examined from samples collected over a broad geographic area to examine regional differences in diet (Fig. 1). In the laboratory, 20 age-0 pollock were haphazardly chosen from the preserved samples. Fish were measured to the nearest millimeter (standard length; SL) and weighed to the nearest 0.001 g, and the stomach (from the esophagus to pylorus) was excised. Relative fullness of the stomach was visually ranked on a scale of 0 to 5 as follows: 0 = empty; 1 = trace amount of food; 2 = 25% full; 3 = 50% full; 4 = 75% full; and 5 = 100% full. The entire stomach contents were then blotted on blotting paper to remove excess moisture and weighed to the nearest 0.001 g.

The stomach contents were separated under a dissecting scope. The relative condition of the contents was determined on a scale of 0 to 4, ranging from totally digested to fresh prey. Gut contents were identified only to major taxonomic category (order). Each taxon was enumerated and weighed individually for every stomach.

Data Analysis

To examine variations in feeding intensity, we calculated the percent body weight (%BW) of the total stomach content weight (wet weight in grams) for each fish:

$$\%\mathrm{BW} = \frac{(\text{stomach content weight } \times 100)}{(\text{total body weight} - \text{stomach content weight})}.$$

For indices to characterize the time of day when age-0 pollock feed, we used 1) %BW, 2) fullness code, 3) digestion code, and 4) percentage of stomachs containing at least some food. Collection times were grouped into 4-h intervals to examine diel variation at smaller increments of time. Because of the highly skewed nature of the %BW values and the number of empty stomachs, we chose to use the median values and to test for differences using nonparametric statistics. Diel differences in feeding intensity among time intervals were tested with a Kruskal-Wallis one-way nonparametric analysis of variance (ANOVA). When significant differences were observed, we performed an a posterori pairwise test of adjacent intervals using a Mann-Whitney *U*-test to determine the time period in which the changes occurred (Zar, 1984). To minimize the effects of geographic variability, we used the same analyses to separately examine stomachs collected during the five hauls (Stations 111–117 in Table 1) at different times but at the same location (semidiel series).

Daily ration (R_d) was estimated from the diel trajectory of stomach content weights following the approach of Sainsbury (1986). We fitted two models to the median values of %BW for each collection period using a nonlinear least-squares iteration as implemented by the MAXIMS program (Jarre-Tiechmann, 1992). The first (Model I) assumes that the ingestion rate is constant, whereas the second (Model II) assumes that it is linearly related to stomach contents (see Sainsbury, 1986 and Jarre et al., 1991 for derivation of the two models). Assuming a single feeding period per day, Model I is defined as

$$R_d = \int_{t=F_b}^{t=F_s} J dt = J(F_s - F_b),$$

where F_b is the time at which feeding begins, F_s is the time feeding stops, and J is the ingestion rate (%BW/h). Model II contains an additional parameter (S_∞) to specify an asymptotic consumption level:

$$R_d = \int_{t=F_b}^{t=F_s} \left[S_\infty * (E - J2) - J2 * S_t\right] dt,$$

where E is the instantaneous rate of evacuation (per hour), $J2$ is the instantaneous rate of ingestion (per hour), and S_t is the stomach contents at time t (Jarre et al., 1991). Both models assume an exponential evacuation rate, which has been observed for older juvenile and adult walleye pollock in laboratory experiments (Dwyer et al., 1987; Smith et al., 1989). These models have been shown to provide similar estimates to those from the frequently applied Elliott and Persson (1978) model, but they do not require independent estimates of evacuation rate.

The total collection of fish, including those from the diel series, was grouped into several subsets to examine variability in diet composition. The percent numerical and percent gravimetric composition were used to characterize the diet composition by three factors: area, predator size, and time of day. Trends in dietary variability by geographic area were examined by dividing the collection into three areas (Fig. 1) designated as Area I (Kodiak Island), Area II (east of Shumagin Islands), and Area III (west of Shumagin Islands). To examine dietary variability by predator size, we divided the entire range of available age-0 pollock lengths into six size categories (<60 mm, 60–69 mm, 70–79 mm, 80–89 mm, 90–99 mm, and >100 mm). Finally, to examine diel changes in major prey taxa consumed, we grouped the collection into three time periods: day (0930–1930 ADT), twilight (1930–2220 and 0700–0930), and night (2220–0700). Differences in the presence or absence of major prey taxa among these subsets were compared individually for each factor (area, size, and time of day) using the variance test of binomially distributed data. For tests that exceeded the tabulated 0.05 χ^2 value, we rejected the null hypothesis of similar diets (Snedecor and Cochran, 1967). Because of the large number of empty cells, we were not able to test for interaction effects among these factors. Finally, to quantify absolute changes in the biomass of the major prey groups among the different times of day, areas, and size classes, we also examined the mean weight of prey consumed at each level within each of the factors.

Results

Because the highest catches of age-0 fish occurred in Area II (Wilson et al., 1996), most of our age-0 fish stomachs were collected in this area (Fig. 1). Age-0 pollock examined for the feeding habits study showed a similar length-frequency distribution to those from the overall September 1990 survey (Wilson et al., 1996). No significant differences in size composition existed between the three areas (Kolmogorov-Smirnov test corrected for multiple tests).

Feeding Intensity

The relation between size of fish and %BW consumed was examined because size-related variability may be an important factor in the analyses that follow. We tested the null hypothesis that %BW was not a function of fish size. We regressed fish size (standard length in millimeters) on %BW, and found that the slope of the relationship was not significant ($P>0.50$); therefore, the meal size appears to increase isometrically with fish size.

A wide distribution of %BW values was observed (Fig. 2), with a median stomach fullness of 1.64%BW. The distributions of values for each area were highly heteroscedastic, including relatively few extreme values, especially in Area III (Fig. 2), but the distributions were not significantly different among areas (Kolmogorov-Smirnov test).

Box plots of the values of the feeding-intensity parameters for different 4-h periods of the day for the entire data set revealed that prey condition (digestion code) was the freshest at night, with a median value of 2.5 at 0200 (Fig. 3a). The overall trend suggested that prey condition decreased as the day progressed, with the lowest

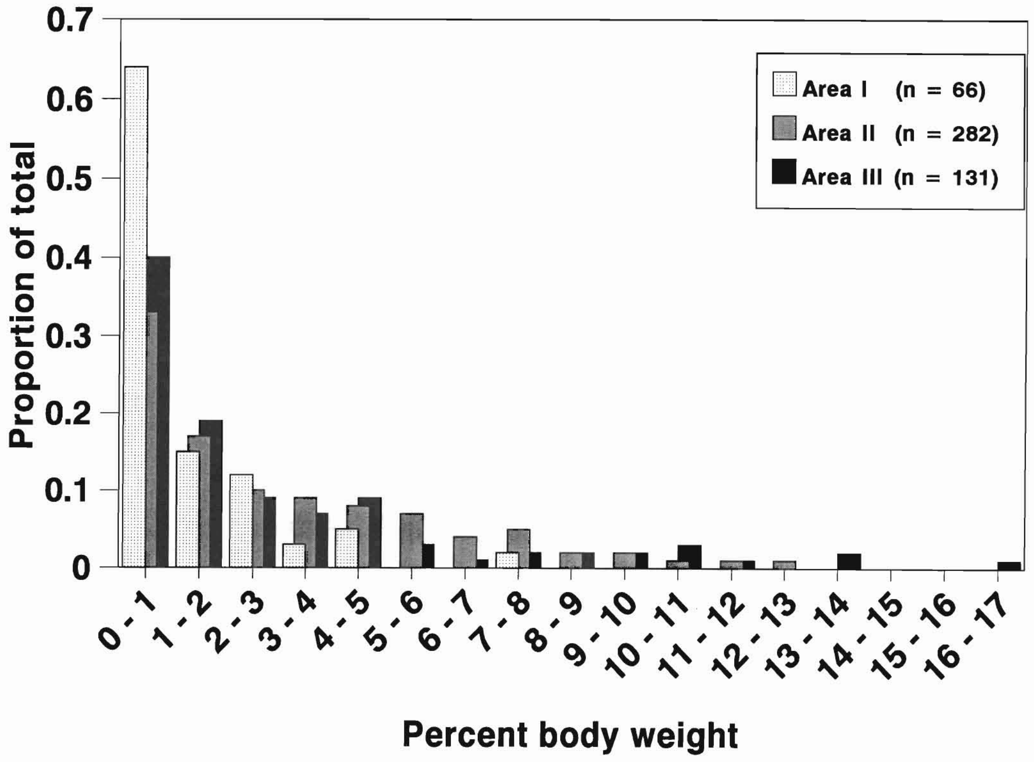

Figure 2
Distributions of relative stomach content weight (as percent body weight, %BW) of juvenile walleye pollock in each area analyzed. Also given is the number of stomachs included in each area (N).

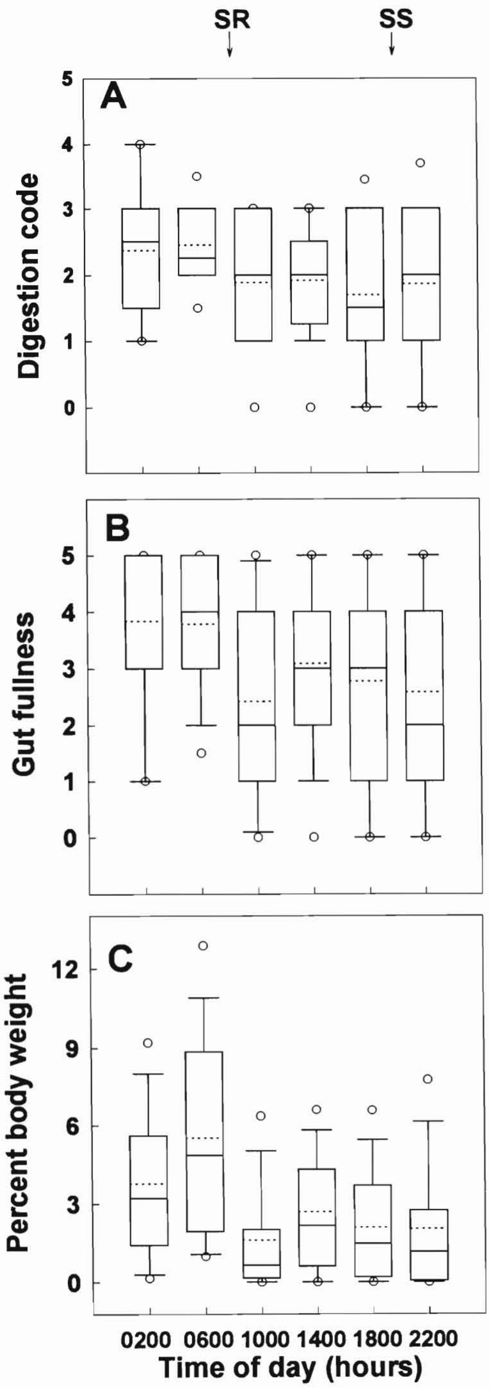

Figure 3
Box plots of (A) digestion code, (B) gut fullness, and (C) percent body weight versus time of day. Diel sampling was binned into 4-h periods and is represented by the midpoint of the period. The solid lines indicate 25th, 50th, and 75th percentiles. Error bars mark 10th and 90th percentiles. Dotted lines indicate mean values. Circles represent 5th and 95th percentiles. Sunrise (SR) was at 0815 and sunset (SS) at 2015.

median value of 1.5 in the period just before dusk (1600–2000). Overall differences in prey condition by time were significant (Kruskal-Wallis test, *H*=56.46; *P*<0.001). Significant pairwise differences in ranked sums occurred between time periods 2 and 3 (0400–0800 and 0800–1200) and 3 and 4 (0800–1200 and 1200–1600; Table 2).

Gut fullness was highest at night, with a median fullness of 5 (Fig. 3b). The gut fullness decreased as the day progressed, with lowest values at 1000 and after dusk (2000). We rejected the hypothesis that gut fullness was equal at different times (*H*=34.50; *P*<0.001). Significant differences in gut fullness detected by a posteriori comparisons were found between 0400–0800 and 0800–1200 and between 0800–1200 and 1200–1600 h (Table 2).

The %BW of stomach contents demonstrated a trend similar to that of gut fullness. The highest values were recorded just before dawn (0400–0800) and decreased as the day progressed (Fig. 3c). The hypothesis that %BW was equal at the time periods examined was rejected (*H*=31.46; *P*<0.001). Subsequent pairwise Mann-Whitney tests indicated that periods 1 and 2 (0000–0400 and 0400–0800), 2 and 3 (0400–0800 and 0800–1200), and 3 and 4 (0800–1200 and 1200–1600) had significantly different %BW values (Table 2).

The semidiel study showed trends similar to those seen in the overall survey (Fig. 4). Median prey digestion was highest at night (0200) and decreased over time. Gut fullness and %BW values were highest at night and decreased steadily until the last sampling at 1745 (Fig. 4). Ranked values for all three feeding-intensity parameters were unequal for all times tested (Kruskal-Wallis test; *P*<0.001 in all cases; Table 3). Pairwise differences in gut fullness were found between time periods 1 and 2 (0245 and 0445) and between periods 4 and 5 (1215 and 1745). Prey-digestion codes showed significant decreases in every pairwise test except for time periods 3 and 4 (1000 and 1200). In contrast, only one significant difference in %BW occurred; it fell between time periods 4 and 5 (1215 and 1745; Table 4).

Median values of %BW were quite variable, especially for the times following peak feeding (Fig. 5). Estimates of daily ration for the two models were 8.45% and 7.37%BW per day for Model I and Model II, respectively (Table 5), at an in situ temperature range of 6–10°C (Wilson et al., 1996). Although both models gave virtually identical fits to the data based on lower mean squared residuals values (Table 5), Model II showed a better fit at the beginning and end of the feeding periods, as well as smaller residuals (Fig. 5).

Overall Diet Composition

Larvaceans (mostly *Oikopleura* spp.) were the most important prey numerically, constituting 67.7% of walleye

Table 2

Results of the Mann-Whitney *U*-test for differences in feeding intensity between adjacent time intervals throughout a 24-hour period. The data are from the whole survey, including the semidiel study.

Time intervals	Gut fullness	Digestion code	Percent body weight
0000–0400 and 0400–0800	$U = 2612$ $P = 0.345$	$U = 2307$ $P = 0.685$	$U = 1820$ $P = 0.015$
0400–0800 and 0800–1200	$U = 4752$ $P < 0.001$	$U = 4168.5$ $P = 0.001$	$U = 5354.5$ $P < 0.001$
0800–1200 and 1200–1600	$U = 2397.5$ $P = 0.007$	$U = 3134$ $P = 0.873$	$U = 2227$ $P = 0.001$
1200–1600 and 1600–2000	$U = 3330.5$ $P = 0.285$	$U = 3501$ $P = 0.090$	$U = 3488$ $P = 0.109$
1600–2000 and 2000–2400	$U = 7604.5$ $P = 0.415$	$U = 6437.5$ $P = 0.163$	$U = 7680.5$ $P = 0.344$

pollock stomach contents (Fig. 6). These were followed by copepods (19.9% by number) and euphausiids (10.7%). Other components of age-0 pollock diet included fish larvae, decapods (mostly crab megalopae), chaetognaths, hyperiid amphipods, and euthecosomatous pteropods, but each contributed less than 2% by number to the overall diet. Euphausiids contributed 80.8% to the diet by weight, followed by larvaceans (8.1%) and copepods (5.4%) (Fig. 6). Fish larvae constituted 0.1% of the diet by number and 1.3% by weight. All other taxa made up less than 2% of the diet by weight.

Prey Composition by Time of Day

Stomach samples collected during the day throughout the survey area contained mainly larvaceans (84.4% by number) (Fig. 6). Euphausiids and copepods were the next important prey items (4.7% and 9.3%, respectively). During twilight hours, the diet composition of

Table 3

Results of the Kruskal-Wallis test for differences in feeding intensity in adjacent time intervals. The results are from the whole cruise and the semidiel study.

Treatment	Gut fullness	Digestion code	Percent body weight
Overall survey	$H = 34.50$ $P < 0.001$	$H = 54.75$ $P < 0.001$	$H = 29.23$ $P < 0.001$
Semidiel study	$H = 54.55$ $P < 0.001$	$H = 31.46$ $P < 0.001$	$H = 85.97$ $P < 0.001$

Table 4

Results of the Mann-Whitney *U*-Test for differences in feeding intensity between adjacent time intervals during the semidiel study.

Time intervals	Gut fullness	Digestion code	Percent body weight
0245 and 0445	$U = 295$ $P = 0.006$	$U = 296.5$ $P = 0.005$	$U = 200$ $P = 1.0$
0445 and 1030	$U = 231$ $P = 0.365$	$U = 241.5$ $P = 0.206$	$U = 239$ $P = 0.291$
1030 and 1215	$U = 241.5$ $P = 0.236$	$U = 268.5$ $P = 0.050$	$U = 218$ $P = 0.626$
1215 and 1745	$U = 298$ $P = 0.006$	$U = 334$ $P < 0.001$	$U = 343$ $P < 0.001$

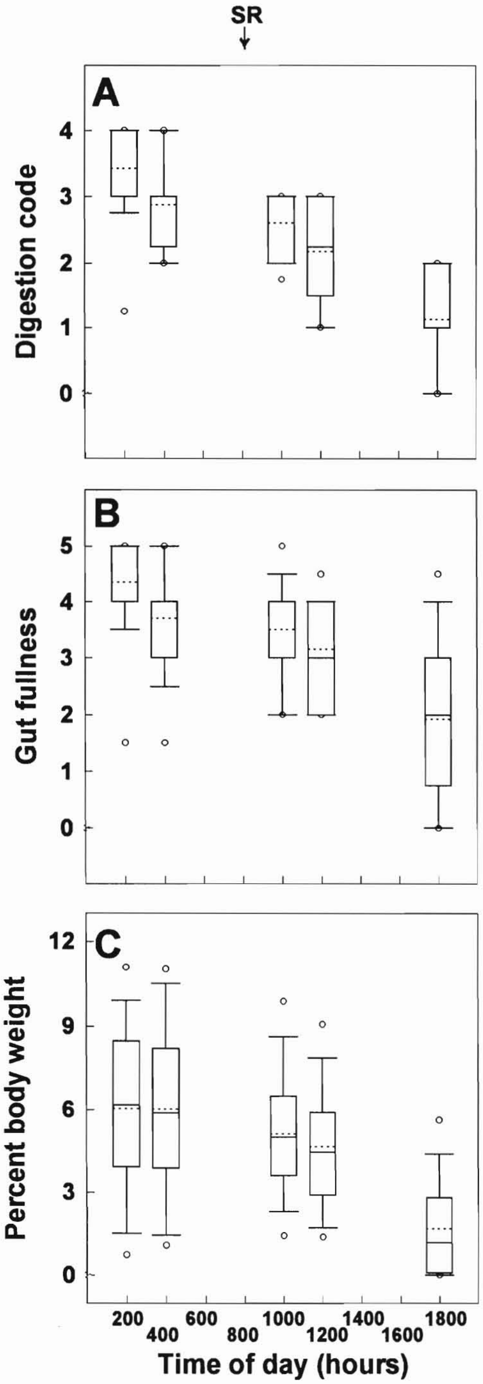

Figure 4

Box plots of (A) digestion code, (B) gut fullness, and (C) percent body weight versus time of day for the semidiel study (5 collections at one station). The solid lines indicate the 25th, 50th, and 75th percentiles. Error bars mark 10th and 90th percentiles. The dotted lines indicate mean values. Circles represent 5th and 95th percentiles. Sunrise (SR) was at 0815.

juvenile pollock shifted dramatically to mostly copepods, reflected in the substantial increase of their numerical percentages (82.4%), whereas the number of larvaceans decreased markedly (3.4%). There were no pronounced changes in the numerical percentage of

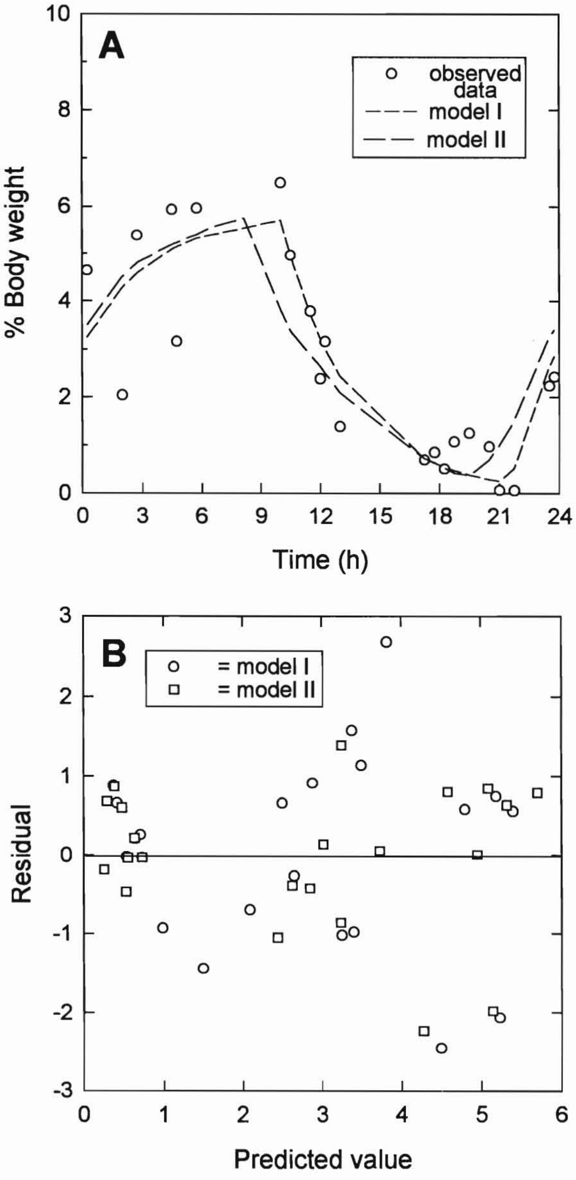

Figure 5

(A) Food consumption estimated from the diel trajectory of median percent body weights (circles). Model I is fitted with the assumption that the ingestion rate is constant. Model II is fitted with the assumption that the ingestion rate is linearly related to amount of food present in the stomach (see text for explanation of models). (B) The residuals for each of the models.

euphausiids from day to twilight, but numbers increased at night. At night, prey consumption shifted back to larvaceans (68.3%). Variations in the gravimetric composition of the diet among time periods were less pronounced, with euphausiids constituting the majority of the diet by weight for all three time periods.

Prey Composition by Area

Diet of age-0 pollock in the Kodiak Island region (Area I) consisted mostly of euphausiids (76.8%), with copepods ranked as the second most important prey item (10.3%) numerically (Fig. 7). Hyperiid amphipods, mostly *Themisto pacifica*, made up 2.6% of the diet by number. In Area II (east of the Shumagin Islands), pollock diets differed somewhat from those around Kodiak Island, containing mostly larvaceans (39.9%) and copepods (39.8%), with a substantial decrease in the incidence of euphausiids in the diet. Samples collected in Area III (west of the Shumagin Islands) contained mostly larvaceans (92.3%). Copepods numerically contributed 4.8% to the diet in this area. By weight, euphausiids were the most important prey item in the diet in all areas, especially Area I.

Prey Composition by Size

The smallest fish sampled (49.5–59.9 mm SL) contained high numbers of copepods (41.6%), but larvaceans and euphausiids were also important (32.8% and 21.6%, respectively; Fig. 8). Euphausiids contributed the most by weight (72.8%) to the diet of this size-group, followed by copepods (20.2%). There was a gradual numerical shift from copepods to larvaceans up to the largest size category examined (Fig. 8). Fish longer than 100 mm SL, however, consumed almost entirely euphausiids (98.1% on a numerical basis), although the sample size was limited for this size category. Euphausiids dominated the diet of all size categories by weight, to the almost complete exclusion of other prey items in the largest size category (Fig. 8).

An examination of the mean weights of stomach contents by major prey category revealed some interesting trends in consumption (Fig. 9). Larvaceans were the dominant prey by weight in stomachs collected during the day, whereas euphausiids were dominant during the other two periods. Geographic differences were very pronounced: euphausiids were the dominant

Table 5

Parameter estimates for two models of the diel feeding cycle of juvenile walleye pollock in the Gulf of Alaska using the median values for stomach fullness (percent body weight, %BW) during each time period. See text for explanation of the models.

Parameter	Model I	Model II
Feeding period begins (h)	1915	2130
Feeding period ends (h)	810	1000
Ingestion (%BW/h)	1.43	1.10
Evacuation (%BW/h)	0.25	0.28
Asymptotic consumption (%BW)		5.87
Daily ration (%BW/d)	8.45	7.37
Mean squared residuals	1.13	1.12

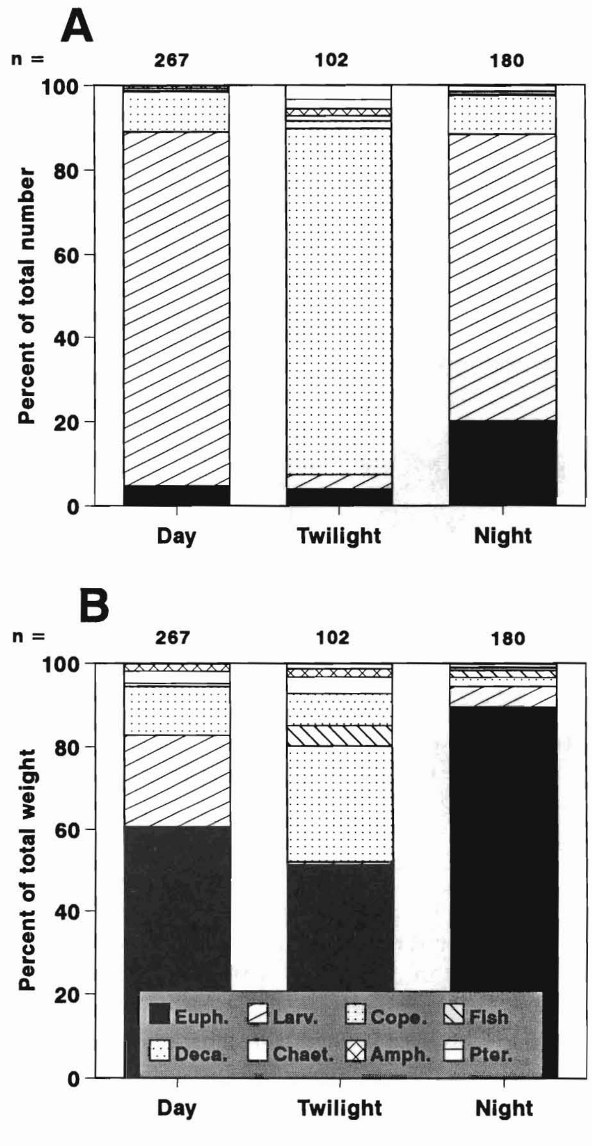

Figure 6

Prey of walleye pollock by time of day in terms of percentage of (A) total number and (B) total weight of the major prey categories.

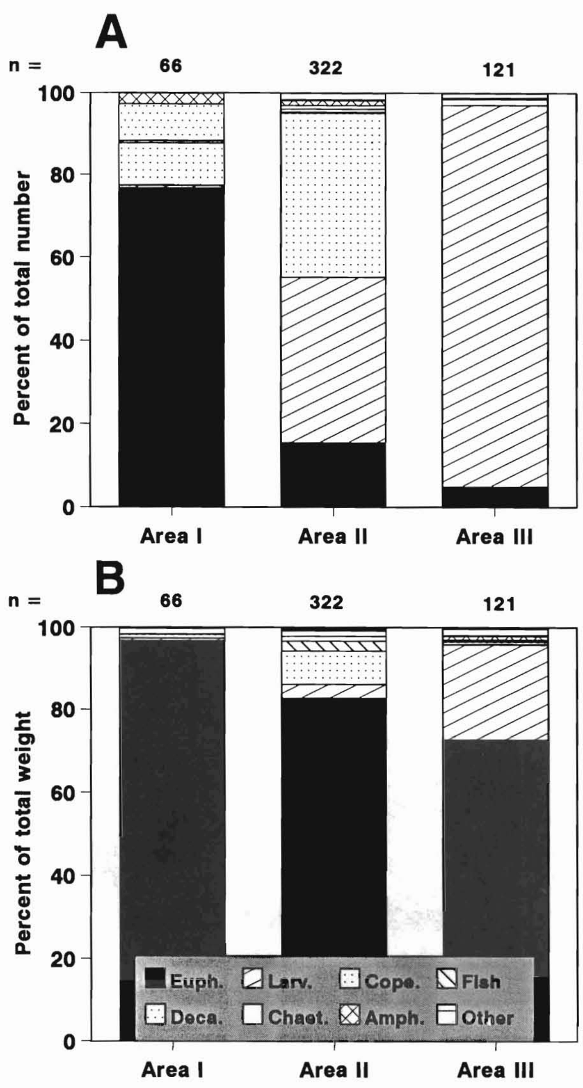

Figure 7
Prey of walleye pollock by geographical area in terms of percentage of (A) total number and (B) total weight of the major prey categories. The three areas are shown in Figure 1.

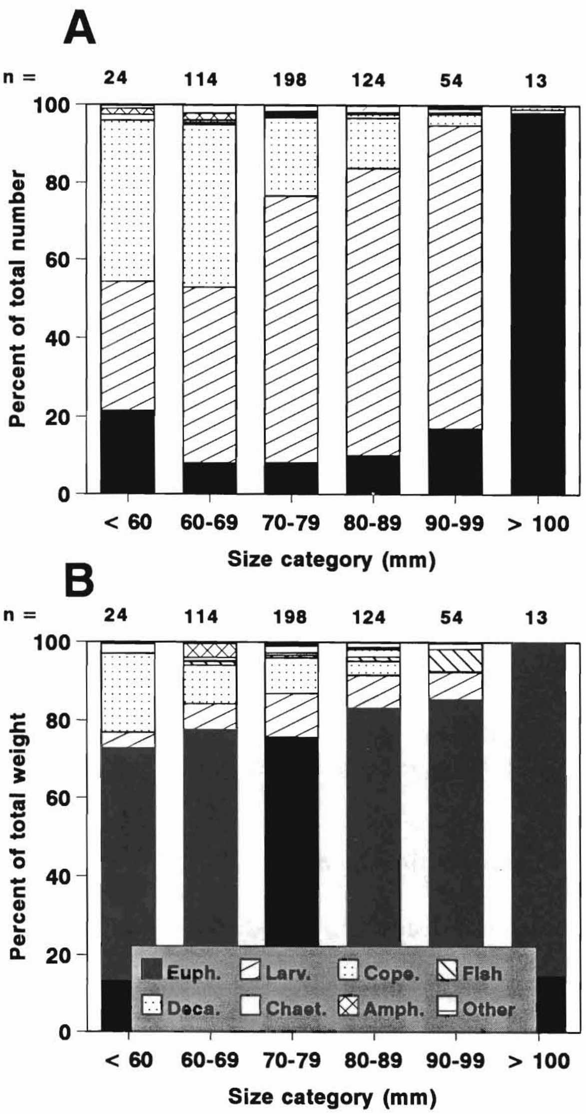

Figure 8
Prey of walleye pollock by fish size in terms of percentage of (A) total number and (B) total weight of the major prey categories.

prey in Area I, and euphausiids and larvaceans combined were dominant in Areas II and III (Fig. 9). Amphipods showed a substantial increase in Area III relative to the other areas. Euphausiids were the dominant prey for all size categories, and larvaceans were important only in the intermediate categories (70–79 mm and 80–89 mm SL).

Analysis of Dietary Variation

Significant differences in the frequency of the major prey taxa in the diets of age-0 pollock by all three factors were found (Table 6). Thus we could reject the null hypothesis that the diets were similar within each factor. Hyperiid amphipods were the only taxon that did not show significant variation (P=0.05) by time of day. Comparison by size of fish demonstrated that copepods, euphausiids, and decapods showed significant variation, whereas the occurrence of larvaceans and hyperiid amphipods did not show significant variation with size of predator (P>0.05). Areal analysis showed that the distribution of feeding on copepods, hyperiids, and larvaceans was highly variable (P<0.05), whereas the distribution of feeding on decapods and euphausiids did not show significant variations.

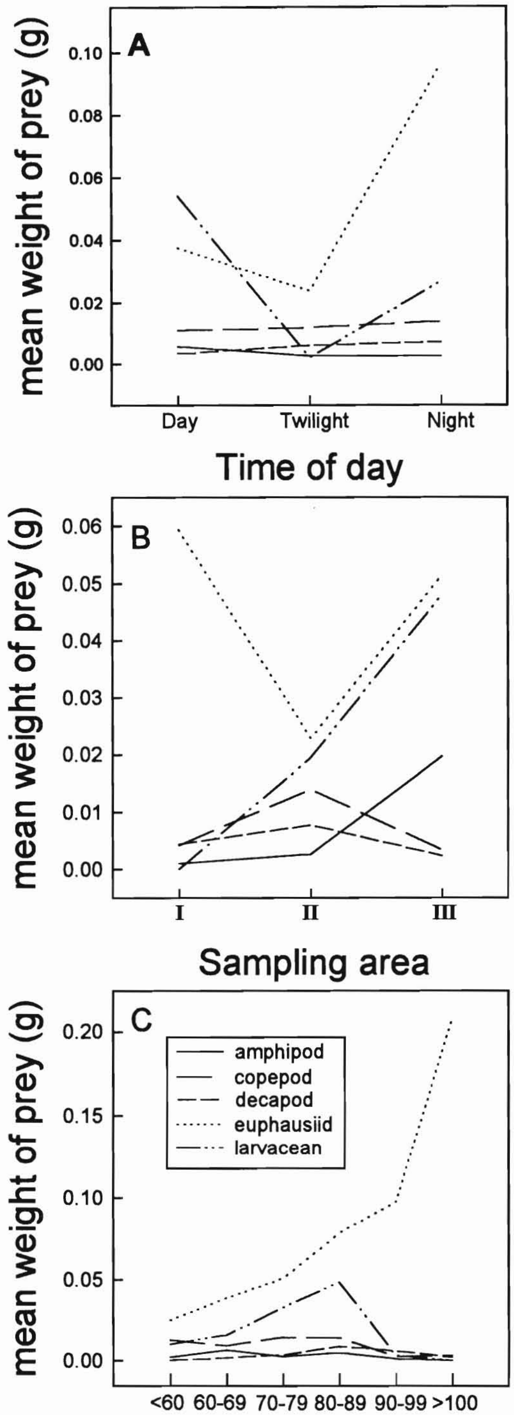

Figure 9

Prey composition by mean weight for (A) time of day, (B) sampling area, and (C) fish size category for the dominant prey categories.

Discussion

Our finding that age-0 walleye pollock fed mainly at night was surprising in light of previous observations that the larvae feed mainly in daytime or in crepuscular periods (Kamba, 1977; Kendall et al., 1987; Canino et al., 1991; Canino and Bailey, 1995). Walline (1983), working with more limited data on stomach fullness of juvenile pollock from the Bering Sea, concluded that there was no discernable feeding periodicity, but he did observe that the percentage of empty stomachs peaked in the evening hours and then declined at night, which is consistent with our findings. The increased amount of well-digested food and chyme present in age-0 pollock stomachs collected during the day led Krieger (1985) to suggest that the period of peak feeding switches from day to night during the fall months. Evidence for diel periodicity in feeding of adult walleye pollock is equivocal in the results of Dwyer et al. (1987) for the Bering Sea, but their data suggest that food items found in the stomachs at night were less digested than those recovered during the day (Livingston[5]).

What benefits do juvenile pollock derive from feeding at night rather than during the day, when visual acuity and contrast are far greater? Bailey (1989) found that juvenile pollock in the Bering Sea formed dense aggregations in deep water during the day but migrated and subsequently dispersed in the surface layer at night. Similar diel differences in distribution were observed in acoustic data collected during our sampling in the Gulf of Alaska (Brodeur and Wilson, 1996). In laboratory studies, juvenile pollock have been shown to avoid high light intensities and to seek out relatively low light levels (Olla and Davis, 1990). Apparently, light levels in surface waters were sufficient to facilitate feeding even at night, even though the moon was not full and there was extensive cloud cover during most of our sampling. A benefit to foraging in surface waters at night is that many diel vertically migrating prey, such as copepods and euphausiids, move to the surface at dusk (e.g., Marlowe and Miller, 1975; Cooney, 1989). Juvenile pollock may also decrease their risk of predation by spending time at the surface when major surface-feeding predators such as seabirds and marine mammals are not foraging (Hatch and Sanger, 1992; Springer, 1992).

Our estimates of daily ration as a percentage of body weight were comparable with the two models, but the results from Model II, which assumed that ingestion was proportional to the stomach contents, fit the data slightly better at the time of initiation and cessation of feeding. We also found the statistical fit (mean square errors) of both models to be substantially better when

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[5] Livingston, P. A. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way N.E., Seattle WA. 98115-0070. Pers. commun.

Table 6

Results of the chi-square analysis of each factor independently for major prey taxa of juvenile pollock. The data are from the whole cruise, including the diel study.

Prey	Time	Size	Area
Copepods	$\chi^2 = 20.8$ $P < 0.001$	$\chi^2 = 19.9$ $P = 0.001$	$\chi^2 = 18.5$ $P < 0.001$
Euphausiids	$\chi^2 = 107.5$ $P < 0.001$	$\chi^2 = 11.3$ $P = 0.046$	$\chi^2 = 0.7$ $P = 0.70$
Larvaceans	$\chi^2 = 11.8$ $P = 0.003$	$\chi^2 = 7.0$ $P = 0.22$	$\chi^2 = 14.8$ $P < 0.001$
Decapods	$\chi^2 = 16.0$ $P < 0.001$	$\chi^2 = 13.1$ $P = 0.02$	$\chi^2 = 3.3$ $P = 0.19$
Hyperiids	$\chi^2 = 5.9$ $P = 0.05$	$\chi^2 = 3.8$ $P = 0.57$	$\chi^2 = 9.1$ $P = 0.01$

we used median rather than mean values because of the influence of several very large values, and we recommend using median values when fitting these models. To be reliable, the models that we fit to the feeding trajectory require a synchronized switch from feeding to nonfeeding modes for the entire population (Sainsbury, 1986). As in many other studies on diel feeding behavior, our data are most variable during these transition periods and would benefit from increased sampling intensity during these times.

Previous field studies on the daily ration of age-0 pollock do not exist for comparison with our results. Springer (1992) summarized a number of laboratory and field studies of daily consumption rates of walleye pollock and found them to be quite variable (<0.1% to 8.6%BW) depending on size, temperature, and season. It is not surprising that our ration estimates are at the high end of this range, since many of the other field studies were done on slower-growing adults at the lower temperatures of the Bering Sea (maximum temperature <4°C) rather than on relatively fast-growing juveniles at 6–10°C like those we collected. The laboratory studies on small juveniles are consonant with our results (Springer, 1992).

All of the taxa that we identified from the stomachs of juvenile pollock were pelagic zooplankton, which is consistent with previous studies suggesting that age-0 pollock are planktivores feeding mainly on copepods and euphausiids (Kamba, 1977; Walline, 1983; Grover 1990, 1991; Livingston[2]). The gradual ontogenetic shift from copepods to euphausiids documented by Bailey and Dunn (1979) for pollock from larger size groups also appears in our data; evidently, the costs of foraging on copepods exceed the nutritive benefits for larger walleye pollock. However, we did not note any dramatic shifts in diet between adjacent size groups that might indicate an ontogenetic change in habitat (Mahon and Neilson, 1987). Krieger (1985) found that the consumption of epibenthic prey (e.g., cumaceans, shrimp, and mysids) increased dramatically during winter, suggesting that age-0 fish may be more associated with the bottom substrate then. Similar foraging on epibenthic prey was observed among age-1 pollock collected in Shelikof Strait during March and April (Brodeur and Wilson, 1996). Unlike some other researchers (Lee, 1985; Grover, 1991), we did not find copepod eggs in the guts of juvenile pollock. This may have been because we examined larger fish and not because there were no reproductive copepods at this time of year. The low frequency of fish found in the stomachs indicates that age-0 pollock in our study area are neither piscivorous nor cannibalistic on smaller juvenile pollock (Sogard and Olla, 1994), but the availability of small fish prey appeared to be limited during our sampling period (Brodeur, unpubl. data).

The extensive consumption of larvaceans by juvenile pollock has not been adequately documented, although larvaceans have been reported as prey of age-0 pollock (Walline, 1983; Krieger, 1985; Lee, 1985; Livingston[2]). Larvaceans can be very abundant and aggregated in coastal waters, particularly in late summer, and thus may serve as an important link in the food web between the lower trophic levels and larval and juvenile fishes (Alldredge and Madin, 1982; Gadomski and Boehlert, 1984; Knoechel and Steel-Flynn, 1989). Larvaceans are more difficult to recognize and enumerate than crustacean prey because they are digested faster in predator's stomachs, so our estimates of consumption of these prey may be conservative. Because of their patchy distribution and relatively small size without their large mucous houses, these prey may be inadequately sampled by plankton-collecting gear. Intact larvaceans may have a low nutritive value by themselves, but by consuming and concentrating phytoplankton, they may serve as concentrated energy sources for both predaceous zooplankton and juvenile walleye pollock (Knoechel and Steel-Flynn, 1989).

Juveniles collected at twilight contained the most copepods. This could be attributed to the comigration of copepods and juvenile pollock to and from the surface during crepuscular periods. Since euphausiids migrate to the surface at night (Alton and Blackburn, 1972; Bailey et al., 1992), pollock are able to prey on them in the surface layers. Pollock showed significant differences in consumption of larvaceans by time of day: the highest percentages of stomachs containing larvaceans were collected during daylight hours. Though little is known about their behavior or vertical distribution in the northern Gulf of Alaska, larvaceans were found in high concentrations outside their gelatinous houses in windrows at the surface during late afternoon off California (Alldredge, 1982). If age-0 pollock migrate to the surface before dusk, then their chances of encountering larvaceans increase. Variability was seen in hyperiid and decapod consumption by time of day: the highest consumption occurred in twilight hours. It is unclear how pollock detect these crustaceans, but they may be encountering them during their crepuscular ascents or descents through the water column.

Some dietary variability was apparent among differing sizes of pollock. Smaller fish (<60 mm) had the highest percentage of copepods in their stomachs, and the incidence declined as fish size increased. Larvaceans were most common in the intermediate size groups but were not consumed by the larger fishes, possibly because it was not energetically favorable for large fish to feed on such small prey items. Euphausiids showed significant variability with fish size, with the highest mean weight found in larger fish. Though smaller fish also preyed on euphausiids, the larger juveniles (>80 mm) have larger gape sizes and faster swimming speeds, which are needed to capture and ingest the larger and more evasive euphausiids. Decapod consumption increased as fish size increased, which may also be due to the increased capture efficiency of larger fish.

Though pollock diet varied by area, no differences were seen in fish condition among the three areas (a Kolmogorov-Smirnov test showed no significant differences among the three areas for fish we examined; see also Wilson et al., 1996). If condition index is used as a long-term indicator of fish growth and survival, then fish collected in the different areas would be expected to have similar chances of surviving. However, fish caught in Area II demonstrated a wide range of condition index values, with several specimens showing very low values, indicating that some fish may not have received an adequate daily ration. Although we found that stomach fullness was as high in Area II as in the other areas, it is difficult to draw clear conclusions without knowing the migratory patterns of juvenile pollock. If these fish were just passing through or had recently settled in the area in which they were sampled, they may have been exposed to different prey fields and to beneficial feeding opportunities which affected their condition more than their very recent feeding history would indicate.

We need to learn more about the Gulf of Alaska juvenile pollock population size, distribution, and migration patterns, as well as the patterns of their major prey, to ascertain whether age-0 pollock are food-limited in this environment. With a finer-scale sampling scheme and data on prey availability and vertical overlap, along with incorporation of environmental data, we may be able to infer more about juvenile pollock feeding regimes. Bioenergetic modeling that combines feeding data with information on pollock juvenile growth rates may yield some clues about whether juveniles in this population are feeding at or near their optimal levels.

Acknowledgments

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Hatch Date and Growth Estimation of Juvenile Walleye Pollock, *Theragra chalcogramma*, Collected in the Bering Sea in 1989 and 1990

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ABSTRACT

Age-0 walleye pollock, *Theragra chalcogramma*, ranging from 6 to 108 mm fork length, were collected in the Bering Sea in the summers of 1989 and 1990. Trawl surveys showed a wide distribution of juvenile fish in the eastern continental shelf area, and limited distribution in the Aleutian Basin. The ages, in days after hatching, of juvenile fish selected from a wide area were estimated by counting otolith daily growth increments. The mean number of daily growth increments of juvenile pollock collected in 1989 was 98; in 1990 the mean number was 104. Back-calculated hatch dates of both years ranged between mid-April and early June, and peaks were observed between late April and mid-May. Allowing for the days required from spawning to hatching, spawning was estimated to have peaked in middle to late April. These spawning periods were in agreement with those on the southeastern Bering Sea continental shelf. Although it is known that pollock spawn from February to March in the Aleutian Basin area, only a few juvenile pollock that had been spawned during this period were observed. Either the survival rates of basin-spawned fish were very low, or the fish were transported out of the survey region. Early growth patterns in 1990 were estimated by the back-calculation method, using daily growth increments.

Introduction

Natural fluctuations in population size are commonly observed between age classes of walleye pollock, *Theragra chalcogramma*, and variations of biomass are thought to largely be dependent upon the strength of these year classes. However, processes affecting year-class strength are still largely uncertain. It is known that there are separate spawning stocks of walleye pollock in the Bering Sea (Hinckley, 1987). One is located in the Aleutian Basin, and several others are located over the continental shelf. These adult stocks have different biological characteristics, including spawning period. Pollock spawn from February to March in the Aleutian Basin surrounding Bogoslof Island, from April to June in the southern part of the eastern shelf, and from June to August in the northern part of the eastern shelf (Hinckley, 1987; Mulligan et al., 1989). The linkages between basin and shelf components are not well understood.

The otoliths of many fish species contain growth increments, concentric microstructures generally formed on a daily basis. Growth increments yield information about the early life history of the fish, such as hatch date and growth rates. In previous studies (Nishimura and Yamada, 1984; Bailey and Stehr, 1988), the increments of larval and juvenile walleye pollock otoliths were shown to be laid down on a daily basis.

The major objective of this study is to examine the relationship between surviving juveniles and spawning stocks by estimating hatch dates in different geographical areas. This paper provides preliminary estimates of hatch date and growth of juvenile pollock collected in 1989 and 1990.

Materials and Methods

Juvenile walleye pollock were sampled at 38 stations in the Bering Sea between July and October in 1989 and at 34 stations between July and September in 1990. Samples were collected with midwater trawl nets deployed from a land-based dragnet trawler (*#28 Seiju Maru* in 1989 and *#128 Daian Maru* in 1990) chartered as a research vessel for echo-integration midwater trawl surveys. These surveys were a cooperative effort between the National Research Institute of Far Seas Fisheries, the National Research Institute of Fisheries Engineering, and the Alaska Fisheries Science Center. The forward part of the net body was constructed from lengthwise ropes, and the mesh size above the codend was 45 mm in 1989 and 100 mm in 1990. A net liner of 4-mm mesh was attached inside the codend to collect juvenile fish in both years. Sampling was carried out within a few hours after sunset by trawling in the subsurface layer at depths of 20–40 m. Towing speeds on average were 3.4 knots in 1989 and 5.0 knots in 1990. Net depths and vertical and horizontal openings of the nets were measured by a SCANMAR net monitoring system. Average vertical and horizontal net openings were 28.7 m and 18.9 m in 1989, and 12.0 m and 19.7 m in 1990. The collected juvenile pollock were frozen and stored. Fork lengths were measured and otoliths (sagittae) were dissected out from 40 individuals randomly selected from each station.

The survey area was divided into the Aleutian Basin area and the southern and northern parts of the eastern continental shelf. The shelf area was divided into north and south by the 58°N parallel.

Otoliths were measured along the longest axis and embedded in epoxy resin on a glass slide. Embedded otoliths were ground with carbon paper (#800–#1200) perpendicular to the otolith flat plane along the long axis (frontal section). Polished otolith specimens were selected if they included the otolith nucleus on the ground surface and were thin enough to transmit light under a light microscope. These specimens were polished with lapping film, cleaned, and etched with 0.2 M EDTA for 4 minutes. The early increments of narrow width were counted under 600× magnification. As the increments increased in width, the magnification was changed to 300×. Hatch date was estimated by subtracting the number of increments from the sampling date.

Otolith specimens from the 1990 samples were used for early growth estimation. The specimens were photographed, and diameters of 10 increments from the outer margin were measured on each photograph. Each diameter was converted to total length by means of an otolith length–total length relationshop (Nishimura and Yamada, 1988).

Results

Juvenile Distribution and Size Composition in 1989

Juvenile pollock were distributed extensively on the eastern continental shelf. In the Aleutian Basin, a small concentration was observed in the southeastern area (Fig. 1). Juveniles were collected from early to middle August on the southern shelf and basin, and from middle August to late September on the northern shelf. Juveniles from the southern shelf and basin area showed similar size ranges between 40 and 80 mm, with modes at about 60 mm (Fig. 2). Juveniles from the northern shelf were larger, ranging from 40 to 110 mm, with a mode around 80 mm, because this region was sampled later.

Juvenile Distribution and Size Composition in 1990

Sampling was conducted between late July and early August on the eastern continental shelf, and between late August and late September in the Aleutian Basin. Juvenile pollock were distributed mainly in the southern part of the eastern continental shelf. A small concentration was observed in the northern shelf and basin areas (Fig. 1). Although there was not an obvious difference in the modes of fish size between the northern shelf and the southern shelf (about 50 mm), juveniles collected from the southern shelf ranged widely in size. Juveniles collected in the basin area had a larger mode than those collected in the shelf area, and the size range extended to 90 mm, again because of later sampling (Fig. 3).

Hatch Date Estimation in 1989 and 1990

Otoliths were taken from 176 fish (size range: 33.2–94.5 mm) from 1989 samples. The fish were selected from 5 stations on the southern shelf, 2 stations on the northern shelf, and 1 station in the southeastern basin. The otoliths of 156 juvenile fish (size range: 32.8–88.2 mm) from 1990 samples were examined. The fish were selected from 2 stations on the northern shelf, 10 stations on the southern shelf, and 3 stations in the basin.

A nucleus of about 20 μm diameter was observed in the central part of each otolith, and daily growth increments were deposited concentrically around the nucleus (Fig. 4). The first few increments around the nucleus were narrow, but increments widened gradually with increasing age. The increments were clearly observed by light microscopy. Numbers of daily growth increments ranged from 60 to 139 in 1989 (Table 1). Despite differences in sampling dates and area, all groups were estimated to be hatched during almost the same period from late April to early June in 1989 (Fig. 5). The peak hatching period was estimated to be in mid-May. The frequency distribution of hatching dates in 1989 was unimodal (Fig. 5).

Otoliths from the 1990 samples showed increment numbers ranging from 60 to 167 (Table 1). As in 1989, and despite the differences in sampling dates and areas, it was estimated that most of the fish hatched from mid-April to mid-May in 1990 (Fig. 5). Exceptions in-

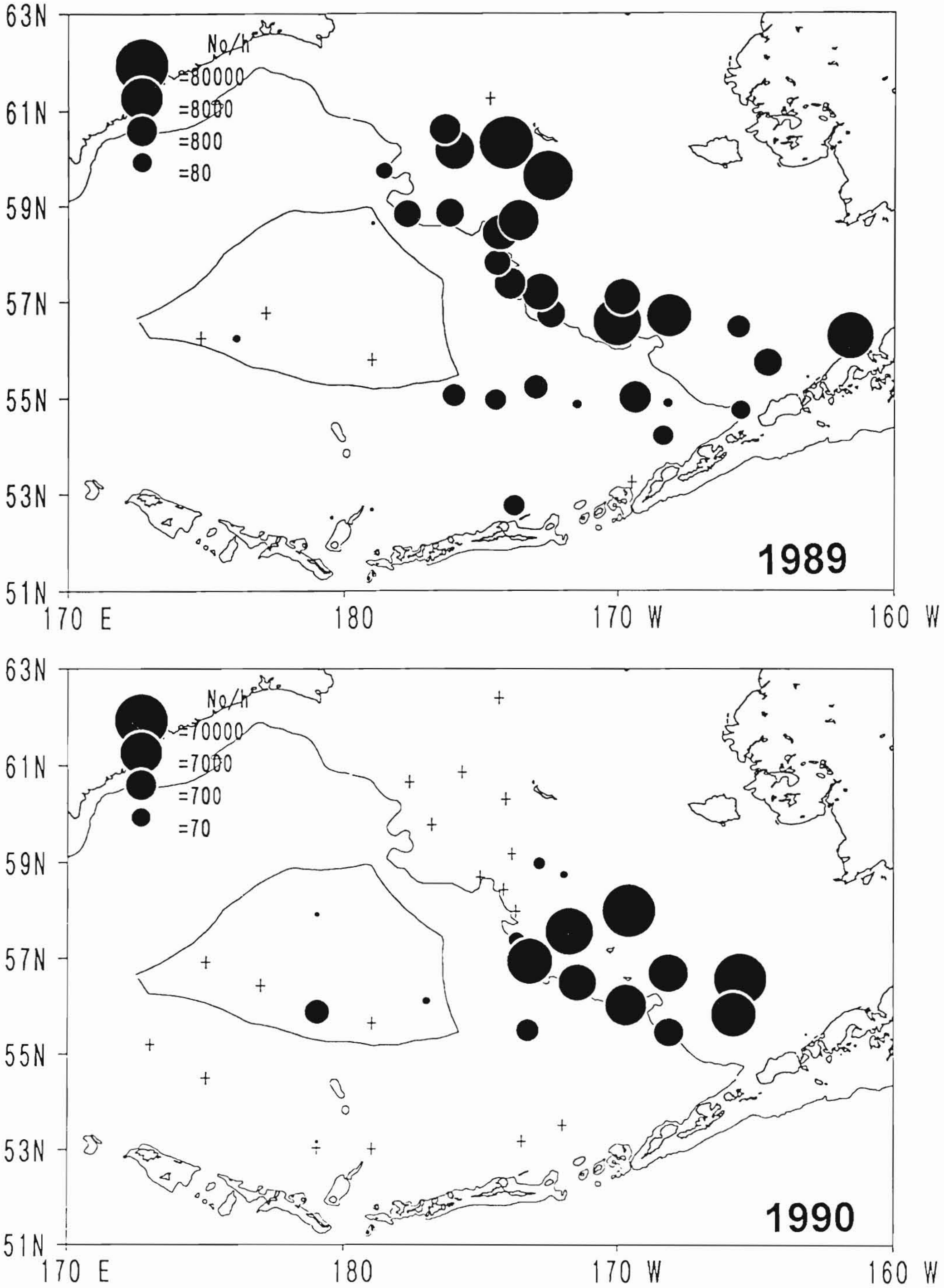

Figure 1

Catch (no/h) of juvenile walleye pollock at sampling stations during 1989 and 1990 summer surveys. A zero catch is shown by +. The isobaths represent 200 m depth.

cluded the juveniles collected at two stations (24 and 25) on the southern shelf that hatched later (between late May and early June), and two individuals collected from the basin that hatched earlier (in late March). Juvenile fish collected on the southern shelf in 1990 showed a bimodal hatching period. The major mode was in late April, about 3 weeks earlier than the major mode in 1989. The hatching period estimated for the juvenile fish collected in the basin area was broader than that for the shelf fish.

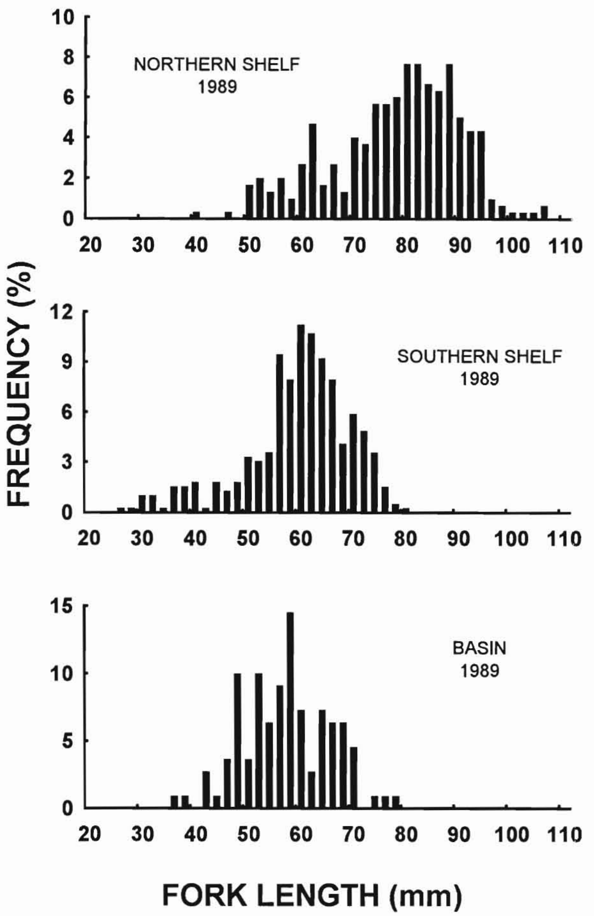

Figure 2
Size composition of juvenile walleye pollock collected from the northern shelf (north of 58°N), southern shelf (south of 58°N), and basin, in the summer of 1989.

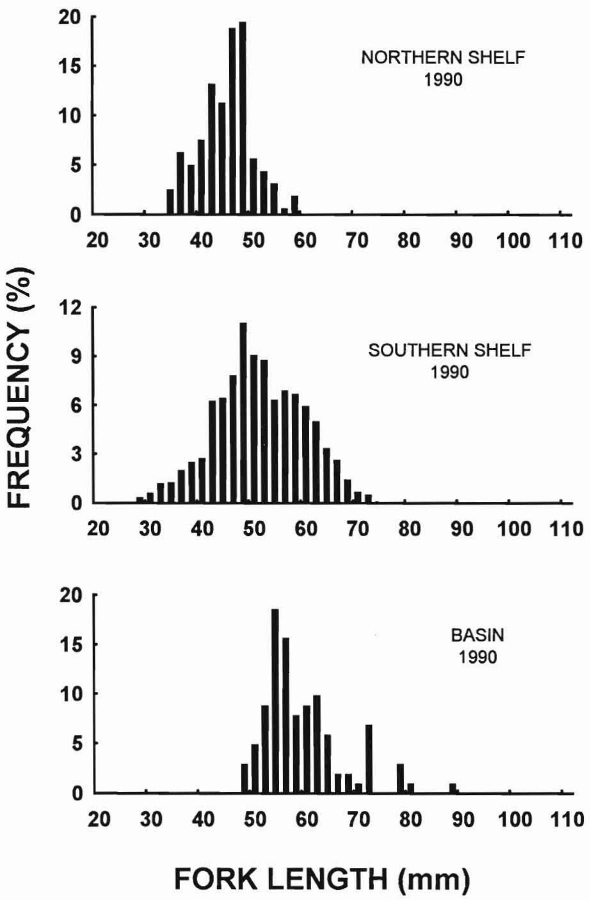

Figure 3
Size composition of juvenile walleye pollock collected from the northern shelf (north of 58°N), southern shelf (south of 58°N), and basin, in the summer of 1990.

Early Growth Estimation in 1990

Figure 6 shows back-calculated body length at 10-day intervals for 39 juveniles from the shelf and 22 from the basin in 1990. Juveniles collected on the shelf show comparably uniform and favorable growth, whereas those collected in the basin show substantial variation. Growth in the basin juveniles began to stagnate between 90 and 120 days after hatching. Growth stagnation was not clear in the shelf samples, because of the younger age ranges. Assuming a body length at hatching of 4.5 mm, the following logistic growth curves were calculated for the shelf and basin samples by using Ricklefs's (1967) method:

$$BL = 115.5/(1+e^{-0.030\,(day-101.7)})$$

for shelf samples and

$$BL = 84.0/(1+e^{-0.032(day-84.7)})$$

for basin samples.

Discussion

Nishimura and Yamada (1984) reported that daily growth increments in the otoliths of larval and juvenile walleye pollock can be seen with scanning electron microscopy. Bailey and Stehr (1988) incubated eggs obtained from Puget Sound in the laboratory, and found that daily growth increments are visible by light microscopy when larvae are fed sufficiently and their growth is satisfactory. Under conditions of low growth, however, early growth increments are narrower and impossible to observe with the resolving power of a light microscope. To get the most accurate counts, it is desirable to

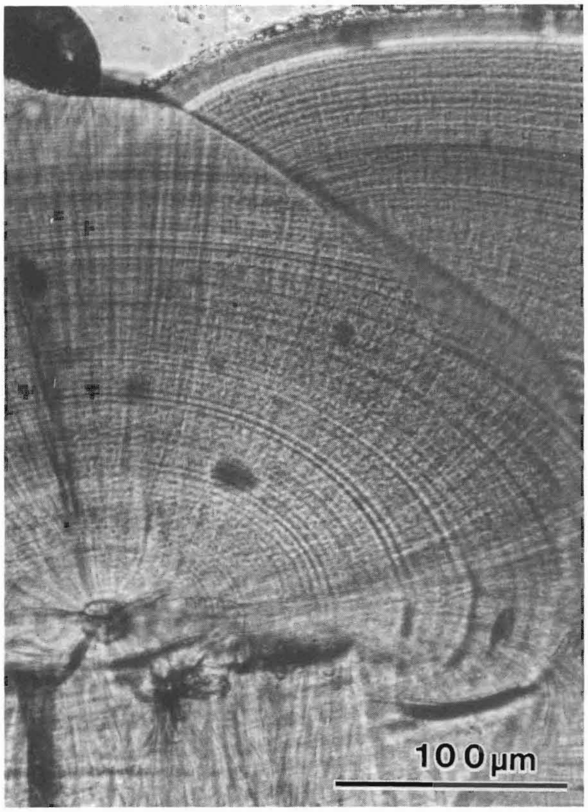

Figure 4
Light micrograph of otolith from juvenile walleye pollock (58.5 mm FL), collected in the Bering Sea in the summer of 1989.

use a scanning electron microscope, but preparation and observation of SEM specimens are extremely time consuming. On the other hand, counting with the light microscope is easy and efficient when many specimens are analyzed. We used 600× magnification to avoid contamination with immersion oil, which is required for observation at 1000×, allowing for future SEM observation. Because our otolith specimens were thin and polished on both sides, the increments were relatively easily identified. Although a few increments may have been missed, and counting errors may have occurred, the degree of error would not greatly affect the results. Therefore, we consider that gathering substantially more data by light microscope offered greater value than a small number of SEM counts.

Hinckley (1987) proposed the existence of three separate spawning stocks in the Bering Sea. Spawning occurred between January and March in the basin, between March and June over the southeastern continental shelf and slope, and between June and August over the northwestern shelf and slope. Our results from both 1989 and 1990 showed that juvenile walleye pollock were distributed mainly on the continental shelf and slope area. On the other hand, only a few juvenile fish were observed in the Aleutian Basin. This distribution pattern suggests that larvae and juvenile fish spawned in the basin area may have moved to the shelf region or that they did not survive in significant numbers in the basin.

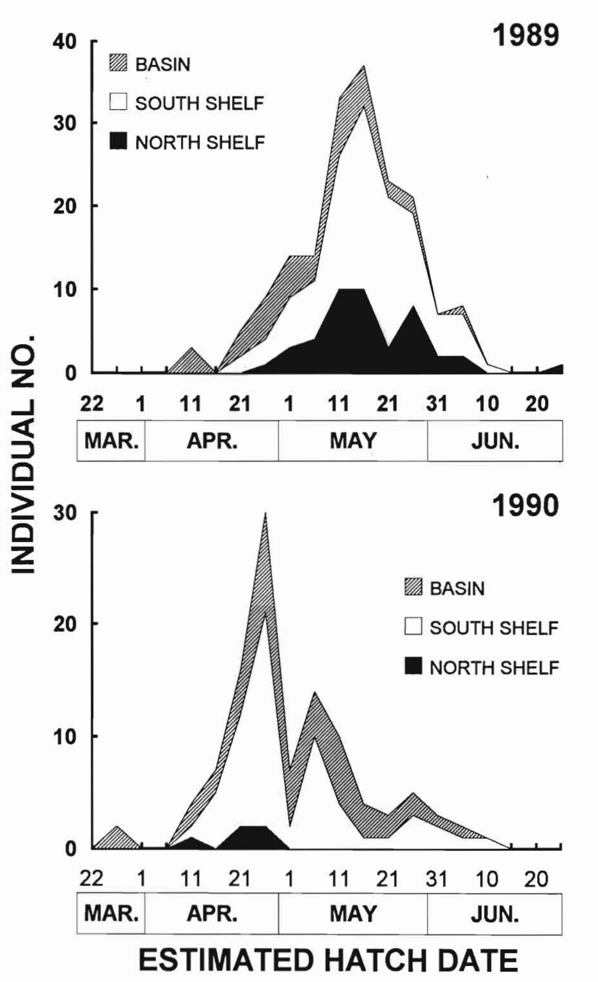

Figure 5
Frequency distribution of estimated hatch date of juvenile walleye pollock collected in the Bering Sea in 1989 and 1990.

The hatching periods estimated by back-calculation from counts of otolith daily growth increments were from mid-April to mid-June in both years, except for two individuals hatched in March 1990. The time from spawning to hatching is estimated to be about 25 days at 3° to 4°C (Okada, 1986), and about 14 days at 5° to 6°C (Haynes and Ignell, 1983; Nakatani and Maeda, 1984; Nishimura and Yamada, 1984). Water temperature in

Table 1

Fork length, otolith daily growth increment number, and estimated hatch date of juvenile walleye pollock collected in 1989 and 1990 in the Bering Sea.

Year class and area	Number of specimens	Fork length (mm)		Increment number		Estimated hatch date	
		Range	Average	Range	Average	Range	Average
1989							
Northern shelf	44	68.1–94.5	83.7	80–139	118.0	29 Apr–29 Jun	19 May
Southern shelf	96	33.2–77.2	60.9	60–114	89.0	24 Apr–13 Jun	18 May
Basin	36	42.1–78.1	60.4	77–117	99.0	13 Apr–5 Jun	7 May
1989 total	176	33.2–94.5	66.5	60–139	98.0	13 Apr–26 Jun	16 May
1990							
Northern shelf	5	40.9–55.3	47.0	94–112	99.9	11 Apr–29 Apr	22 Apr
Southern shelf	104	32.8–71.7	54.1	60–120	96.2	9 Apr–10 Jun	2 May
Basin	47	49.9–88.2	61.0	93–167	121.9	30 Mar–5 Jun	4 May
1990 total	156	32.8–88.2	55.9	60–167	104.1	30 Mar–10 Jun	2 May

the larval environment is thought to be about 3°C (Nishiyama et al., 1986; Okada, 1986). Allowing 25 days from spawning to hatching, the spawning period of these fish was estimated to be from late March to late May in both 1989 and 1990. This spawning period coincides with the spawning period on the southeastern continental shelf and slope. These results suggest the possibility that the juvenile fish collected in this study originated mainly from the southern shelf spawning stock.

Two fish collected in 1990 were estimated to be spawned in early March, which matches the spawning period of the basin stock. From a winter hydroacoustic survey in 1989, the spawning biomass in the Bogoslof area was estimated to be about 2 million tons (Wespestad[1]). In spite of considerable spawning biomass in the basin, we found only a few (0.7% of the total) juvenile fish that were estimated to have originated in the basin stock. At several stations in 1989 and 1990, larger fish ranging from 100 mm to 220 mm were collected by midwater trawling. We also succeeded in collecting fish larger than 100 mm by bottom trawling without a net liner at several stations on the shelf. These larger fish were determined by otolith analysis to be age-1 fish, and we could not find age-0 juveniles of comparable size. These results suggest that the larvae spawned in the basin area did not survive to the juvenile stage in 1989 and 1990, and further suggest that some shelf-spawned juveniles migrated or were transported off the shelf area into the basin. This concept is sup-

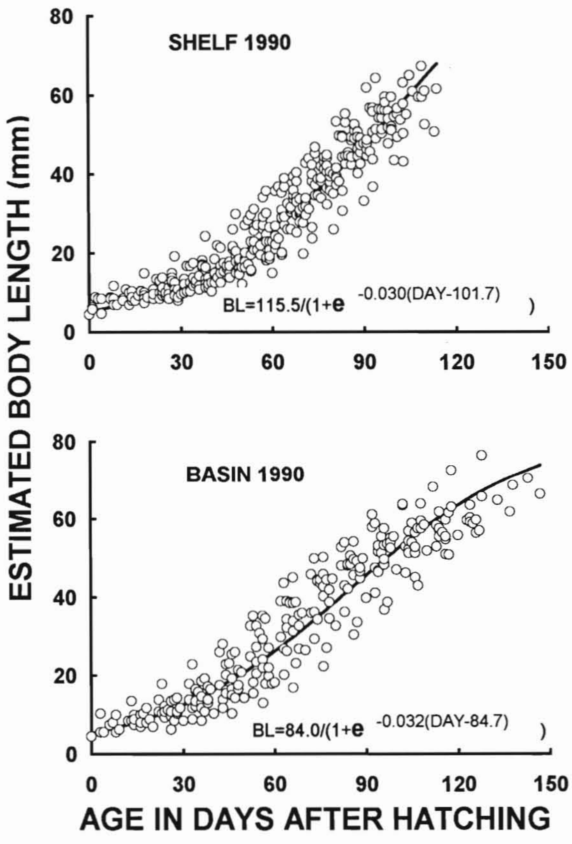

Figure 6

Back-calculated length at age of juvenile walleye pollock collected in the Bering Sea in 1990. Open circles represent back-calculated body length at 10-day intervals for 39 individuals of the shelf samples and for 22 individuals of the basin samples. The growth equations were calculated using Ricklefs's (1967) method.

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[1] Wespestad, V. G. 1991. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1992. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

ported by satellite drifter trajectories that headed mainly offshore (Reed and Stabeno, 1990).

The range of the estimated hatching period was almost the same in 1989 and 1990, but the mode in 1990 appeared in late April, about 3 weeks earlier than in 1989. Hatch date distribution in 1990 closely resembles that observed in 1979 by Walline (1985). Hatch date frequency distributions showed a unimodal pattern in 1989 and a bimodal pattern in 1990. One explanation for the bimodal distribution might be a separate spawning period in 1990. At the same time, we cannot rule out the possibility that selective mortality may influence hatch date distributions of surviving larvae. Oceanographic information will be necessary to distinguish between these two possibilities.

In this study, estimated hatch date distribution was not corrected for mortality. Size-specific mortality rates of larval and juvenile walleye pollock in the Bering Sea are unknown. In future analyses, mortality estimates combined with the effect of advection will be required.

The growth curve estimated for the shelf juveniles in this study closely resembles that estimated for the juveniles collected in the Gulf of Alaska (Yoklavich and Bailey, 1990; Brown and Bailey, 1992). Nishimura and Yamada (1988) observed geographical differences in early growth of juvenile pollock in the adjacent waters off Hokkaido. The growth curves obtained in this study show moderate growth, between the fastest and slowest growth observed in the waters off Hokkaido.

According to the estimated growth equations, the asymptotes of growth in the first year are 115.5 mm for the shelf samples and 84.0 mm for the basin samples. The first annual rings of one-year-old fish collected in the Bering Sea were estimated by back-calculation to be formed between about 120 mm and 170 mm (Nishimura, unpublished data). Considering the growth stagnation before annual ring formation, the estimated asymptote of 115.5 mm for the shelf samples appears to be a reasonable estimation. On the other hand, the estimated asymptote of 84.0 mm for the basin samples seems too low. The fate of juvenile pollock in the basin will become the object of additional attention in the future.

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Diseases and Parasites of Juvenile Walleye Pollock, *Theragra chalcogramma*, from the Gulf of Alaska, 1986–1988

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ABSTRACT

From 1986 to 1988, 1,582 walleye pollock, *Theragra chalcogramma*, between 40 and 120 mm in length were collected from the Gulf of Alaska by midwater shrimp trawl for a study on the diseases of juvenile fish. A number of parasites were encountered, varying in prevalence and distribution in each year of collection. Trematodes were the most often encountered group of parasites: they were found at approximately all sampled stations and at relatively high frequencies. The prevalence of most parasites (e.g., digenetic trematodes, nematodes, myxosporeans, bacterial epibiont) increased with fish size, suggesting that they were acquired through feeding and that they had no deleterious effects on health. The exception was a microsporidan that infected skeletal muscle. This protistan parasite tended to be more prevalent in small fish than in larger ones, suggesting that infected fish were removed from the population either through predation or because the parasitized host died. The geographic distribution patterns of the parasites do not entirely support the existence of a single population of walleye pollock in the Gulf of Alaska because neither host nor parasite distribution can be explained by the region's hydrography.

Introduction

Determination of the disease component of natural mortality rates for wild fish populations is beset with many problems. Foremost, the effects of disease vary considerably with the life-history stage of the fish (Munro et al., 1983). Second, sample sizes are typically insufficient to determine the incidence of infection; as a result, prevalence is more often reported. Third, although mortality of wild fishes is the most visible effect, the relationship of disease to sublethal effects (e.g., reduced growth rates and fecundity, diminished avoidance of predators) is unknown and may represent a significant proportion of natural mortality. Fourth, natural mortality rates are unknown, not constant, and generally vary with age (Munro et al., 1983). Finally, underlying the previously stated problems is the fact that the causes of population fluctuations are essentially unknown and unpredictable. This paper reports on the results of a continuing histopathological baseline study that attempts to examine the role of disease in the population dynamics of Gulf of Alaska walleye pollock, *Theragra chalcogramma*. Current data on the distribution patterns and prevalence of infectious and noninfectious diseases of juvenile walleye pollock (1986–88) are reported here.

Methods

Schools of juvenile walleye pollock, *Theragra chalcogramma*, were sought using the ship's echo sounder during 1986, 1987, and 1988 surveys of juvenile walleye pollock in the Gulf of Alaska. Favorable targets were then sampled with a 24-m high-opening shrimp trawl. Twenty or more fish were arbitrarily chosen from the haul at randomly selected stations. Incisions were made along both sides of the body cavity of all fish, and in dorsal body musculature of fish longer than 70 mm. The fish were then placed in 10% neutral buffered formalin and transported to the laboratory. Before processing, the standard length of each fish was determined and each was sliced into five cross sections. The five segments were then dehydrated through a graded ethanol series, embedded in paraffin, sectioned at 3–5 µm, and stained with hematoxylin and eosin. All cases were read blind.

Overall parasite prevalence was determined and plotted for each 10-mm increment of fish size. Parasite distribution and prevalence for each sampled station were also determined and plotted.

Results

Samples

During the three-year survey period, 307 hauls (1986, *N*=107; 1987, *N*=119; 1988, *N*=81; Fig. 1) were made in the attempt to collect sufficient numbers of juvenile walleye pollock for various studies. In 1986, hauls were restricted to the central and eastern Alaska Peninsula regions and around Kodiak Island. In 1987 and 1988, hauls were made along the entire Alaska Peninsula and around Kodiak Island. Specimens for disease studies were collected from 70 hauls (1986, *N*=6; 1987, *N*=33; 1988, *N*=31), resulting in the collection of 1,582 juvenile walleye pollock during the three-year sampling period (1986, *N*=146; 1987, *N*=661; 1988, *N*=775). We have examined 1,476 of these fish (1986, *N*=142, or 97%; 1987, *N*=648, or 98%; 1988, *N*=686, or 89%). The size of collected juveniles ranged between 40 and 120 mm, but collections at both ends of the range were few (Table 1). For this reason, our discussion will focus on the size groups from 50 through 100 mm.

Host Size–Parasite Prevalence Relationships

Few noninfectious anomalies were encountered in samples from all the collection years. These anomalies appeared to be of little significance to this study and will not be discussed. The most frequent observations are presented below, along with their prevalence in each year and in the combined collection.

Bacteria—A filamentous, bacterial epibiont was found colonizing the rectal epithelium of juvenile walleye pollock collected in 1988; it was absent in samples from the two previous years. The importance of the bacterial epibiont is unknown because even under the heaviest infestation, it did not appear to adversely affect the epithelium of the rectum.

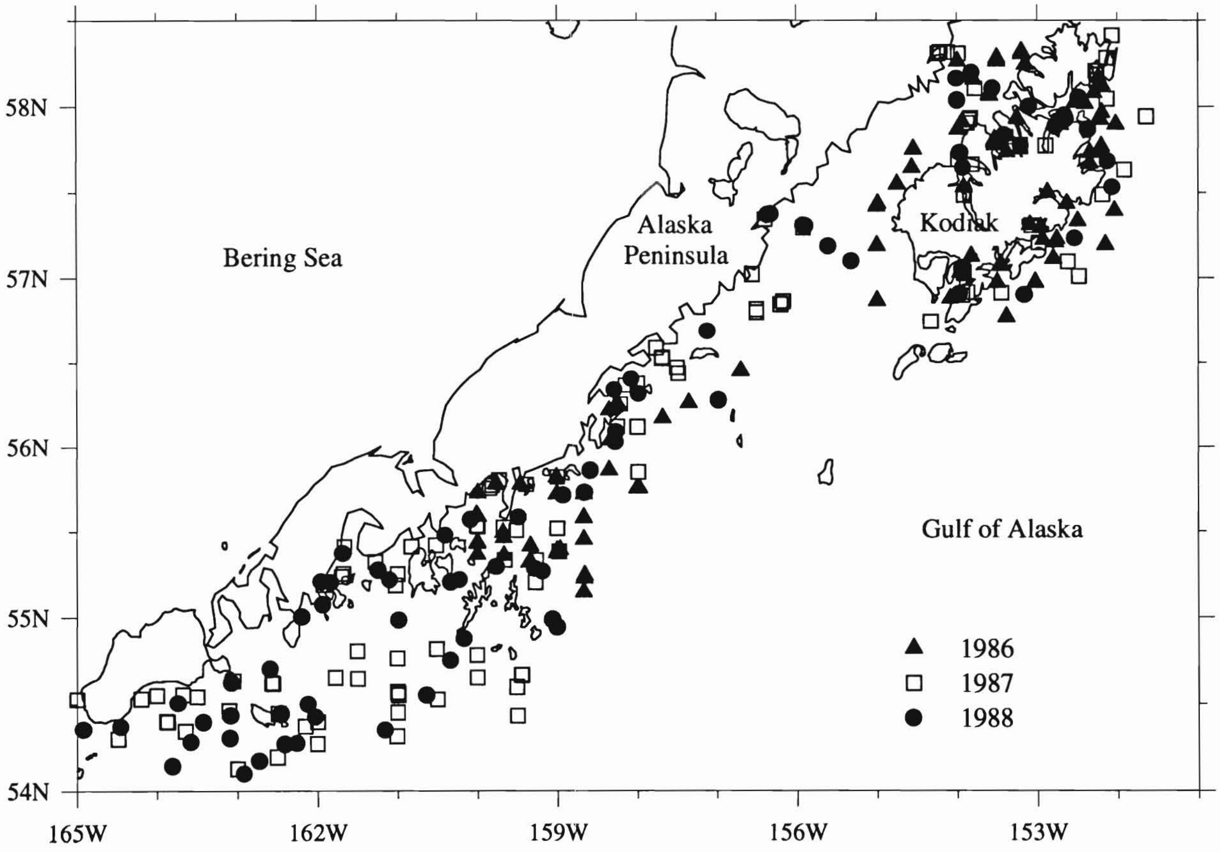

Figure 1
Haul positions for collections of juvenile walleye pollock, *Theragra chalcogramma*, by year.

Table 1
Sample sizes for each 10-mm size category of juvenile walleye pollock.

	Size (mm)									
Year	40	50	60	70	80	90	100	110	120	Total
1986	0	7	28	31	21	29	20	6	0	142
1987	0	98	139	120	111	105	64	5	1	643
1988	2	22	152	198	159	89	22	0	0	644
Total	2	127	319	349	291	223	106	11	1	1429

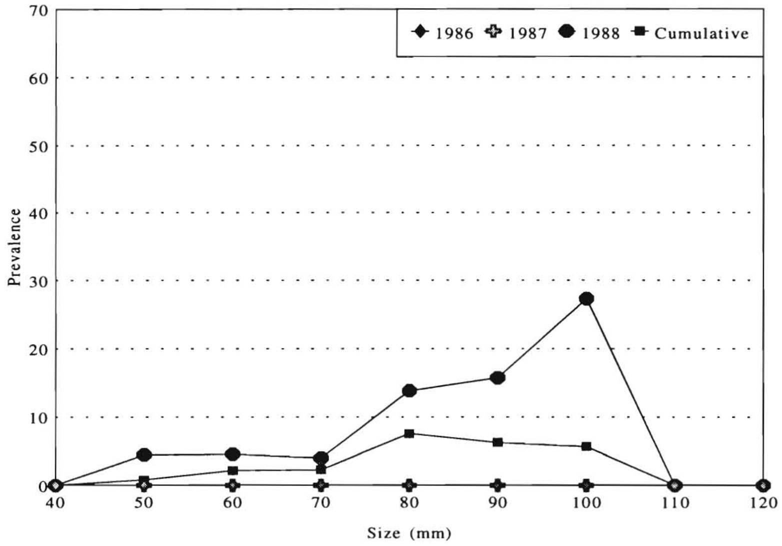

Figure 2
Relation between fish size and prevalence of a filamentous bacterium in Gulf of Alaska juvenile walleye pollock, 1986–88.

The bacterium first became evident in 50-mm fish (Fig. 2) and remained at the same prevalence for the subsequent two size groups. In 1988, the infestation rate increased markedly in fish larger than 70 mm, to 28%. Overall, prevalence increased slightly in fish between 50 and 70 mm, reached a maximum of 8.5% in 80-mm fish, and then dropped slightly in the 90- and 100-mm groups.

Microsporida—A microsporidan of the genus *Pleistophora* was routinely found in the skeletal muscle of juvenile walleye pollock. Infections qualitatively ranged between light (restricted to isolated muscle fibers) and severe (including several adjacent muscle fibers). No host response was directed at the microsporidan until the surrounding sarcolemma was breached, at which time a marked granulomatous response appeared.

Microsporidan infections for 1987 and 1988 generally fluctuated between 0 and 11% for the 50–100-mm size groups (Fig. 3). In 1986, however, nearly 30% of the 50-mm group was infected by *Pleistophora*; microsporidan prevalence dropped to less than 5% in the 60-mm group, and did not exceed 10% in the subsequent size groups. Overall prevalence (10%) was highest in the 50-mm group and gradually declined with increase in fish size.

Myxosporea—Two myxosporeans were found in the kidneys of juvenile walleye pollock. Neither was identified to species; they were similar in morphology to myxosporeans of the genera *Sphaerospora* (Dyková and Lom, 1982) and *Chloromyxum* (Dyková and Lom, 1988). Neither was present in sufficiently large numbers to cause marked changes in parasitized cells of the proxi-

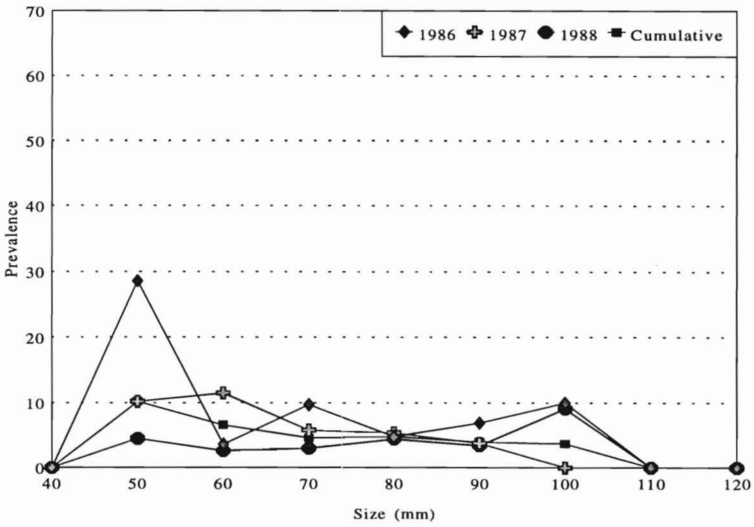

Figure 3

Relation between fish size and prevalence of a microsporidan, *Pleistophora* sp., in Gulf of Alaska juvenile walleye pollock, 1986–88.

mal or distal tubules of the kidney. *Sphaerospora* sp. was the most frequently encountered myxosporean, but several mixed infections were observed. Intracellular *Sphaerospora* stages were rare, but presumed trophozoites were abundant in the lumena of the proximal and distal tubules. A large proportion of presumed trophozoites adhered to the epithelia of the proximal and distal tubules. *Chloromyxum* sp. was typically found attached to the proximal tubule epithelium of the kidney via a stalk (Morado and Sparks, 1990), but even in the heaviest of infections, few changes were evident in the host cells.

Overall, *Sphaerospora* prevalence increased with fish size, reaching a maximum (33%) in walleye pollock of 110 mm (Fig. 4); each year's collections generally presented a similar trend. The highest *Sphaerospora* prevalence (33%) was found in the 110-mm group in 1986.

Chloromyxum was much less prevalent than *Sphaerospora* (Fig. 5). The cumulative data suggested an infection pattern of gradual increase with increase of fish size, but prevalence varied slightly among sizes and years. The highest *Chloromyxum* prevalence was observed in the 100-mm group in 1988.

Digenetic Trematodes—Digenetic trematodes, probably members of the genera *Lepidapedon, Podocotyle,* and *Steganoderma* (Arthur, 1984), were routinely encountered in fish from all three collection periods (Fig. 6). All parasites were adults that possessed ova, regardless of host size. Most were encountered in the intestine, although they were common in the lumena of the pyloric caeca. Cell and tissue changes were restricted to the immediate area of parasite attachment; because infestations were relatively light, no remarkable organ changes were observed. In 1987 and 1988, trematodes were significantly prevalent in juvenile walleye pollock of the 50-mm group, after which prevalence increased with fish size in 1987 and decreased with fish size in 1988. In 1986, trematode infections did not become notable until the fish reached 80 mm. The highest trematode prevalence (60%) was observed in 110-mm fish in 1987.

Cestodes—The prevalence of adult cestodes, probably of the genera *Abothrium, Bothriocephalus,* and *Scolex* (Arthur, 1984), increased with fish size in the 1986 and 1987 samples (Fig. 7); the cumulative data presented a similar tendency. Cestode prevalences for 1988 remained relatively constant for the 50- to 80-mm groups and then diminished in larger size groups. In general, in 1988 cestode prevalence was lower than in 1986 and 1987. Adult cestodes were found attached to the mucosa of the stomach, intestine, and pyloric caeca, but because infestations were relatively light, no remarkable organ changes were observed.

Larval Nematodes—Larval nematodes, probably members of the genera *Anisakis, Contracaecum,* and *Hysterothylacium* (Margolis and Arthur, 1979), were frequent in juvenile fish and typically found in the mesenteries of all organs and tissue, especially the liver. In all in-

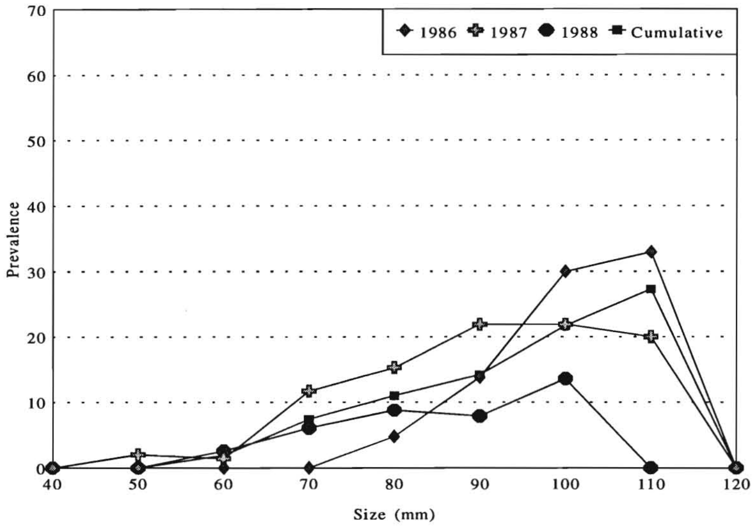

Figure 4
Relation between fish size and prevalence of a myxosporean, *Sphaerospora* sp., in Gulf of Alaska juvenile walleye pollock, 1986–88.

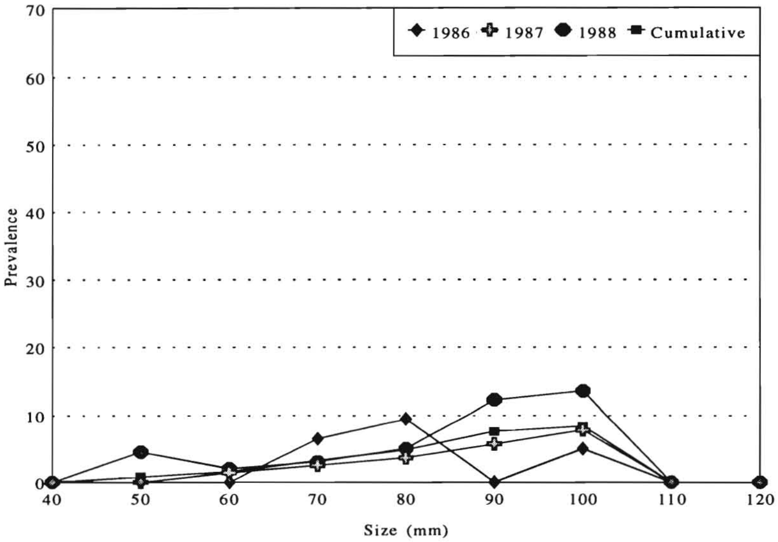

Figure 5
Relation between fish size and prevalence of a myxosporean, *Chloromyxum* sp., in Gulf of Alaska juvenile walleye pollock, 1986–88.

stances of infection, a host response to the larval nematodes was evident as an encapsulation. Response was confined to the area immediately around the nematode, but because infections were relatively light, no remarkable organ changes were observed. In one specimen, the apparent migratory path of a larval nematode was observed in the liver. An acute inflammatory reaction directed at host cell damage, the nematode, and the introduction of bacteria was present at the final destination of the nematode.

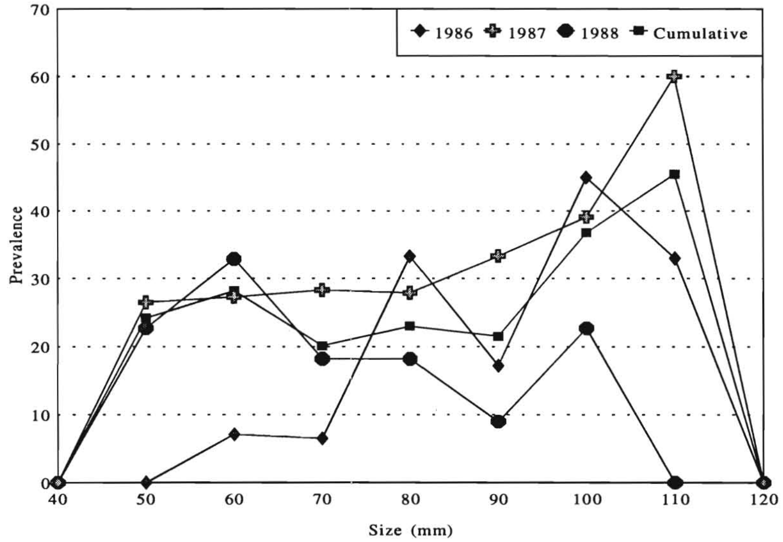

Figure 6
Relation between fish size and prevalence of digenetic trematodes in Gulf of Alaska juvenile walleye pollock, 1986–88.

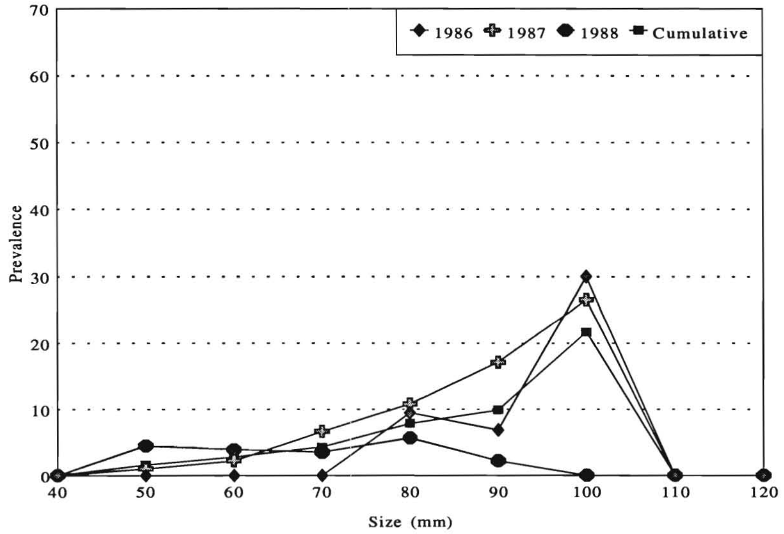

Figure 7
Relation between fish size and prevalence of unidentified cestodes in Gulf of Alaska juvenile walleye pollock, 1986–88.

In 1986, nematode prevalence fluctuated considerably, reaching peaks in the 50- and 80-mm size groups and a low in the 70-mm group (Fig. 8). The pattern of the cumulative data and that for 1987 indicated that infection generally increased with increase in fish size. Nematode prevalence for 1988 presented a curve that peaked in the 80-mm size group.

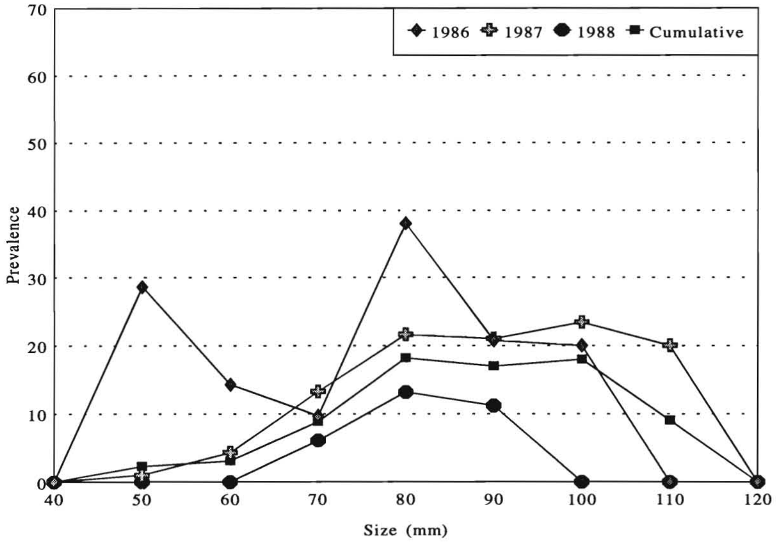

Figure 8

Relation between fish size and prevalence of unidentified larval nematodes in Gulf of Alaska juvenile walleye pollock, 1986–88.

Site-Specific Parasite Prevalence and Distribution

Because fewer stations were sampled in 1986 (*N*=6) than in 1987 and 1988, the site-specific prevalence and distribution patterns of the above parasites are presented here only for 1987 and 1988.

Bacteria—Fish colonized by the filamentous bacterium were collected throughout the survey area. Prevalence was most remarkable at sites off the central and eastern Alaska Peninsula, especially around Kodiak Island (Fig. 9). Site-specific prevalence ranged between 3% and 40%.

Microsporida—In 1987, site-specific prevalence ranged between 3.7% and 50%. Microsporidan infections were widespread in fish collected along the entire Alaska Peninsula and at a few sites around the Kodiak Archipelago (Fig. 10). The 1988 microsporidan distribution pattern was similar to the 1987 pattern, but fewer stations were positive, and site-specific prevalence ranged from 2.5% to 30% (Fig. 10).

Myxosporea—In 1987, *Sphaerospora* infections were restricted to stations sampled off the eastern and central Alaska Peninsula and around Kodiak Island; site-specific prevalence ranged between 5% and 40% (Fig. 11). In contrast to 1987, in 1988 *Sphaerospora* infections were found at stations along the entire length of the Alaska Peninsula, but overall prevalence was lower (Fig. 11); site-specific prevalence ranged between 5% and 26.3%.

The distribution patterns of *Chloromyxum* for 1987 and 1988 were similar to the *Sphaerospora* patterns of 1987 and 1988 (Fig. 12). *Chloromyxum* was less frequently encountered than *Sphaerospora*: site-specific prevalence ranged between 5% and 20% in 1987, and between 4.8% and 20% in 1988.

Trematodes—In 1987, site-specific prevalence ranged from 5% to 55% (Fig. 13). Trematode-infected fish were widely distributed throughout the sampling area: nearly all sampled stations had infected fish. The 1988 distribution pattern is similar to that of 1987, but in 1988, 40% of the fish collected at one station at the far western end of the survey were infected with digenetic trematodes. The station was located at Unimak Pass, a channel between the Bering Sea and the Gulf of Alaska. Site-specific prevalence in 1988 ranged from 4.8% to 40%.

Cestodes—In 1987, cestode-infected fish were generally found in the central and eastern Alaska Peninsula regions and around Kodiak Island (Fig. 14); only one station in the western Alaska Peninsula region had cestode-infected fish. Site-specific prevalence in 1987 ranged between 5.3% and 44.4%. The 1988 distribution was more widespread, but site-specific prevalence was generally lower (Fig. 14), ranging between 4.5% and 10%.

Nematodes—In 1987, nematode-infected juvenile walleye pollock were common in the central and eastern

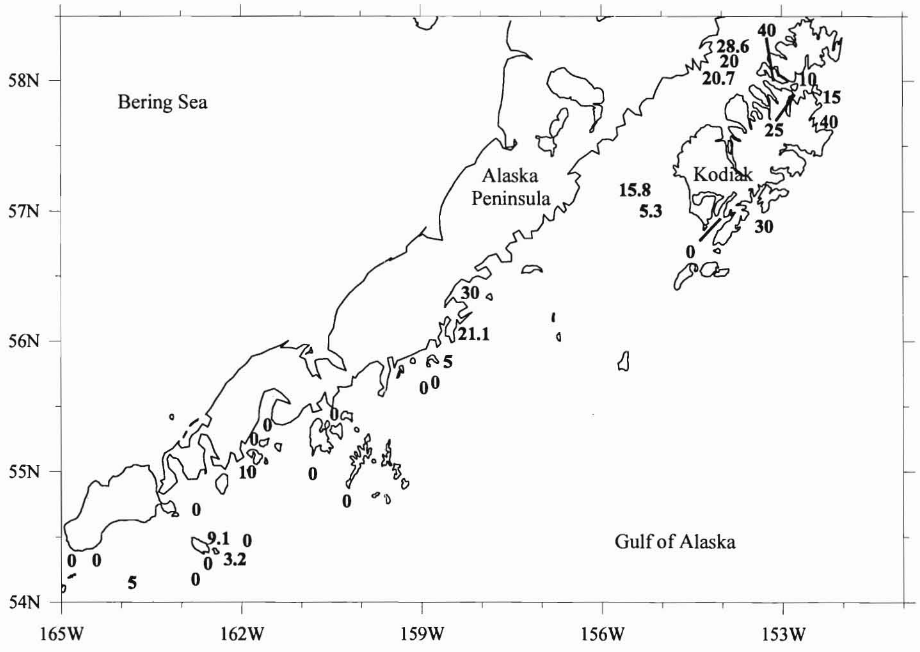

Figure 9

Site-specific prevalence of a filamentous bacterium in juvenile walleye pollock, 1988.

Alaska Peninsula regions and around Kodiak Island (Fig. 15) and less frequent in the western Alaska Peninsula region. In 1988, nematode infection was widely distributed throughout the survey area, but as before, it was less common at the western end of the survey. Prevalence generally seemed lower during 1988: site-specific prevalence ranged between 5% and 55% in 1987, and between 5% and 23.8% in 1988. Fewer positive stations were found in 1988 than in 1987.

Discussion

Infectious disease affects individuals in different ways. Death of the host is the most obvious outcome, but a condition that either directly or indirectly retards growth or swimming performance is equally important because it compromises survival (Munro et al., 1983). Juvenile fish unable to grow or to school with their cohort are more susceptible to predation. A loss in swimming efficiency probably affects the host's ability to find and capture prey. Thus an important factor to consider in assessing the impact of disease on the condition of its host is the organ or tissue affected and the severity of the disease.

Two different myxosporean parasites were found in juvenile walleye pollock. Both *Chloromyxum* and *Sphaerospora* are obligate parasites that infect kidney proximal and distal tubule epithelia and are classically defined as coelozoic even though their initial development occurs within epithelia. Their subsequent developmental stages appear free in the lumena of target organs (Dyková and Lom, 1988). *Chloromyxum* sp. uses a stalk to attach plasmodia to a parasitized cell (Morado and Sparks, 1990). In contrast, sporoblasts of *Sphaerospora* develop freely in proximal tubule epithelium without evidence of an attachment structure. Neither parasite appears lethal, and both generally cause inconspicuous infections in fish (Lom et al., 1985). Little is known about the pathogenesis of *Chloromyxum*. In contrast, *Sphaerospora* infections tend to be more common in juveniles than in adults and are reported to be scarce in feral fish (Lom et al., 1985). This study confirms that *Sphaerospora* infections are common in juvenile fish, and also shows that infections are prevalent in wild fish.

The microsporidan parasite *Pleistophora* sp. develops within skeletal muscle and causes significant disruption of myofibers, but death resulting from direct infection is unlikely. Rather, because of the site of infection, heavy parasitization can greatly affect muscle function and thus swimming efficiency. Thus the host's ability to feed or avoid predation is reduced. This probably explains the general profile of reduced prevalence with increased fish size.

Most adult digenetic trematodes live in the digestive tract lumen, attached to intestinal mucosa via muscular suckers. Large numbers of digenetic trematodes can reduce the host's fitness to survive, but this is not typical. Even though trematode infections were common, the number of trematodes per fish was not sufficient to cause cell or organ changes in infected juvenile walleye

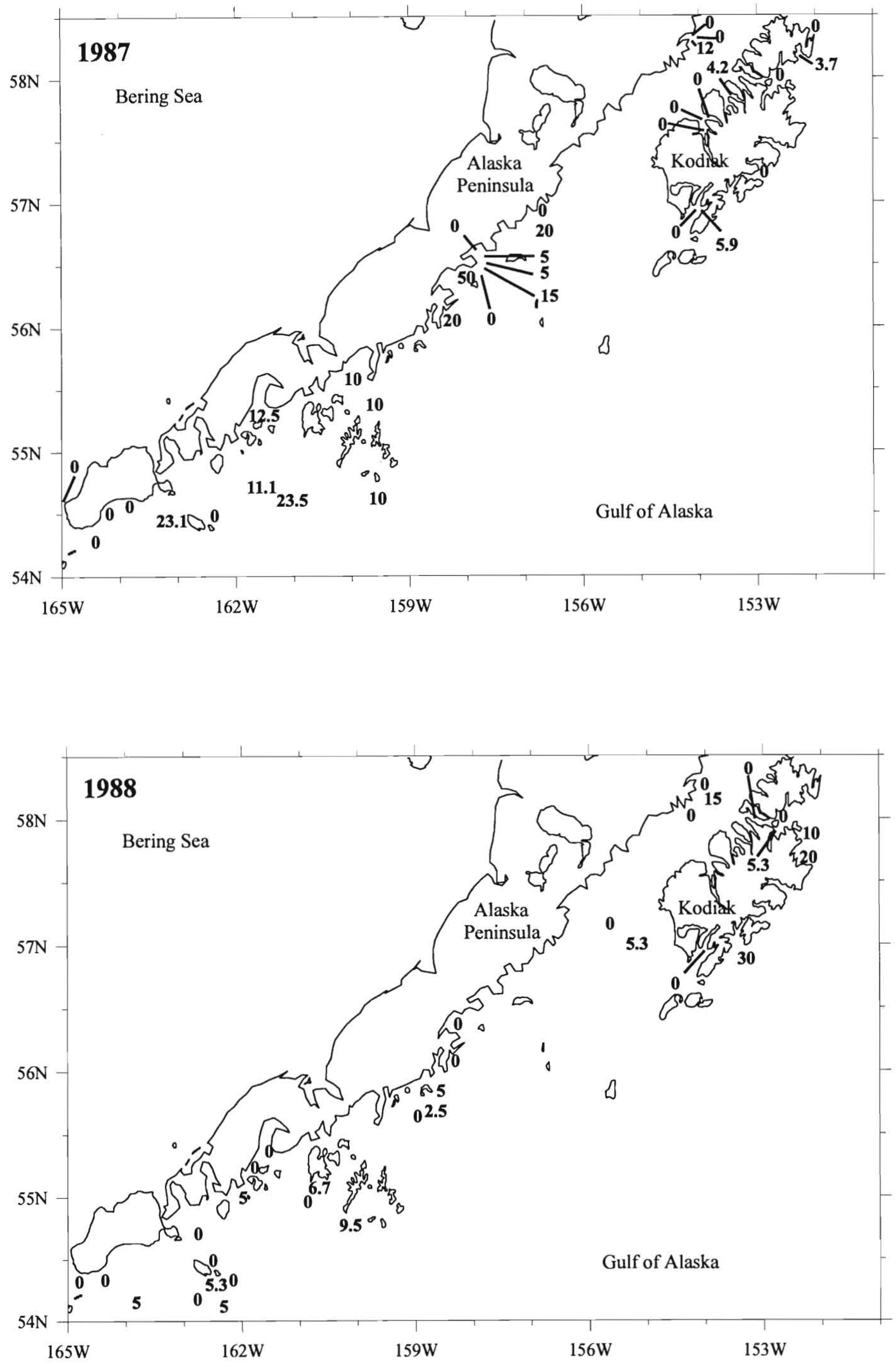

Figure 10

Site-specific prevalence of *Pleistophora* sp. in juvenile walleye pollock in 1987 (above) and 1988 (below).

pollock. In general, this taxon was the most often encountered parasite; it was found at nearly all sampled stations and at relatively high frequencies.

In marked contrast, juvenile nematodes must perforate the gut epithelium to find their preferred site of residence. During penetration and migration to their preferred site, pathogenic or opportunistic bacteria may be introduced into the underlying connective tissue and coelom. When the nematodes reach their preferred site, the host responds by encapsulating them. Heavily parasitized fish may therefore possess organs or tissues in which the parenchyma has been significantly

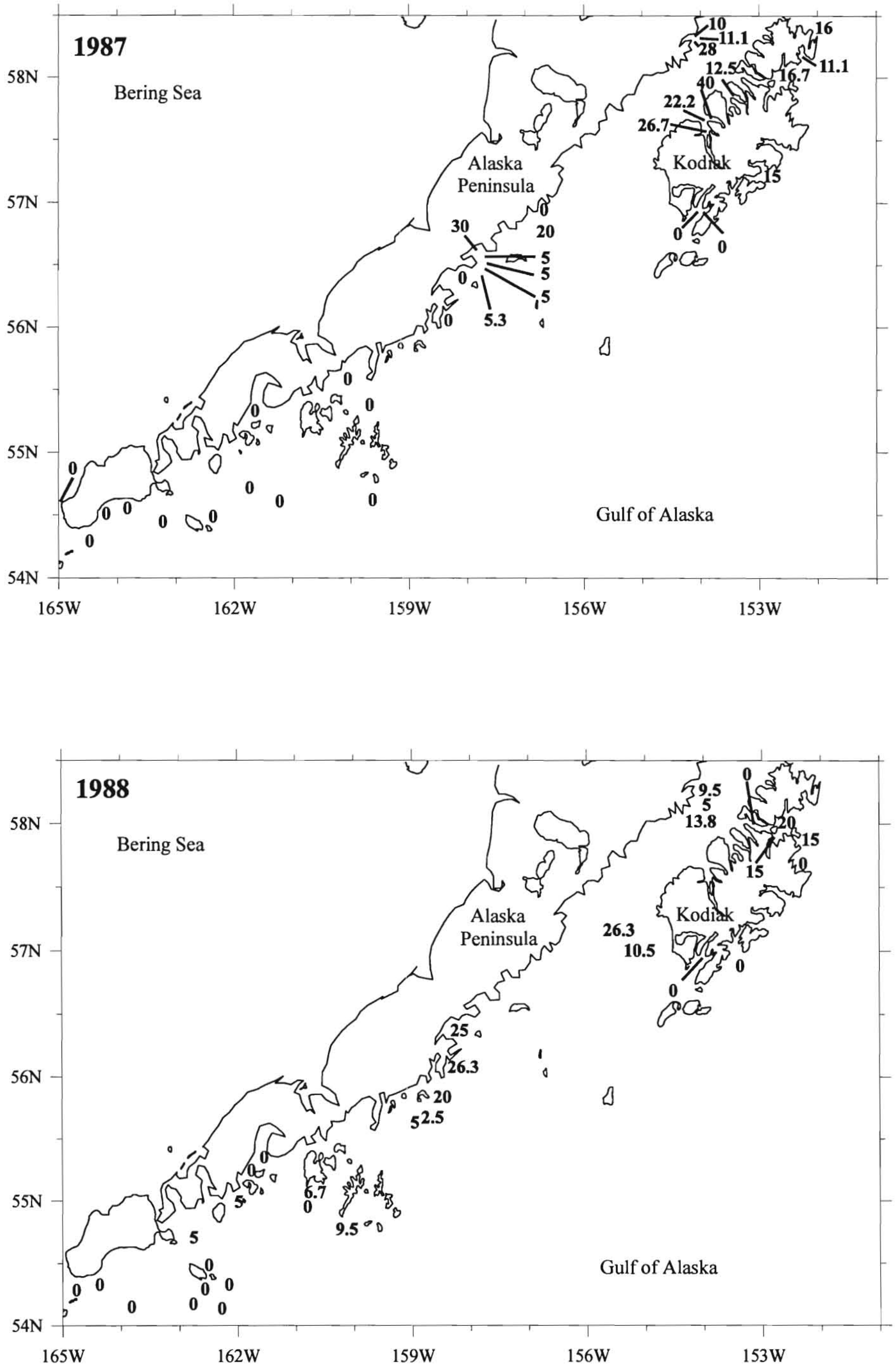

Figure 11
Site-specific prevalence of *Sphaerospora* sp. in juvenile walleye pollock in 1987 (above) and 1988 (below).

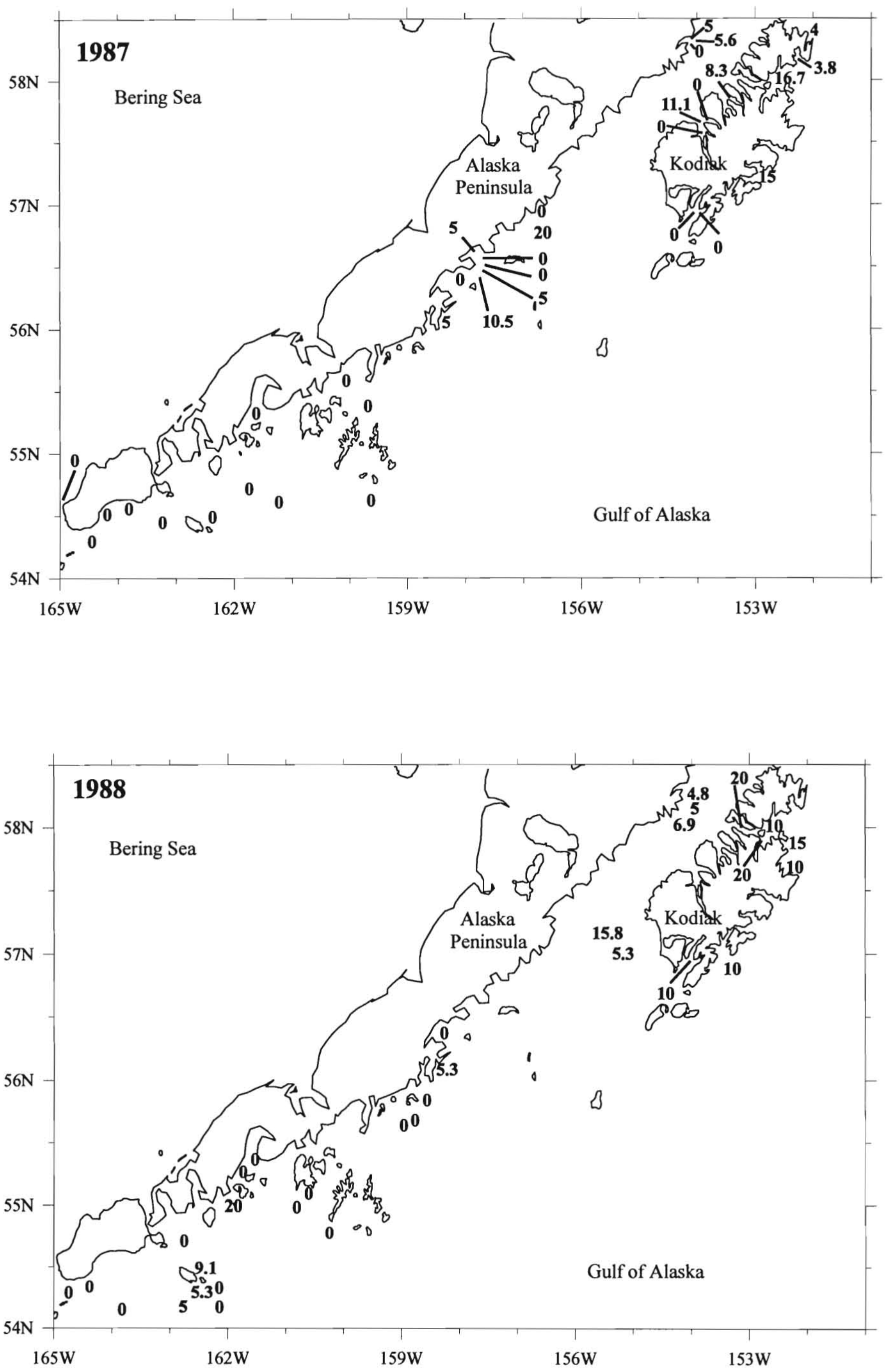

Figure 12
Site-specific prevalence of *Chloromyxum* sp. in juvenile walleye pollock in 1987 (above) and 1988 (below).

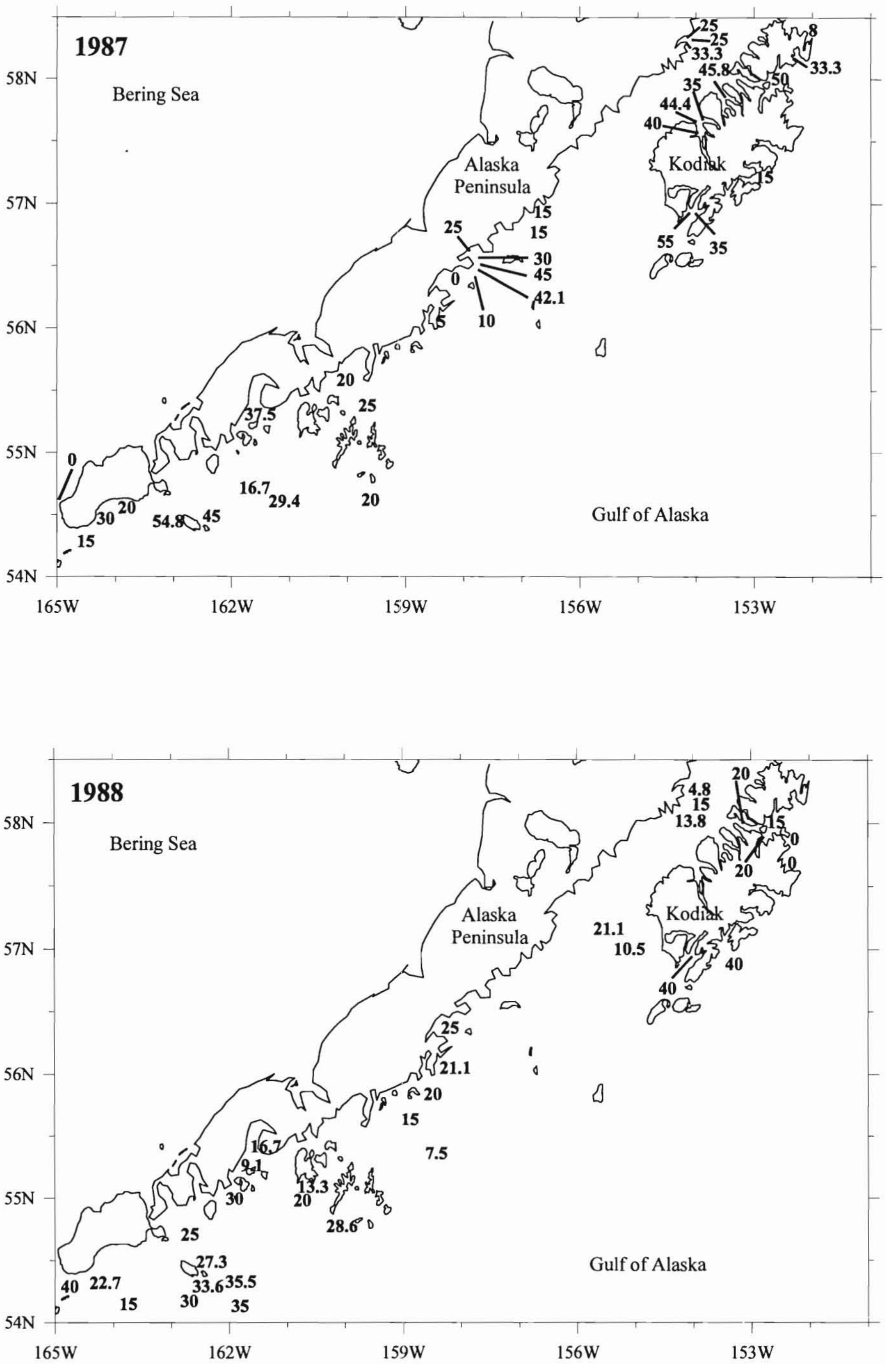

Figure 13

Site-specific prevalence of unidentified trematodes in juvenile walleye pollock in 1987 (above) and 1988 (below).

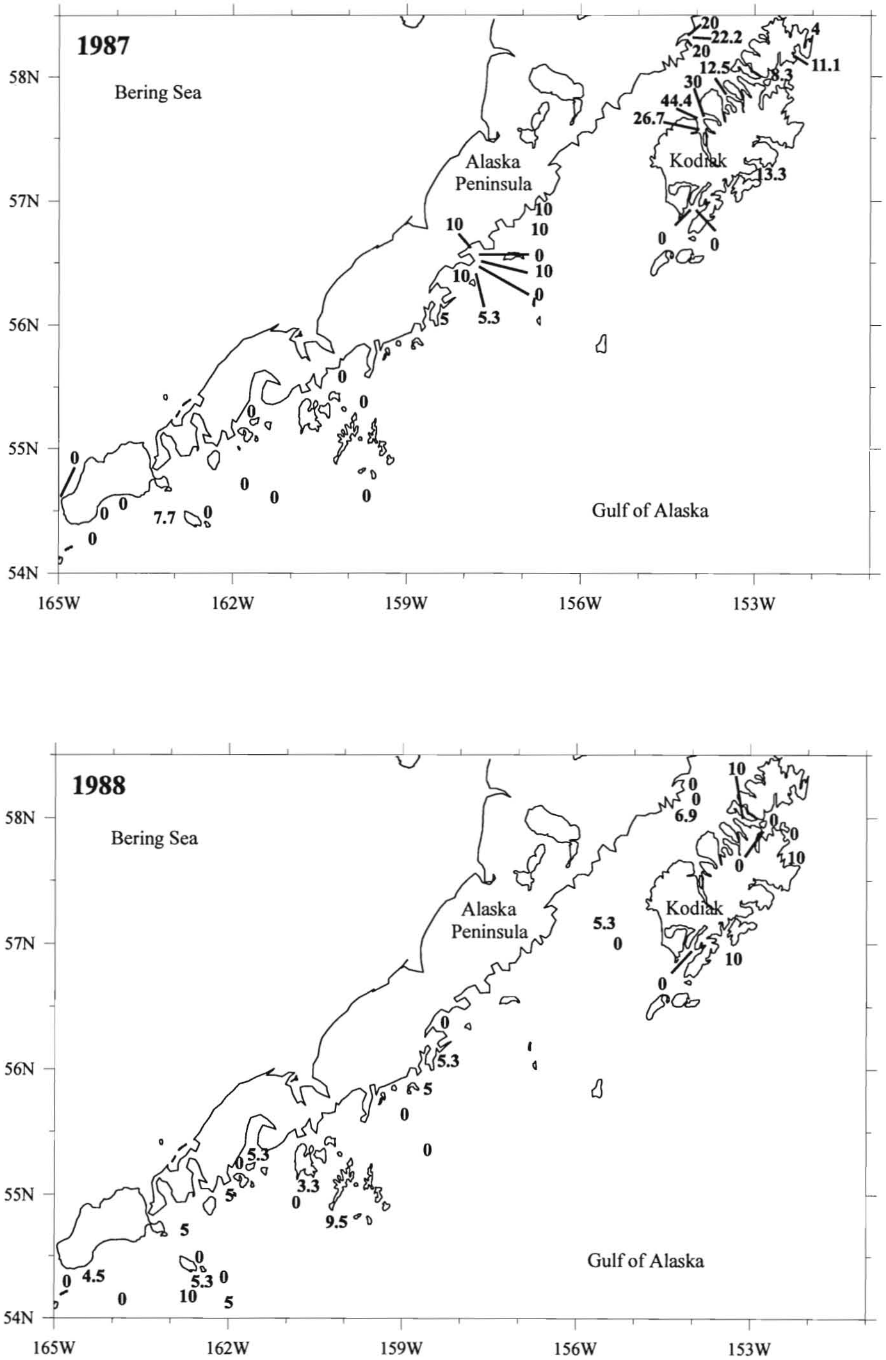

Figure 14
Site-specific prevalence of unidentified cestodes in juvenile walleye pollock in 1987 (above) and 1988 (below).

replaced by connective tissue. Indeed, liver function and size of Baltic cod, *Gadus morhua*, parasitized by juvenile nematodes are inversely proportional to the level of nematode infection (Margolis, 1970). However, a correlation between parasitism and tissue function was not obvious in juvenile walleye pollock.

The major spawning site of Gulf of Alaska walleye pollock is a trough off Cape Kekurnoi. Eggs and larvae subsequently drift to the southwest, out of Shelikof Strait and parallel to the Alaska Peninsula (Kim and Kendall, 1989; Kendall and Picquelle, 1990; Hinckley et al., 1991). But the distribution patterns of parasites in

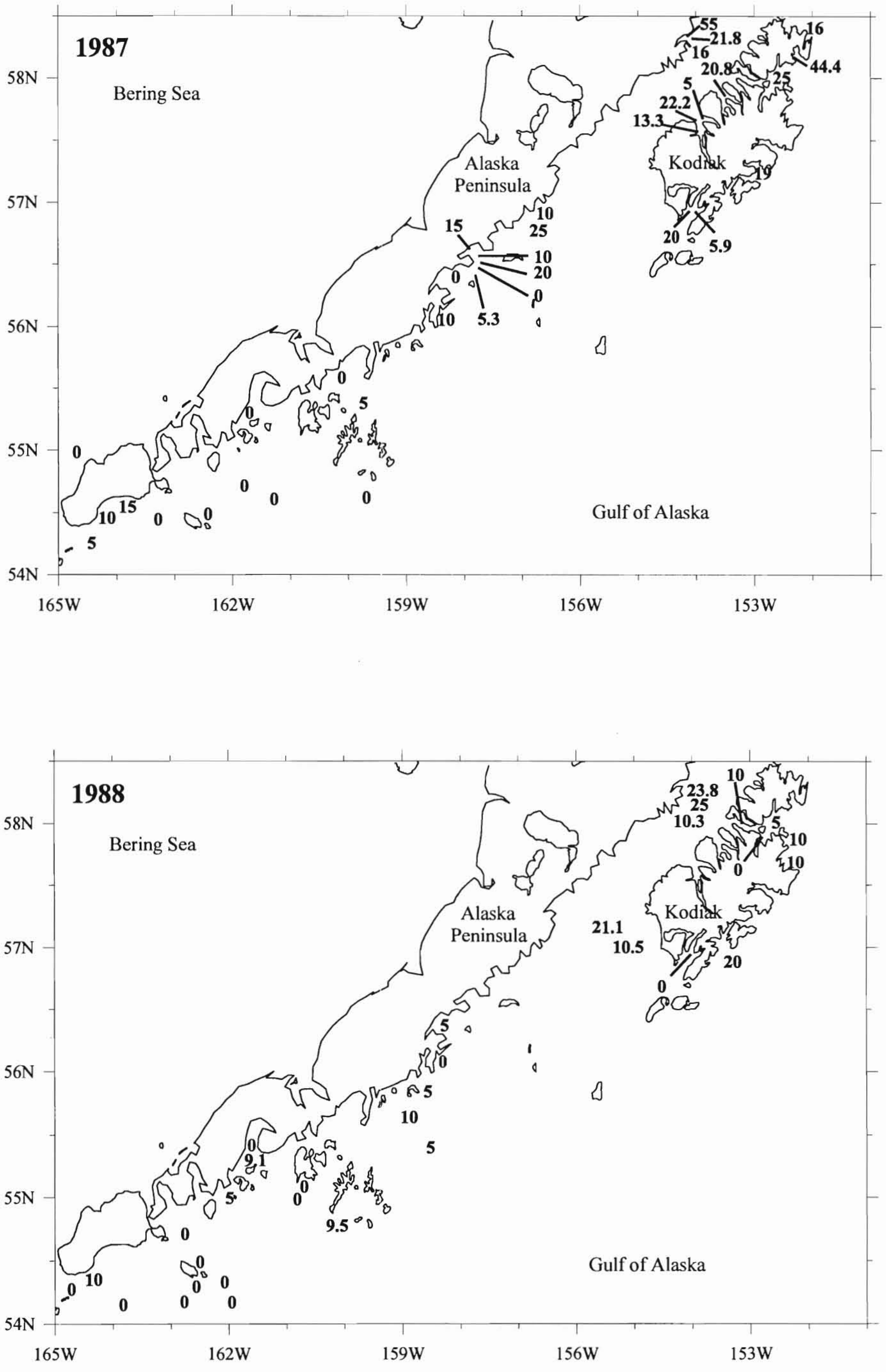

Figure 15
Site-specific prevalence of unidentified nematodes in juvenile walleye pollock in 1987 (above) and 1988 (below).

juvenile walleye pollock throughout the survey area suggest that it is unlikely that recently hatched fish from the Shelikof Strait spawning population populate all bays around Kodiak Island, especially Marmot Bay. It thus appears likely that smaller and possibly distinct spawning populations exist throughout the Gulf of Alaska.

Parasites are often unique to particular ecosystems. This principle has been frequently used to help identify various fish stocks (MacKenzie, 1983; Moller and Anders, 1986; Rhode, 1993). Juvenile parasite stages are the most useful for this purpose because they are acquired early, remain viable within the host for several years, and—because they are acquired throughout the host's life span—may reflect the host's migration through various ecosystems. All the parasites encountered in this study, but especially the nematodes and digenetic trematodes, should be identified to species, since this may provide information on the existence of one or more walleye pollock stocks in the Gulf of Alaska. Knowledge of the parasite fauna of exploited fishes may also provide information about stock composition at the time of harvesting.

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Growth of Juvenile Walleye Pollock, *Theragra chalcogramma*, in the Gulf of Alaska

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Recruitment of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska can be influenced by processes affecting survival during the late larval and early juvenile phases of life. As part of an ongoing study of factors affecting recruitment dynamics of pollock, we monitored length-at-age growth rates by otolith micro-increment analysis of age-0 pollock caught in annual surveys from 1985 to 1991. Aggregated seasonal length-at-age data were used to infer growth rates that could be compared by geographic region and year. Both geographic and interannual differences in growth rates were detected. Mean growth rates can vary by 40% between years. Intra-annual differences in growth rates by geographic region can vary by a similar amount. There were no obvious relationships between growth rates and gross approximations of age-0 juvenile density and sea surface temperature. However, age-0 growth rates in the relatively high recruitment years of 1985 and 1988 were high compared with those in the weak year classes of 1987 and 1991.

The Growth of Walleye Pollock, *Theragra chalcogramma*, and Structure of Scales during the First Year of Life

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Comparative studies of the juvenile growth of walleye pollock, *Theragra chalcogramma*, are of great importance both in population investigations and for estimating production. Scientists at TINRO have recently conducted research on walleye pollock growth during the first year of life which has involved study of the first annulus on calcified structures and of juvenile pollock size in different regions (Fig. 1).

The great difference in spawning times between areas of winter and spring reproduction causes wide variation in the size of juveniles in Far Eastern seas. In various areas of the Bering Sea, the mean size of juveniles in late autumn ranges from 7 to 11 cm. An analogous situation occurs in Pacific waters off Kamchatka and in the northern Sea of Japan. In the Sea of Okhotsk, juvenile pollock are generally smaller (6.5–10 cm); in late autumn the mean size of juveniles in the south is 12–13 cm. Evidently, differences in mean size (1.5 cm or more) of juveniles in the western Bering Sea and Sea of Okhotsk can be explained by differences in their food supply; mesoplankton biomass is over twice as high in the western Bering Sea as in the Sea of Okhotsk.

In November–December, and even by the end of the winter, the sizes of juvenile pollock are scarcely different from the sizes of those collected in October. This indicates a significant slowing of the growth rate of juveniles in late autumn despite a lack of change in their feeding. A slight increase in growth is observed the following spring. The long duration of spawning and the different growth conditions result in a great range in juvenile sizes at the end of the first year of life. In the western Bering Sea and Sea of Okhotsk during October–November and January–March, the size distributions of pollock include specimens from 4 to 6 cm as well as from 12 to 14 cm, which may cause errors in defining ages by length distribution. Because of the great temporal extent of spawning in many areas where there are differences in transport by currents, body length increases with distance from spawning grounds. In the western Bering Sea, the difference in juvenile

Table 1

Mean values of parameters measured on the first annulus of walleye pollock scales from different regions of the Sea of Okhotsk and the Sea of Japan.

Region	Radius (microns)	Number of sclerites	Mean intersclerite distance (microns)
Sea of Okhotsk			
South Kuril Islands	638.9	13.4	47.7
Okhotksy region	448.4	9.4	47.7
Northeastern Sakhalin	429.6	9.5	45.2
Yamsko-Tauysky region	410.3	8.9	46.1
Southwestern Kamchatka	388.7	8.2	47.6
Northwestern Kamchatka	363.8	8.0	45.7
Iono-Kashevarovsky	363.8	7.4	45.1
Sea of Japan			
Tatarsky Strait	412.5	7.3	56.5
Southwestern Sakhalin	436.0	8.5	50.8
Peter the Great Bay	505.5	10.9	47.5

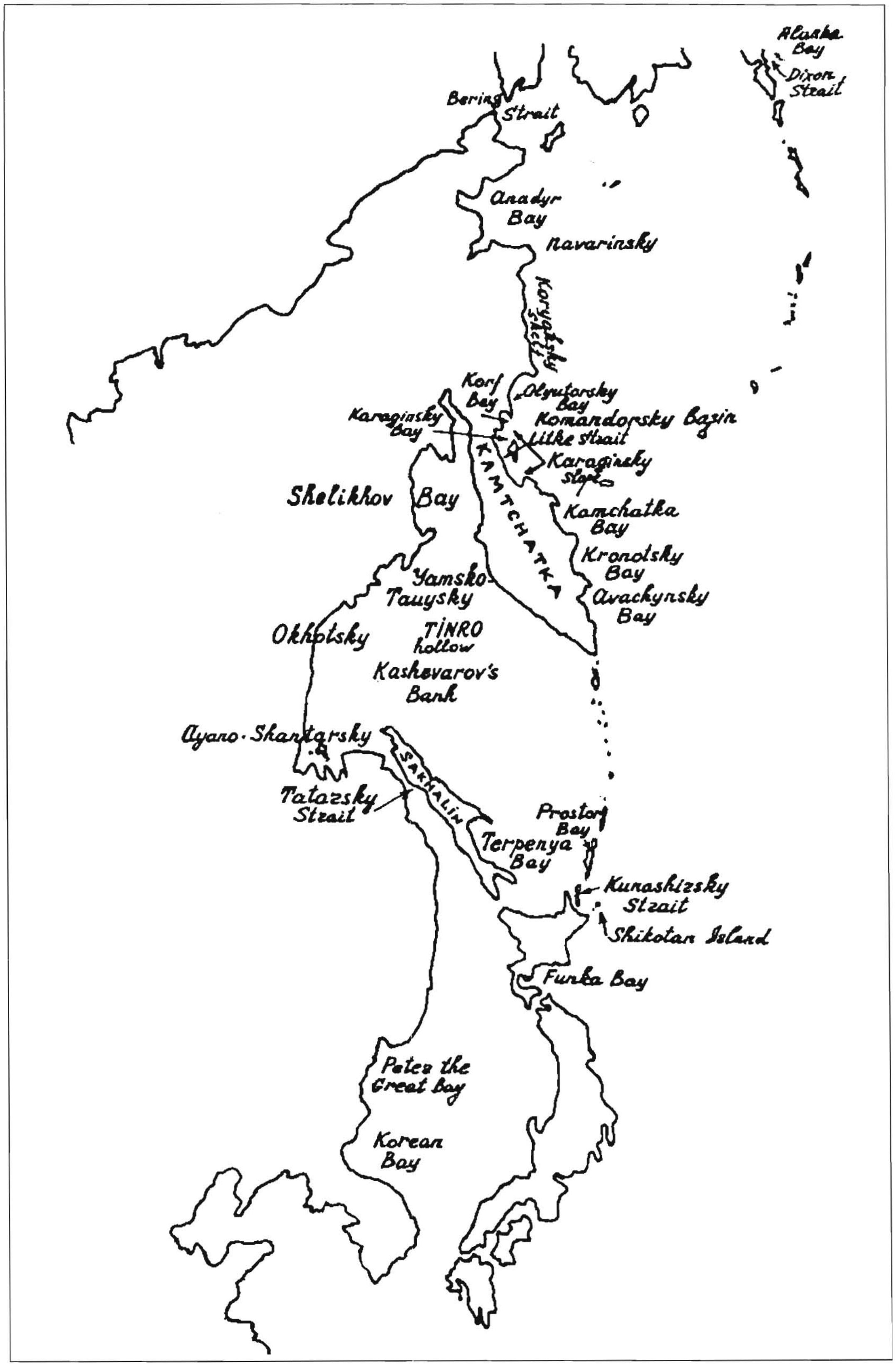

Figure 1
The investigation regions.

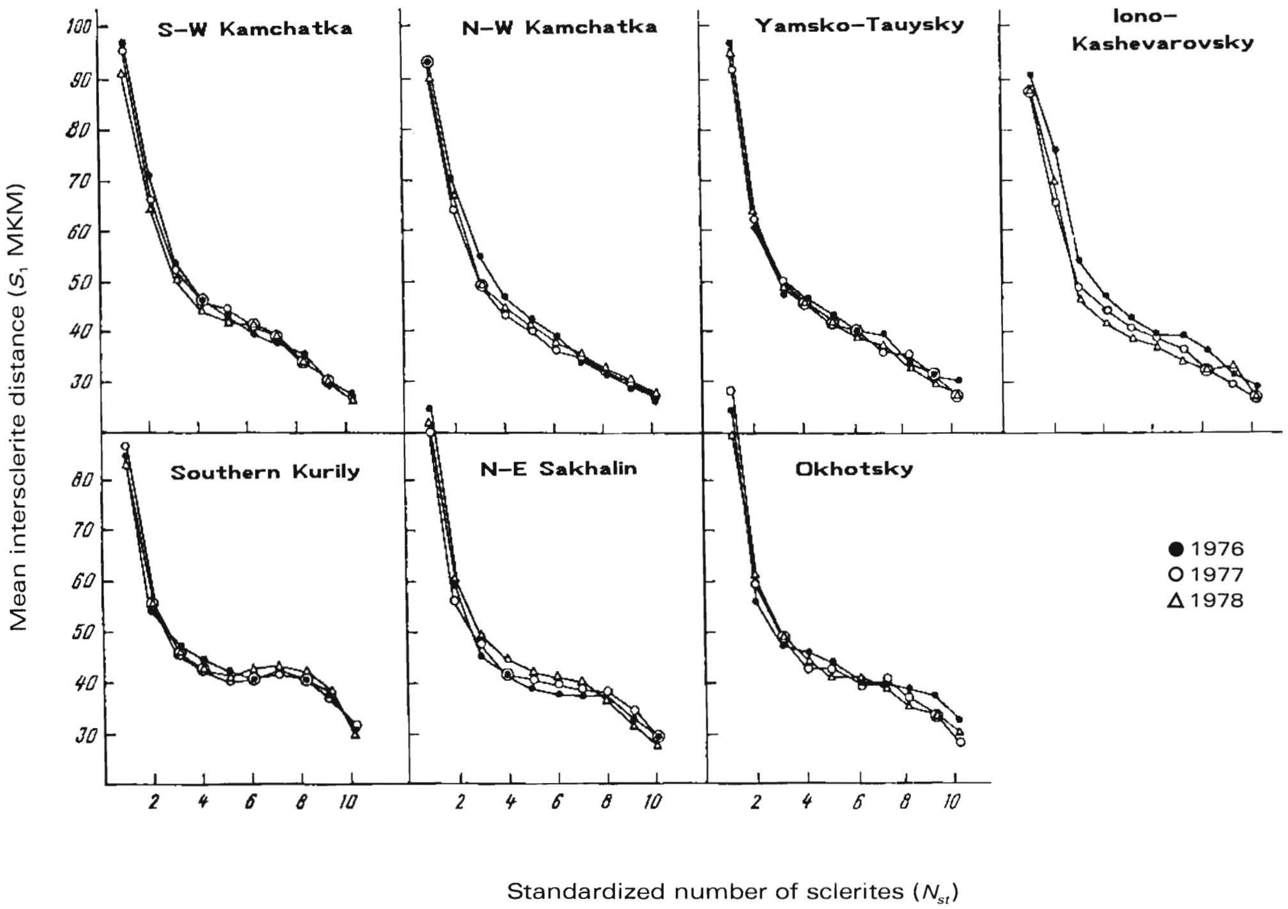

Figure 2

Scleritograms of the first annulus for pollock from different regions of the Sea of Okhotsk, for 1976–78.

mean length is 0.6–1.6 cm in catches from the shelf, slope, and Aleutian basin waters. Our data indicate that growth is controlled by factors such as the temperature of water and food supply interacting with population density.

The characteristics of the first-year annulus in pollock scales reflect the variability of juvenile growth in the various areas of the Far Eastern seas (Fig. 2). The sizes of annuli from the Sea of Okhotsk vary from 364 microns (7.4 sclerites) in the Iono-Kashevarovsky area to 639 microns (13.4 sclerites) in the south Kuril Islands area (Table 1). The larger walleye pollock juveniles (9.6–13 cm) in the Sea of Japan have a lesser range of size of the first-year annulus than those from the Sea of Okhotsk, mainly because of greater intersclerite distance. The first-year annuli of fish from Peter the Great Bay and the south Kuril area are characterized by an additional ring in the center. The presence of this ring is connected with a cessation of growth that occurs as juveniles are vertically displaced to demersal layers.

Distribution, Recruitment, and Survival of Juvenile Walleye Pollock, *Theragra chalcogramma:* What Role Does Behavior Play?

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Behavioral responses of age-0 juvenile walleye pollock, *Theragra chalcogramma*, to both abiotic and biotic factors may play a major role in controlling distribution, recruitment, and survival. Success in extrapolating results from laboratory to field depends on how well the laboratory environment permits juveniles to fully express their behavioral potential. Under laboratory conditions, the vertical distribution of juveniles was shown to be influenced by a variety of extrinsic and intrinsic factors. Distribution above and below a thermocline was influenced by light intensity, food distribution, level of hunger, presence of predators, and ontogenetic differences in behavioral thermoregulation. Differences in food availability and distribution were shown to affect the way in which juveniles either dispersed or aggregated into distinct schools. Juveniles respond to a hierarchy of interacting environmental factors, which may be modified by their internal state and ontogenetic development. Defining the behavioral response ascribed to any one factor is insufficient for prediction of juveniles' behavior when faced with multiple factors in the natural environment.

Electron Microprobe Analysis of Otoliths of Juvenile Walleye Pollock, *Theragra chalcogramma*, from Alaska: A Pilot Stock Separation Study

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Dissolved oceanic constituents incorporated into the otoliths of fish may serve as chemical tracers for reconstructing the early life history of marine fish. Wavelength-dispersive spectrometers on an electron microprobe were able to detect Na, Mg, P, S, Cl, K, Ca, and Sr concentrations on the outer margins of otoliths from 57 juvenile walleye pollock, *Theragra chalcogramma*, from five locations in the Gulf of Alaska and eastern Bering Sea. Discriminant analyses that used various combinations of Na, P, K, Sr, and standard length of fish showed that 60%–70% of the samples could be assigned to the correct capture locality. Although the concentrations of some of the measured elements were correlated with standard length of the fish, there were measurable differences among localities when concentrations were length-corrected, mainly because of differences in Na and K concentrations. Elemental composition of otoliths potentially could be used to assign fish from a mixed-stock fishery to original stocks, information that is greatly needed for the effective management of fish stocks.

Ecology and Growth of Juvenile Walleye Pollock, *Theragra chalcogramma*: Summary and Recommendations for Future Research

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There has recently been considerable progress in understanding the ecology and growth of larval walleye pollock, due to the large programs conducted by the United States and Japan. Fewer studies have been conducted of the juvenile stage of walleye pollock, however. This stage is usually more dispersed, harder to sample quantitatively (because of lower abundances and greater mobility), and is believed to have a lower instantaneous mortality rate (but a longer duration) than the larval stage. This lower instantaneous mortality rate suggests that "internal" processes such as feeding and growth (i.e., starvation) may be less important to population fluctuations than "external" causes of mortality such as predation. In practice, however, partitioning the major sources of mortality, and therefore variability in juvenile abundance, is very difficult because of assumed interaction effects such as predator selection of starved or disease-weakened fish. Studies of the feeding and growth of juveniles are therefore crucial to a complete understanding of the population dynamics of walleye pollock.

This commentary presents a view of future directions for research on the ecology, feeding, and growth of juvenile walleye pollock. It is based on presentations and discussions that took place during the Juvenile Pollock Workshop. In the session on ecology and growth, five papers and three posters were presented, of which three papers and four abstracts have been included in this volume. I will first discuss specific points from these presentations, then discuss broader research issues, and conclude with suggestions for the types of analyses that might be considered in future field programs.

Merati and Brodeur (1996) present important information and questions on the diets and feeding activities of juvenile walleye pollock. They conclude that feeding occurred predominately at night, which is contrary to the conclusions of previous studies on the larval stages. How, then, do the juvenile fish detect their prey in darkness, and how do they maintain contact with their conspecifics? What might be the reason for the switch from the larval behavior? Merati and Brodeur's conclusion about the timing of feeding is important for comparisons with prey distributions and for modeling and behavioral studies. Interestingly, they did not find any sharp ontogenetic changes in diet, and prey composition changed gradually with time of day and with fish size. However, they sampled a limited size range of fish (49–113 mm); broader comparisons should include sizes of juvenile pollock that inhabit greater depths. The strongest variations in diet were attributed to location effects, and it would be useful to compare diet composition with the local concentration of plankton in each of the areas sampled to determine the degree of prey selectivity. Also of interest would be an assessment of the nutritive values of the different prey from the different areas, perhaps coupled with laboratory studies of prey "desirability."

Nishimura, Mito, and Yanagimoto (1996) present a tantalizing study of growth estimates and stock origin based on otoliths. Otoliths provide an excellent means to develop growth histories of individual fish, to identify the temporal spawning distribution (of survivors), and thereby to infer possible spawning location and stock origin. If the spawning areas are sufficiently different in location, as may be the case for the three areas in the Bering Sea (Hinckley, 1987), then the microelemental composition of the otoliths may also be used to identify the spawning areas and stock origins of the fish (e.g., see Norcross et al., 1996). The elemental composition (e.g., the Sr/Ca ratio) of the otoliths may also indicate the temperatures experienced by the larvae and juveniles during growth, which—when combined with oceanographic surveys and circulation modeling—could be a powerful tool for reconstructing past distributions. Development of growth histories would be particularly useful for comparing the hatch dates of survivors from different spawning populations that experienced significant oceanographic and biological events. Such growth histories can be compared with particle trajectories and feeding dynamics derived from circulation and trophodynamic models. However, the potential for a long spawning period and multiple spawnings by individual fish (e.g., Sakurai, 1993) might complicate the process of distinguishing separate spawning populations. Evidence of the variability of growth histories is provided by Brown and Bailey (1996). Using otoliths of age-0 pollock from the western Gulf of Alaska over the period 1985–91, they found geographic and interannual differences in growth rates that range up to 40%.

Shuntov, Temnykh, and Radchenko (Temnykh and Radchenko, 1996), who also looked at fish ages derived from scales and estimated from age–length conversions, caution that growth rates (and therefore size-at-age) may differ substantially among juvenile pollock from different areas, possibly due to zooplankton densities, temperature, and population densities of juvenile pollock.

Morado and McFee (1996) provide a different view of feeding and growth in their study of the diseases and parasites that might inhibit growth of the host fish. In a sense, such parasites can be considered predators, particularly when they increase the mortality of the host. Parasites may be important to consider if they affect the growth of fish despite sufficient food, and/or if they increase the host's susceptibility to predation. They may also contribute to the identification of stock origins.

Although not included in its entirety in this volume, the presentation by Olla et al. (1996) (also see Olla et al., 1995) introduced a number of questions about the ecology and growth of juvenile pollock and the ability to use this information in management. They showed that the distribution of juvenile pollock above and below a thermocline was influenced by a number of physical, behavioral, and physiological conditions such as light, food, level of hunger, presence of predators, and ontogenetic differences in response to temperature. In addition, differences in food availability affected the degree to which juveniles dispersed or aggregated into distinct schools. The authors concluded that using behavioral responses to single factors was insufficient for predicting responses to the multiple factors experienced in the real world. Some of these results have been described in Olla and Davis (1990), Ryer and Olla (1992), and Sogard and Olla (1993).

Recruitment predictions using feeding and growth characteristics of larval and juvenile fish have been less common, and perhaps less successful, than predictions using physical processes alone (e.g., Sinclair, 1988; Mullin, 1993). Houde (1987) suggested that recruitment variability may be dominated by physical processes (such as transport to or from appropriate areas), with the remaining variability due to biological processes such as feeding and predation (which themselves may be physically mediated; e.g., Rothschild and Osborn's [1988] turbulent contact-rate hypothesis). Since a principal goal of research on walleye pollock early life history is recruitment prediction, one of the first tasks should be to estimate which stocks or areas are likely to have recruitment dominated by physical processes, and which stocks might be more influenced by biological processes. Studies on the ecology, feeding, and growth of juvenile stages for recruitment predictions should be most profitable in these latter areas. Circulation models are one tool for assessing the extent of particle retention and dispersion in an area and therefore the relative importance of physical and biological processes to recruitment variability.

An important point that can be drawn from all the presentations in this workshop concerns the long duration of the "juvenile" stage in walleye pollock. The juvenile stage is defined as lasting from about 60 days to 2–3 years of age by the traditional limits, from postmetamorphosis to recruitment to the adult fishery. This implies a size range from 25 mm to 300 mm, and a change in capabilities from planktonic to fully nektonic. The juvenile stage therefore includes large changes in prey and predator fields, and a very large reduction in numbers. Perhaps this stage should be viewed as several stages, each with possibly different ecologies, growth patterns, vertical and horizontal distributions, and relationships with the environment. Consideration should also be given to the concept of a threshold size or condition factor that is critical for pollock to survive to the next stage. Habitat (distribution) differences might be used as one criterion for separating these stages, supplemented with information on diet and behavior, although as Olla et al. (1996) pointed out, differences in the latter may be very subtle but still important. The age of juveniles is probably the best determinant of a particular stage, but age determinations (from otoliths) are time-consuming and expensive for large sample sizes. Length is probably not a good indicator of stage within the juvenile phase since it is likely to be influenced by temperature, food, and other growth conditions that vary among locations and years. Prey, predator, or competitor fields that remain with the pollock as they grow through the various juvenile stages (such as cannibalism or parasitism) may have a greater effect on pollock growth and survival than fields which the juvenile pollock encounter for only short periods. Their relative effects could be estimated by multiplying some measure of instantaneous mortality or growth success for a factor by its duration.

None of the papers presented in this session considered animals longer than 130 mm; all examined what Dwyer et al. (1987) have defined as age-0 fish. There is a need to examine older juveniles, possibly those inhabiting deeper depth zones or shallow nearshore areas. A variety of sampling systems will be necessary to adequately capture these various juvenile life-history stages.

Gelatinous zooplankton may play several important roles in the ecology and growth of juvenile walleye pollock, yet they are often difficult to sample quantitatively. They can be competitors with pollock for zooplankton prey (e.g., copepods); they can be prey for pollock (e.g., *Oikopleura*); or they may possibly be commensal with pollock by providing a refuge from predators or perhaps a prey-aggregation mechanism (as has been suggested by Koeller et al. [1986] for haddock in the northwest Atlantic). Merati and Brodeur (1996) observe that *Oikopleura* sp. were a common and abundant prey item in pollock 50–115 mm long (the size range that they sampled). Large "jellyfish" are also very abundant in summer during acoustic and trawl surveys of the Bering Sea and Gulf of Alaska, and the associations of juvenile pollock with these potential hosts should be examined. The nutritive value of gelatinous zooplankton should also be examined, since they may serve as alternate prey when other food is scarce.

The amazing flexibility of behavioral responses by juvenile pollock to almost all stimuli, as presented by Olla et al. (1995, 1996) (and by Temnykh and Radchenko, 1996) is potentially a great hurdle in modeling their ecology and growth. The problem is compounded by observations that such plasticity seems to develop as the juveniles become more competent, with fish smaller than 40 mm being more predictable in their responses. Determination of the significance of such variability, and whether it should be considered in population-level models, is crucial. Individual-based modeling approaches that incorporate such behavioral plasticity (e.g., Tyler and Rose, 1994) are one method of determining the importance of this variability to population-level characteristics. For example, how critical is the observation that pollock avoid cold water except when they are sufficiently hungry? One solution may be to integrate individual responses to multiple stimuli by using population-level responses (e.g., population means, which ignore individual variability). Indices that represent processes occurring on long time scales may also integrate over short-term (behavioral) variability. Such indices for growth success include otolith daily growth rings, morphological condition factors, and indices of nutritional condition such as carbon and nitrogen composition, RNA/DNA ratios, and lipid analyses (e.g., Hakanson et al., 1994). Comparison of the variability of indices (with different time scales) among fish in a school or sample should also identify how long the school remained together within the same feeding conditions.

Although the ability to detect the condition of individual larvae is reasonably well developed—e.g., by means of the biochemical indices mentioned above—the ability to detect food limitation of larval and juvenile fish populations and its effect on survival remains an active problem in fisheries research (e.g., Mullin, 1993). It is still difficult to determine the effective prey concentration for larval and juvenile fishes, considering large-scale processes such as vertical migration, and small-scale processes such as turbulence and predator–prey contact rates. The problem can be expressed in terms of the carrying capacity of a particular area, such as the Bering Sea, for juvenile pollock. However, if the long juvenile period of walleye pollock does represent several distinct stages, then perhaps there should be several carrying capacities. The large larval and juvenile populations of walleye pollock in the Gulf of Alaska and the Bering Sea might make it possible to detect food-limitation effects and carrying capacity limits in these areas. Population-level behavioral responses may also be a valuable and novel method for assessing carrying capacity and food-limitation concepts. For example, Olla et al. (1996) noted that school dynamics of juvenile walleye pollock will change if they are under stress from lack of food, so that the interfish distance becomes smaller. Unfortunately, a similar response can also be elicited in the presence of predators engaged in active predation, although it was observed that the effect did not persist long after the predator had departed.

A program to investigate the ecology and growth of juvenile walleye pollock should consider several approaches. It should first recognise that there may be several stages within the juvenile phase, possibly each with different sampling requirements. The distributions of these stages should be mapped to identify contrasting areas of abundance. It would be particularly useful for study of carrying capacity problems if these areas persisted over several years. Condition and growth characteristics of fish from each contrasting area could then be compared with several indices having different time scales of response to food stress. These include:

- behavioral:
  small-scale fish distributions (interfish distances)
- otoliths:
  age confirmation
  hatch-date analysis (also for confirmation of stock origin)
  elemental analysis
  time history of growth, for comparison with oceanographic and meteorological events
- feeding success:
  stomach fullness and contents identification (short timescale)
  biochemical: RNA/DNA, proteins, lipids (intermediate timescale)
  morphometrics, e.g., condition factor (longer timescale)
  stable isotope composition of various body organs, for possible identification of trophic position and geographic location of feeding

- parasites:
  stock origin
- modeling:
  early life-history distributions (circulation modeling) and growth potential (trophodynamic modeling)
  sensitivities to various behavioral strategies

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Interdecadal Comparisons of Walleye Pollock, *Theragra chalcogramma*, Cannibalism in the Eastern Bering Sea

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ABSTRACT

Diet composition and cannibalism of walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea were compared over a series of years in the 1970's and the 1980's. No significant interdecadal differences in diet composition were found. The contribution of copepods to the diet, as measured by percent weight of stomach contents, was related more to predator size than to year. The percent weight of euphausiids in the diet was relatively constant by year for the 1985–89 period and was similar between the two walleye pollock size groups (<40 cm and ≥40 cm) over all the years. Amphipods contributed little to the diet (<4% by weight) for most years regardless of size or year, except for 1974. There was a definite trend in the percent weight of walleye pollock in the diet by predator size and by year. Cannibalism rates were highest in larger walleye pollock, and rates for both size groups showed similar declines from 1971 to 1989. In the 1985 to 1989 period, the weight percentage of pollock in the diet was highly correlated (r^2=0.99) with an index of age-0 and age-1 walleye pollock biomass in each year. This evidence suggests that walleye pollock year-class strength is currently the main factor that determines the level of cannibalism during summer. The lack of fit of the 1970's cannibalism rates to the biomass index of age-0 to age-1 pollock may be due to several factors, including low sample sizes for some years and incomplete knowledge about the absolute level of pollock biomass during that period.

Introduction

Walleye pollock, *Theragra chalcogramma*, is a dominant component of the groundfish complex in the eastern Bering Sea (Bakkala, 1993). The large biomass of walleye pollock relative to that of other groundfish species in the eastern Bering Sea makes pollock important as a predator on populations such as juvenile walleye pollock, and as a competitor with predator populations such as marine birds and northern fur seals, *Callorhinus ursinus*.

The food habits, including cannibalism, of walleye pollock in the eastern Bering Sea have been studied frequently (Mito, 1974; Livingston et al., 1986, 1993; Dwyer et al., 1987; Livingston, 1989, 1991, 1993; Mito[1]). Our intent is not to provide a detailed description of the diet of walleye pollock, but to compare diet composition from two separate time frames. Inspection of patterns in walleye pollock prey consumption over several years may yield important information on how pollock use the prey resources available to them. We examined data obtained during May through September on the eastern Bering Sea continental shelf for two periods (1970, 1971, and 1974; and 1985 through 1989) to determine predator size and year-related patterns in diet composition.

Materials and Methods

A total of 18,422 walleye pollock stomachs were analyzed from samples collected in 1970, 1971, 1974, and 1985–89 (Table 1). These years were analyzed because they were the only years in which pollock stomach samples were obtained over a broad area on the eastern

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[1] Mito, K.-I. 1990. Differences in the weight and composition of stomach content of pollock between areas in the Bering Sea. Document submitted to the Annual Meeting of the International North Pacific Fisheries Commission, Vancouver, Canada, October 1990, 17 p. Fisheries Agency of Japan, National Research Institute of Far Seas Fisheries, 7-1 Orido 5 chome, Shimizu, Shizuoka, Japan 424.

Table 1

Number of stomachs collected, number of hauls, and sampling dates for walleye pollock, *Theragra chalcogramma*, collections in the eastern Bering Sea.

Year	Sampling dates	No. hauls	No. stomachs
1970	7/2–8/2	66	1,678
1971	6/1–9/9	52	1,684
1974	5/5–8/28	116	5,514
1985	6/8–9/30	103	965
1986	5/2–9/30	236	1,927
1987	5/4–9/30	167	2,119
1988	5/2–9/29	218	2,002
1989	6/6–9/29	225	2,533
Total			18,422

Bering Sea shelf during a similar time of year. Samples from 1970, 1971, and 1974 were collected by Japanese scientists aboard research vessels; samples from 1985 through 1989 were collected by Alaska Fisheries Science Center (AFSC) scientists. Although data collected by Japanese and AFSC scientists were available for other years, only samples from the years presented here were taken on the shelf during the same time period (May through September) as our samples from the 1980's. Sample collection and analysis procedures employed by the Japanese scientists is described by Mito[1]; AFSC scientists used the procedures described by Livingston (1991).

Diet composition was determined for two size groups of walleye pollock: <40 cm and ≥40 cm. These size groups were used because previous research on walleye pollock diet in the eastern Bering Sea showed a sharp increase in the amount of cannibalism by fish larger than 40 cm (Dwyer et al., 1987). We considered the following five prey categories which together constituted almost 80% of the diet by weight over all the years considered: walleye pollock (10%); copepods (32%); euphausiids (30%); capelin, *Mallotus villosus* (1%); and amphipods (5%). A sixth category containing miscellaneous and unidentified prey was also used. Diet composition was determined separately for each size group for six geographic strata. Six strata were defined by depth zone (<50 m, 50–100 m, and 100–200 m) and area (north of the Pribilof Islands and south of the Pribilof Islands). In each stratum, percent weight of each prey species in the diet of each size group of pollock was calculated as the average of the percentages at all sampling stations. The percent contribution of each species to the diet of each size group was then estimated for the whole area as the weighted average of the stratum means, with weights being the biomass of the size group in each stratum. Variation in diet composition in terms of percent weight was calculated from the between-station variance in diet composition for a particular predator size group in a stratum.

Calculation of prey biomass consumed (see Livingston, 1991 for details) required predator biomass estimates by size and stratum in the eastern Bering Sea, which were not available for 1970, 1971, and 1974. Walleye pollock biomass estimates by age from the cohort analysis of Wespestad and Dawson[2] were partitioned into strata for 1970, 1971, and 1974, based on the average proportion of the biomass at age in each area, determined from bottom trawl surveys during the 1985–89 period.

The index of age-0 and age-1 walleye pollock biomass available as prey in each year was derived from cohort analysis estimates of age-2 walleye pollock abundance, assuming annual instantaneous mortality rates of age-1 fish to be 0.85/yr (Wespestad and Terry, 1984) and of age-0 fish to be 1.2/yr.

Results

Walleye pollock cannibalism occurred primarily in the middle shelf (50–100 m bottom depth) and outer shelf (100–200-m) zones in the eastern Bering Sea for all years of our study (Fig. 1, 2). Geographic extent of stomach sampling was least in 1974 and 1985 and most comprehensive in 1989. Percent by weight of pollock in the diet varied slightly by location among years, although each year showed several stations with high (>50% by weight) levels of predation on walleye pollock.

Walleye pollock predator biomass was relatively constant throughout all years of the study (Fig. 3). The largest biomass was seen in 1971 (11 million metric tons [t]) and the smallest in 1989 (8 million t), with an average of approximately 10 million t. The biomass by size group was also relatively constant throughout all years (Fig. 3).

Amphipods represented a relatively small portion of the diet of both sizes of walleye pollock in all years except 1974 (Fig. 4). Percent contribution to the diet by weight ranged from 0% to 23%.

Euphausiid prey were found to be equally important in the diet of both size groups of walleye pollock in terms of weight (Fig. 5). However, some interannual variation in the amount of euphausiids in the diet was seen, particularly in 1974 relative to the other years.

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[2] Wespestad, V. G., and P. Dawson. 1992. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1993, p. 1-1:1-32. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

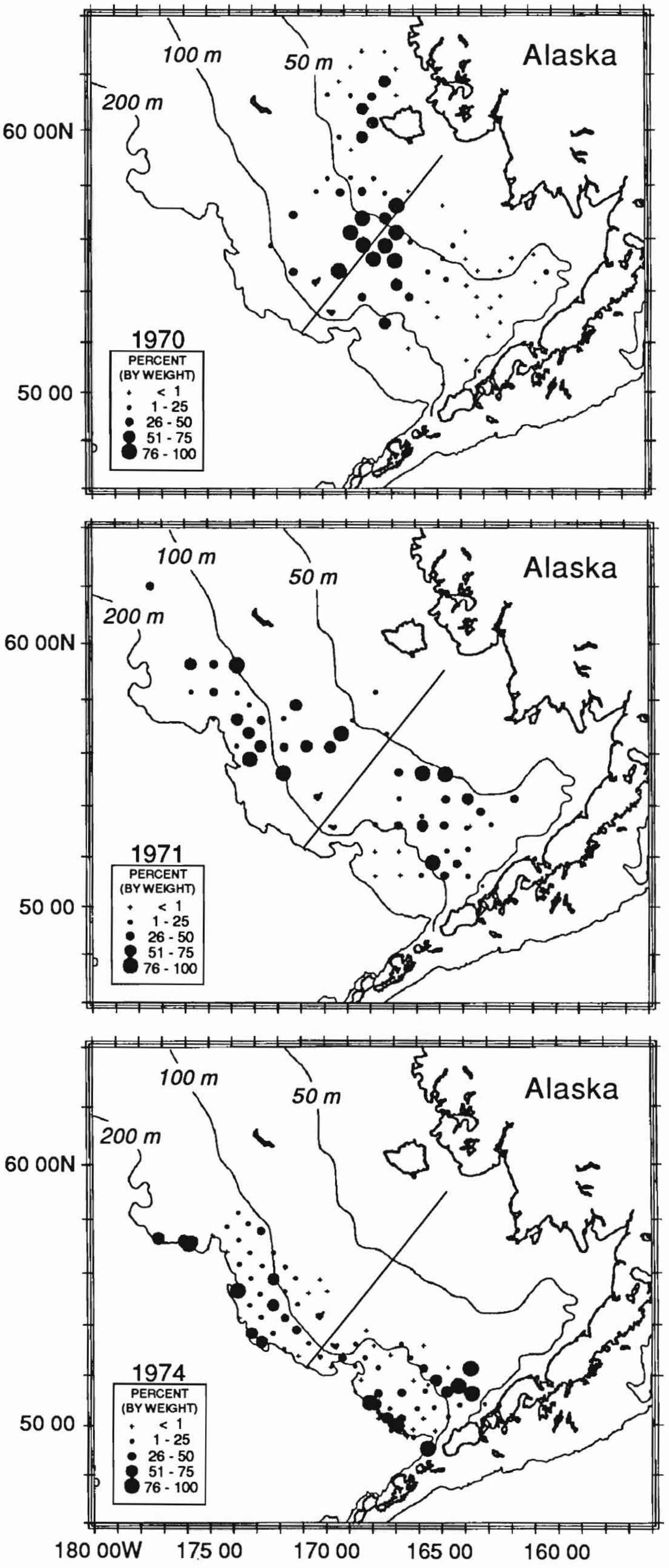

Figure 1

Geographic location of walleye pollock cannibalism in the eastern Bering Sea by percent weight for the years 1970, 1971, and 1974.

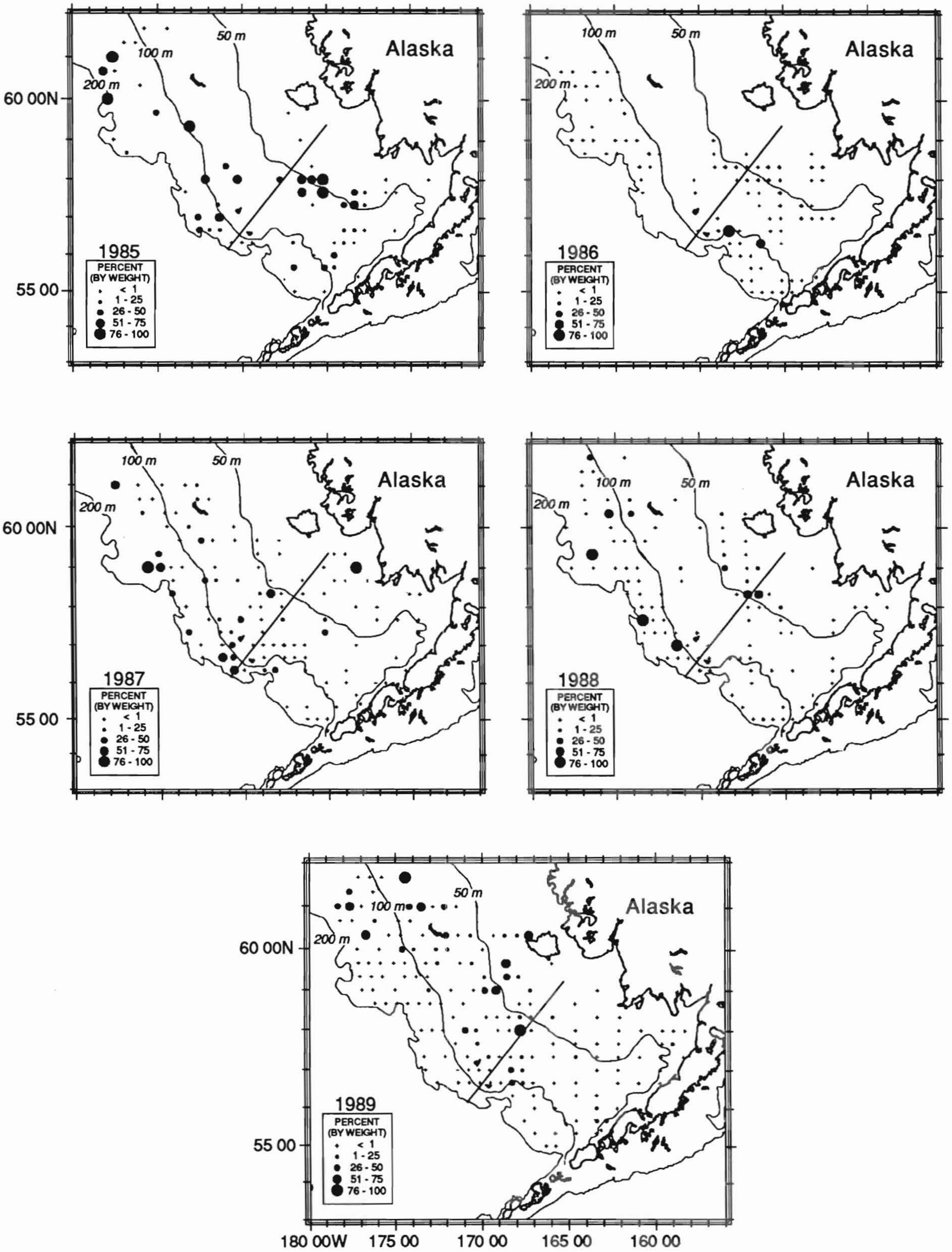

Figure 2

Geographic location of walleye pollock cannibalism in the eastern Bering Sea by percent weight for the years 1985 through 1989.

Although the average fraction of the diet composed of euphausiids in the 1985–89 period was more than double that in the 1970–74 period, there was not a significant difference between the two means (*t* test, $p>0.05$).

The percentage of copepods in the diet of small pollock appeared greater than in that of large pollock for every year except 1970 (Fig 6). The average percent by weight of copepods in the diet of small walleye pollock over all years (43%) was significantly different from that of large pollock (22%) (*t* test, $p<0.05$). Interannual changes in copepod amounts within size groups were mostly nonsignificant.

Walleye pollock were more important in the diet of larger pollock than in the diet of smaller ones (Fig. 7) (*t* test, $p<0.05$). Both predator size groups showed a similar trend in percent by weight of walleye pollock in

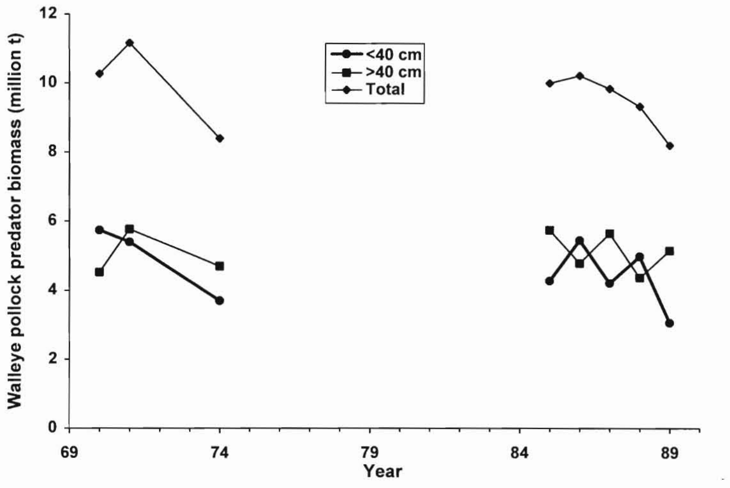

Figure 3
Walleye pollock predator biomass (million metric tons) for the years 1970, 1971, 1974, and 1985–89. Biomass is shown for predators <40 cm and ≥40 cm and for total predators.

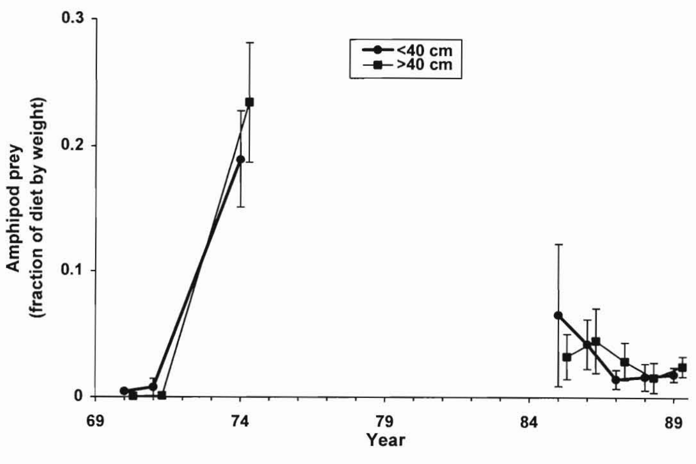

Figure 4
Fraction by weight of amphipod prey in the diet of walleye pollock by predator size group (<40 cm and ≥40 cm) for the years 1970, 1971, 1974, and 1985–89. Error bars show the standard error of the mean. (Data values for large pollock were slightly offset in the x-direction to prevent overplotting.)

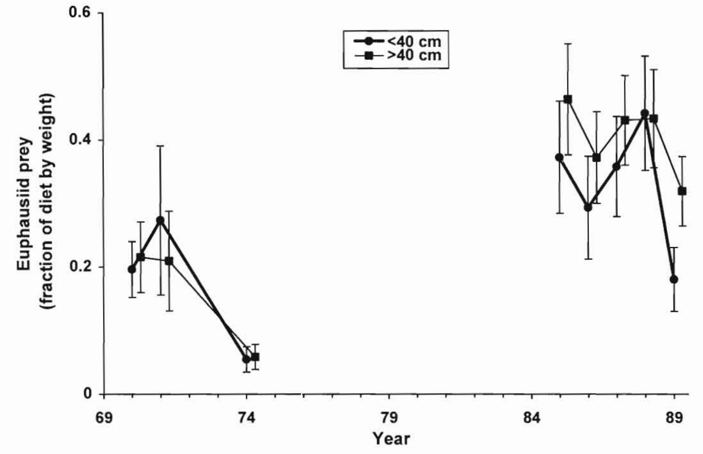

Figure 5
Fraction by weight of euphausiid prey in the diet of walleye pollock by predator size group (<40 cm and ≥40 cm) for the years 1970, 1971, 1974, and 1985–89. Error bars show the standard error of the mean. (Data values for large pollock were slightly offset in the x-direction to prevent overplotting.)

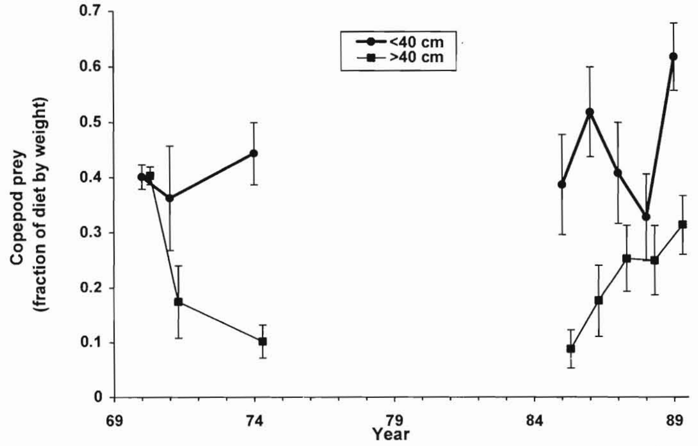

Figure 6
Fraction by weight of copepod prey in the diet of walleye pollock by predator size group (<40 cm and ≥40 cm) for the years 1970, 1971, 1974, and 1985–89. Error bars show the standard error of the mean.

the diet over the study period. Walleye pollock prey appeared to be less important (<10% by weight) for both size groups in the 1985–89 period of this study, but there was not a significant difference between the average contributions of pollock to the diet in the 1970–74 period and the 1985–89 period. The contribution of walleye pollock in the diet by weight (40% for predator size groups ≥40cm, and 12% for groups <40cm) was highest in 1971. There were, however, large variance estimates associated with pollock diet fractions, particularly for 1971. The percent by weight of walleye pollock in the diet for the 1985–89 period was positively correlated (*r*=0.99) with the biomass index of age-0 and age-1 walleye pollock present for a given year (Fig. 8). But

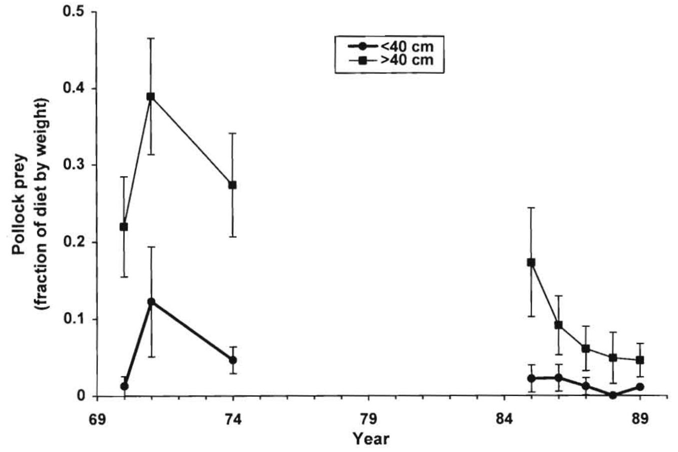

Figure 7
Fraction by weight of walleye pollock prey in the diet of walleye pollock by predator size group (<40 cm and ≥40 cm) for the years 1970, 1971, 1974, and 1985–89. Error bars show the standard error of the mean.

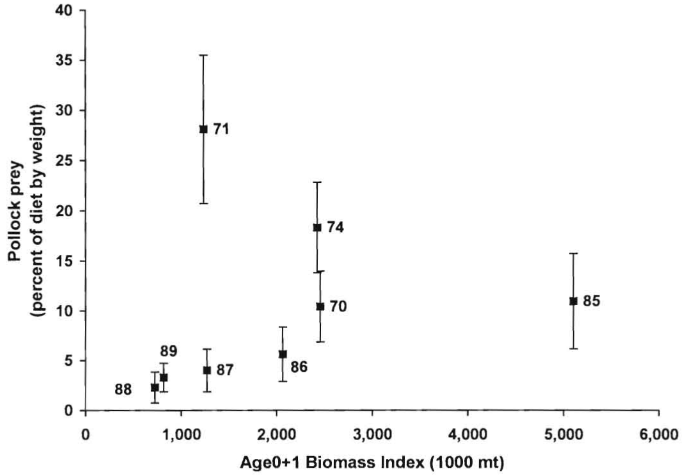

Figure 8
Percent by weight of walleye pollock in the diet of walleye pollock versus the biomass index of age-0+1 walleye pollock for the years 1970, 1971, 1974, and 1985–89. Error bars show the standard error of the mean.

when all years were considered, the correlation was much lower (r=0.16).

Walleye pollock biomass consumed by pollock was highest (3.6 million t) in 1971 and lowest (0.2 million t) in 1988 (Fig. 9). In general, total juvenile pollock biomass consumed through cannibalism was the lowest from 1986 through 1989. This trend parallels that of the percent by weight of walleye pollock in the diet (Fig. 7).

Copepods and euphausiids together constituted over 50% of the prey biomass consumed by walleye pollock during all years except 1974, when they made up only 31% of the biomass consumed (Fig. 9). In 1974, amphipod consumption was highest (23% of prey biomass)

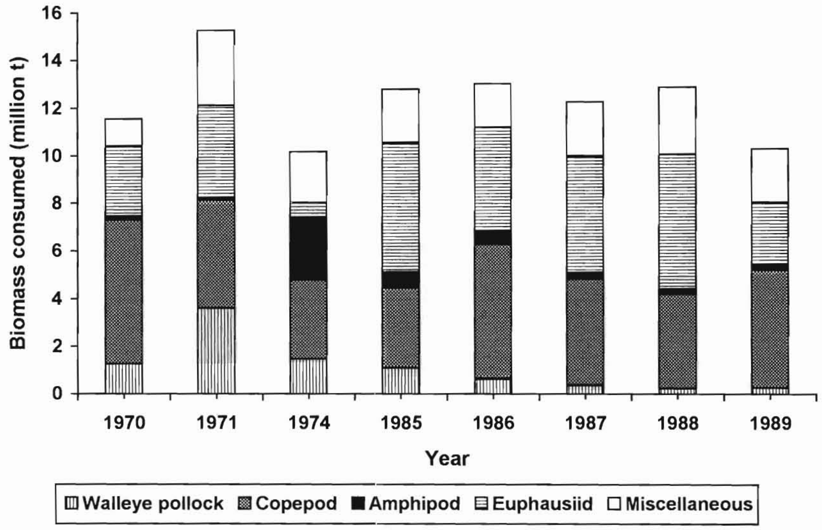

Figure 9

Walleye pollock, copepod, amphipod, euphausiid, and miscellaneous prey biomass (million metric tons) consumed by walleye pollock for the years 1970, 1971, 1974, and 1985–89.

and euphausiid consumption was lowest (6% of prey biomass) compared with other years. Capelin made up less than 1% of the prey biomass consumed in all years.

Discussion

Estimates of total walleye pollock predator biomass and the biomass in each size group (<40 cm and ≥40 cm) were relatively constant throughout all years of the study. Therefore, observed changes in diet composition probably reflect the availability or abundance of prey. Similarly, environmental indices of sea-surface temperature (Decker et al., 1995) and February ice extent (Overland and Pease, 1982; Wilderbuer[3]) show that climate during all the years in this study was similar, with below-average sea-surface temperature and average extent of sea ice. Therefore, observed changes in diet composition were probably not due to changes in production timing or environmental effects on prey distribution.

There appeared to be no size-related differences in the consumption of euphausiids. Euphausiids constituted relatively large fractions of the diet for both size groups during all the study years except 1974. A large percentage of amphipods was noted in the diet during that year; they may actually have been euphausiids, although that cannot be confirmed.

The greatest differences in diet by predator body size were seen for copepod and walleye pollock prey. Copepods were a more important item in the diet of smaller walleye pollock, whereas juvenile pollock prey were more important to larger walleye pollock. Thus small walleye pollock relied primarily on copepods and euphausiids, whereas larger pollock mainly consumed juvenile pollock and euphausiids. In the years when cannibalism was low (1986–89), euphausiids and copepods increased in the diet of larger walleye pollock. Examination of the raw data suggests that other prey, such as shrimp, may also be important during some years.

The most obvious dietary trend implied by these data is that cannibalism rates were size-dependent, with large (≥40 cm) walleye pollock being more cannibalistic. The trend toward cannibalism was the same for both size groups during the two time periods. Although capelin may have been more abundant in the early 1970's than in the 1980's (Fritz et al., 1993), and are consumed by walleye pollock in the Gulf of Alaska (Yang, 1993), they constituted less than 1% of the diet by weight during all the study years. These data contrast with those of Decker et al. (1995), who found a decline in capelin and hyperiid amphipod consumption by marine birds nest-

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[3] Wilderbuer, T. K. 1993. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Cent., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Personal commun.

ing on the Pribilof Islands from the pre-1978 period to the post-1978 period.

Because cannibalism of walleye pollock was highly correlated with the index of age-0 and age-1 abundance for the 1980's period, it appears that cannibalism rates during summer were mostly related to the abundance of juvenile walleye pollock in that period. Previous analyses have shown that the main ages cannibalized are age-0 and age-1 fish, based on prey size frequencies from the 1980's (Dwyer et al. 1987; Livingston et al., 1993). However, no prey size data were available for the 1970's data considered in this study. It is possible that predation on older age groups of walleye pollock could have been the cause of the higher-than-expected percent weight of walleye pollock in the diet for 1971 relative to age-0 and age-1 abundance, but we have no data to support this contention. The lack of correlation between pollock cannibalism rates and the age-0–1 pollock biomass index in the 1970's could also be due to uncertainty in pollock biomass estimates from periods prior to the initiation of shelfwide bottom trawl and hydroacoustic surveys in 1979.

The relation between the index of age-0 and age-1 biomass and percent weight in the diet can also be thought of as a feeding response curve. Within the range of prey biomass observed while our stomach sampling program has been in effect, the predator response is in the portion of the curve where prey intake per predator increases with increasing prey biomass. A nonlinear increase in amount consumed per predator with increasing prey biomass would indicate that compensatory density-dependent mortality was occurring independent of changes in predator biomass. Unfortunately, there are not enough data points to sufficiently distinguish whether this is a linear or nonlinear relationship. Also, we do not have samples from years with very high prey densities, such as 1978–79 or 1982–83, when large biomasses of age-0 and age-1 walleye pollock were present. Thus we cannot determine at what prey density the predator response curve will level off.

The walleye pollock population as a whole consumes more euphausiids and copepods than juvenile pollock prey. Walleye pollock may adjust their diet in the absence of abundant juvenile pollock prey by increasing the consumption of copepods and euphausiids. This strategy could make the energy intake of adult pollock less subject to the interannual variability seen in populations of planktivorous and piscivorous birds in the eastern Bering Sea that rely heavily on the production of either copepods or juvenile walleye pollock in a given year (Springer et al., 1986). However, the effect of cannibalism on the overall population dynamics of walleye pollock in the Bering Sea is a topic of continuing research. A better understanding of adult pollock's functional feeding response at differing prey densities is required to make advances in this area.

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Changes in the Distribution and Size of Juvenile Walleye Pollock, *Theragra chalcogramma*, as Indicated by Seabird Diets at the Pribilof Islands and by Bottom Trawl Surveys in the Eastern Bering Sea, 1975 to 1993

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ABSTRACT

We tested whether the proportion of age-1 walleye pollock, *Theragra chalcogramma*, in the diets of four species of seabirds—black-legged kittiwake, *Rissa tridactyla*; red-legged kittiwake, *R. brevirostris*; common murre, *Uria aalge*; and thick-billed murre, *U. lomvia*—decreased between the 1970's and the 1980's by examining otoliths present in food samples obtained from birds breeding on the Pribilof Islands. We examined the distribution of age-1 walleye pollock on the Bering Sea shelf over the same time period to determine if the changes in age classes of pollock taken by birds were reflected in data from National Marine Fisheries Service bottom trawl surveys. We examined the growth rates and sizes of age-0 pollock taken by the birds, and we sought evidence for mechanisms that might have influenced the distribution and abundance of juvenile pollock in the vicinity of the Pribilof Islands.

We found that the proportion of age-1 walleye pollock in seabird diets decreased significantly from the 1970's to the 1980's. Over the same period, age-1 walleye pollock declined in trawl survey catches in the vicinity of the Pribilof Islands and also in the southern portion of the shelf edge. Although age-0 pollock taken near the end of August were longer in the 1970's than in the 1980's, growth rates of age-0 pollock in August were similar in the two periods. We found no significant correlation between the abundance of age-1 walleye pollock near the Pribilof Islands and in the southern outer domain (strata 32, 42, and 50) and the extent of ice cover along the 170°W meridian. Likewise, there were no significant correlations between the number of age-1 pollock in strata 32, 42, and 50 and the number of adult pollock present in these strata in the same or preceding year. We discuss additional evidence for both interannual and interdecadal changes in the marine environment in the vicinity of the Pribilof Islands. Juvenile walleye pollock were an important component of the diets of breeding seabirds, but—contrary to our expectations—seabird reproductive success was not sensitive to the ratio of age-1 to age-0 pollock in the seabirds' diets.

Introduction

The number of young fledged annually by marine birds breeding on the Pribilof Islands has fluctuated considerably since studies were initiated there in 1975 (Byrd, 1989; Schulmeister, 1991; Springer, 1992; Decker et al., 1995). Additionally, since the 1970's, breeding populations of some seabird species, particularly black-legged and red-legged kittiwakes *(Rissa tridactyla* and *R. brevirostris*), at the Pribilofs have declined (Springer, 1992). The start of the decline in the production of young coincided with a period of increasing sea-surface temperatures and the maturation of the large 1978 year class of walleye pollock, *Theragra chalcogramma* (Springer, 1992; Decker et al., 1995). Explanations for the decrease in kittiwake reproduction during the 1980's have focused on two hypotheses (Springer, 1992). The first emphasized competition between seabirds and adult pollock for forage fish, in particular age-0 and age-1 walleye pollock. The second suggested that seabird population biology was reflecting changes in prey availability driven by changes in ocean temperatures. Changes in the species composition of seabird prey coincided with the warming of surface waters (Decker et al., 1995), but the diets of some seabirds did not return to their former species composition when sea-surface temperatures decreased in the mid-1980's. Decker et al. hypothesized that the birds' diets were indicating a "regime" change in the southeastern Bering Sea that did not track sea-surface temperatures. This concept of a regime shift has been developed independently by others in a number of parallel studies (Beamish, 1995; papers in this symposium).

Throughout the period 1975–90, walleye pollock was an important prey of seabirds breeding on the Pribilof Islands (Decker et al., 1995). Variations in the occurrence and percentage composition of pollock in seabird diets between the 1970's and the 1980's were not consistent among bird species, or between birds breeding on St. Paul and St. George Islands. Although there were significant correlations between estimates of abundance of age-1 walleye pollock on the eastern Bering Sea shelf and their presence in seabird diets in two of six cases examined, Decker et al. (1995) found no statistically significant positive correlations between seabird production of young and estimated abundance of age-1 pollock either in seabird diets or on the eastern Bering Sea shelf.

Past examinations of the role of walleye pollock in the ecologies of Pribilof Islands seabirds relied on aggregated shelfwide estimates of the abundance of age-1 pollock (Springer, 1992; Decker et al., 1995) and did not differentiate between seabirds' use of age-0 and age-1 pollock. We assumed that age-1 pollock would be of greater importance to seabirds because of the greater amount of energy contained in each fish, and because early in the reproductive season, age-0 fish might not be suitable prey because of their small size and their lack of schooling (Sogard and Olla, 1993). We also assumed that the abundance of age-1 pollock near the breeding colonies would be of greater importance to nesting seabirds than would abundances at greater distances from the colonies. Starting with these assumptions, we tested the hypothesis that the production of young by seabirds on the Pribilof Islands would vary with the availability of age-1 pollock near the islands.

We examined walleye pollock otoliths present in food samples obtained from birds, and the distribution and abundance of age-1 walleye pollock on the eastern Bering Sea shelf, using data from National Marine Fisheries Service bottom trawl surveys. We present evidence that a shift in the distribution and abundance of age-1 pollock was reflected in the diets of four species of seabirds, and that age-1 pollock taken by seabirds in the 1980's differed in size from those taken in the 1970's. Contrary to our hypothesis, we found no evidence that variations in the ratio of age-1 to age-0 pollock in the diets of seabirds affected seabird reproductive success on the Pribilof Islands during the study period.

Methods

We investigated the use of walleye pollock by seabirds nesting on the Pribilof Islands, Bering Sea (Fig. 1) from 1975 to 1979, from 1985 to 1989, and in 1992 and 1993. During these periods, we and others also gathered information on the production of young by seabirds nesting on the Pribilof Islands (Byrd, 1989; Springer, 1992; Climo, 1993; Dragoo and Sundseth, 1993; Decker et al., 1995).

We obtained data on the age classes and sizes of walleye pollock consumed by seabirds breeding on the Pribilof Islands by extracting otoliths from samples of food brought to the colonies on St. Paul and St. George Islands. Black-legged and red-legged kittiwakes feed their young by regurgitation. For these species we relied primarily on food regurgitated for chicks to provide samples of what kittiwakes were eating during the chick-rearing phase of the breeding cycle. In contrast, thick-billed murres, *Uria lomvia*, and common murres, *U. aalge*, provision their chicks by bringing them single, large items of prey in their bills. Adult murres themselves eat a variety of prey, including items considerably smaller than those generally fed to chicks (Hunt et al., 1981b). For these two species we collected adults near the colonies to obtain stomach contents, and also examined the prey brought to young. Before chicks hatched, we collected adults of all four species near the colonies to obtain food samples. Immediately after collection, we placed food samples in 80% ETOH for

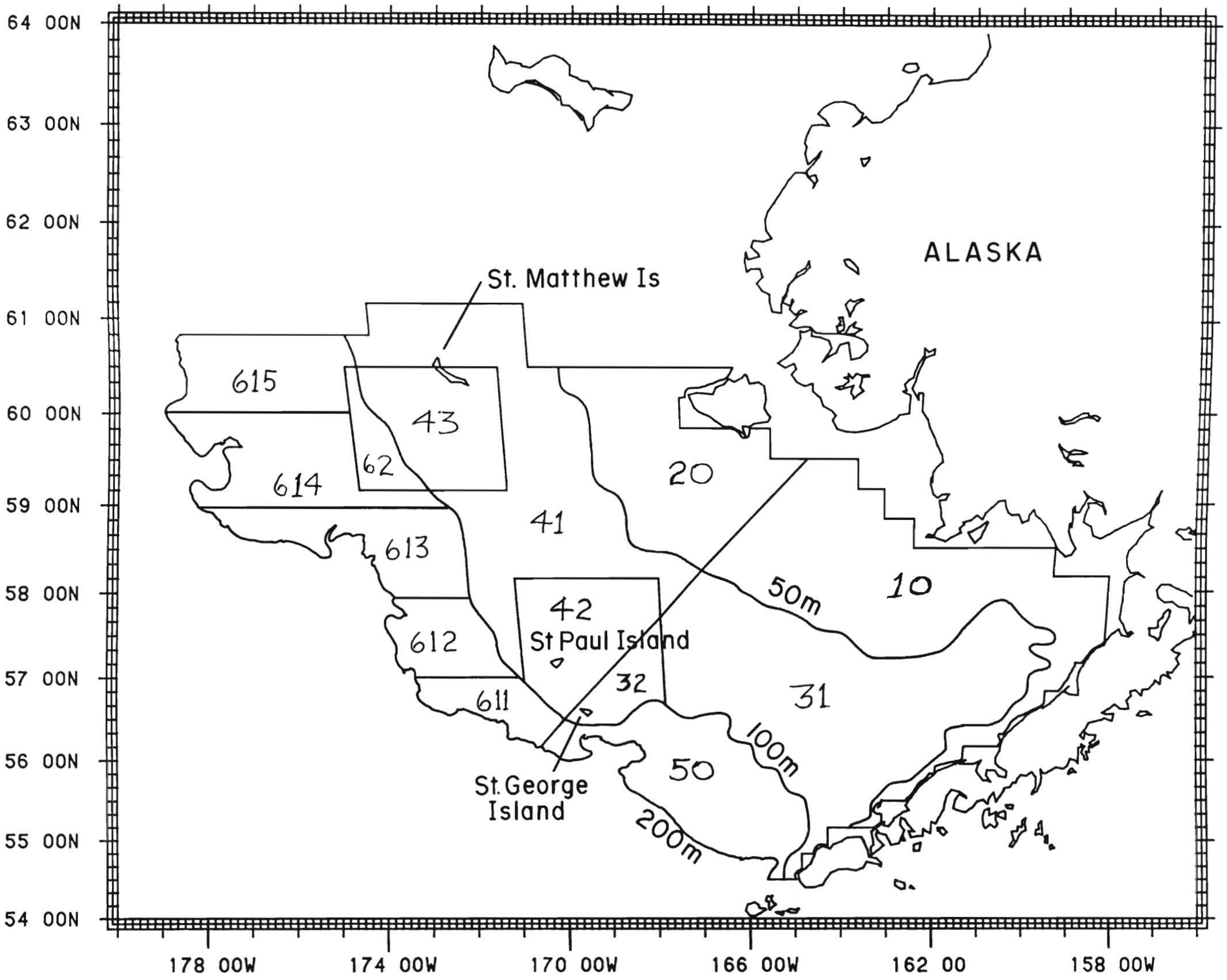

Figure 1

The eastern Bering Sea, showing St. Paul and St. George, the largest of the Pribilof Islands, and the strata (numbered segments) used for assesssing age-1 walleye pollock abundance. The outer domain lies between the 200- and 100-m isobaths, the middle domain between the 100- and 50-m isobaths, and the inner domain shoreward of the 50-m isobath.

preservation until they could be examined in the laboratory. By sampling at the islands, we avoided the potential bias that occurs when birds are collected while they are foraging at aggregations of specific types of prey. Thus our samples are likely to be representative of the prey taken by populations of seabirds nesting at the Pribilof Islands.

As parts of three separate studies, otoliths were measured to obtain estimates of the sizes of pollock taken by seabirds. In each study, otoliths were present in food samples as loose, separate items, and also embedded in the cranial tissue of juvenile pollock, from which they were extracted. The precision of measurements varied between studies: from 1975 to 1979, we either measured all otoliths present, or when the numbers of otoliths of similar size were high, we measured 20 of representative size, which were chosen haphazardly. For samples obtained from 1985 to 1989, we measured all otoliths present. From 1975 to 1979 and from 1987 to 1989, we measured the long axis of otoliths to the nearest 0.1 mm. Otoliths obtained in 1985 and 1986 were measured to the nearest 0.01 mm. To derive pollock body lengths from otolith lengths, we used the relationships described by Nishimura and Yamada (1988): for age-0 pollock,

$$\log_e \text{otolith length (mm)} = -5.808 + 1.622 \log_e \text{body length (mm)},$$

and for age-1 pollock,

$$\log_e \text{otolith length (mm)} = -1.597 + 0.722 \log_e \text{body length (mm)}.$$

With these equations, an otolith measurement precision of 0.1 mm yields an error in estimating the body length of age-0 pollock of ±4.43 mm.

We estimated the lengths of 5,496 (84% of 6,559) fish on the basis of measured otolith lengths. The remaining 16% of estimated fish lengths were based on otoliths whose length was assigned from measurements of representative otoliths in the sample. We used fish lengths based on these assigned otolith lengths only to categorize pollock to age class. In addition to estimating fish lengths from otolith measurements, we measured 73 whole pollock to obtain standard lengths.

Our estimates of fish length based on otoliths are only approximations. Loose otoliths were exposed to the birds' stomach acids before collection and preservation in ethanol, and were eroded to varying extents. Otoliths in bird stomachs that remained imbedded in cranial tissue until we extracted them were less eroded. We were unable to estimate the extent to which erosion had taken place. We therefore assumed that there was no interannual variation in the extent of erosion before preservation in ethanol for otoliths of a given size obtained from bird stomachs. All otoliths were measured within a few months of collection, except otoliths from 1987, 1988, and 1989, which were washed in the year of collection and then stored in ethanol until they were measured in 1992.

We determined the age class of a fish based on the length of its otolith, and on the distribution of otolith lengths obtained in the same time period. During the months when we collected otoliths from seabird stomachs, there was a nonoverlapping bimodal distribution of estimated fish sizes (Hunt et al., 1981b, Fig. 38), and we assumed that fish with estimated lengths less than 100 mm in August were age 0 (Nishimura and Yamada, 1988). Since fish were growing throughout the sampling period, there was no single otolith size that we could use as a criterion for an age class.

To estimate the number of fish represented by our sample, for all years except 1985 and 1986, we matched otoliths of similar size, and assumed that each pair of similar-sized otoliths was contributed by a single fish. For 1985 and 1986, we halved the total number of otoliths measured.

To compare the frequency of seabird use of age-0 and age-1 pollock between the 1970's and the 1980's, we restricted our analyses to the period between 20 July and 20 August, a period during which we had a similar distribution of sampling effort in the two decades (Fig. 2). For this comparison, we used data on fish lengths derived from both measured and estimated otolith lengths, and from measurements of whole fish. To avoid the possibility of pseudoreplication, we used the presence or absence of otoliths of an age class in a stomach or regurgitated food as our dependent variable, since individual fish collected by a bird may have come from the same size- or age-specific school. Thus we assigned a degree of freedom to each sample, rather than to each fish in a sample. We compared the frequency of occurrence of age classes in food samples between the two decades using a chi-square test for independence.

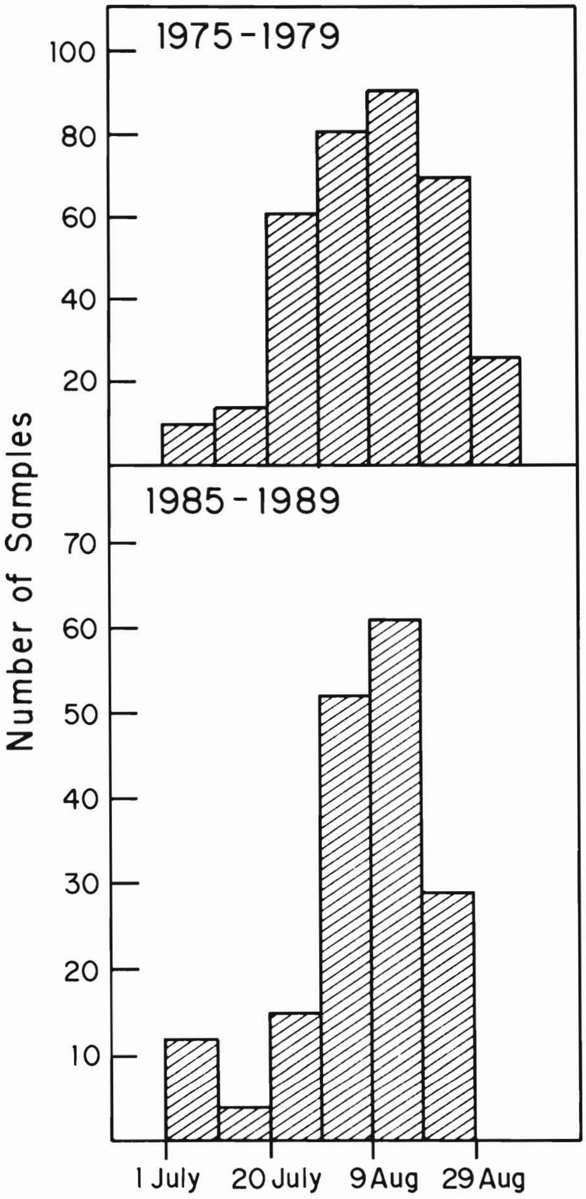

Figure 2
The timing of collections and the number of food samples available for comparison between the periods 1975–79 and 1985–89.

We obtained data on the abundance of age-1 pollock on the eastern Bering Sea shelf from National Marine Fisheries Service (NMFS) bottom trawl surveys. These provide a useful index of year-class strength of age-1 pollock, although the strongest year classes may have been underrepresented because a larger fraction of the age-1 fish were likely to have been too far above the bottom to be caught (Sample and Bakkala, 1989). In addition to the traditional strata employed by NMFS, we requested that a large stratum in the northern outer domain be divided into five substrata at 1° latitude intervals (strata 611 to 615, Fig. 1). This division permitted a finer resolution of the distribution of fish within an area that we expected to be important to foraging seabirds, as revealed by earlier studies (Hunt et al., 1981b).

We estimated interannual and interdecadal differences in the size of age-0 walleye pollock taken by seabirds by using a Mann-Whitney *U*-test to compare the mean size of fish, per bird sampled, brought to the colonies between 10 and 18 August. To minimize the potential for bias in the data due to interannual differences in the dates on which samples were obtained, we chose samples obtained between the narrowest range of dates that would capture a sizable portion of the age-0 fish taken by the seabirds.

To test whether interannual variations in the sizes of age-0 pollock were caused by differences in growth rates in August, we determined the arithmetic slope of the regression of the modal size of fish on date (Hilborn and Walters, 1992). To minimize the effects of interannual variation in sampling dates, we used only those samples obtained between 1 and 30 August each year. We excluded data based on estimates of otolith length derived from representative samples. We tested for a Pearson correlation between sea-surface temperature and growth rates of age-0 pollock by using the mean values of August surface temperatures for a 5°-by-10° grid surrounding the Pribilofs (unpublished NOAA data from Dan Cayan as described in Decker et al., 1995).

We used otoliths collected in different date intervals for each of our tests to extract maximum information from our samples without introducing bias due to differences in the distribution of sampling effort in different years. Thus, for estimates of interannual variation in size, we selected the shortest possible period within which we had numerous samples in each year (10–18 August). In contrast, for calculations of growth rates of age-0 fish, we sought the longest period with relatively similar coverage in each year (1–30 August). We used the period 20 July to 20 August to calculate the ratios between age-1 and age-0 fish in seabird diets because there was a seasonal change in the use of the two age classes, and inclusion of late July samples was less likely to create bias than the inclusion of late August samples, in which age-1 fish were relatively rare.

To correlate interannual changes in the abundance of age-1 pollock in the southern outer domain and around the Pribilof Islands (strata 50, 32, and 42) with variations in winter sea-ice cover, we obtained ice-cover data from the NOAA/Navy Joint Ice Center. As a proxy for total ice cover, we used data on the annual maximum latitudinal extent for the "absolute" (near-0% concentration) ice edge along the 170°W meridian. We used this meridian because it was close to the Pribilof Islands, and because it gave an approximation of the southward extent of ice over the entire eastern Bering Sea shelf.

We also tested the hypothesis that, because of cannibalism or competition, the number of age-1 pollock would be inversely related to the number of age-2 and older pollock present in a stratum. We used data from the bottom trawl surveys of strata 50, 32, and 42. We regressed the abundance of age-1 pollock in a stratum against the abundance of age-2 and older pollock in that stratum in the same year and in the previous year, because cannibalism against young pollock is primarily directed toward age-0 fish in the fall and winter (Dwyer et al., 1987).

We examined the importance of age-1 pollock to successful kittiwake and murre reproduction by comparing breeding success (number of chicks fledged per nest started), as reported in Decker et al. (1995), with the proportion of pollock in seabird diets that was age-1. For this test, we used the number of individual fish of each age class to calculate proportional use. To minimize the effect of interannual variation in the dates on which samples were obtained, we restricted this comparison to the period 20 July to 20 August. To test for differences in breeding success as a function of ratio of age-1 to age-0 pollock, we performed an analysis of covariance, with breeding success as the dependent variable and proportion of age-1 pollock in the diets of each of the four bird species on each island as the continuous independent variable, with bird species as a factor. We required a minimum of eight prey samples containing pollock for a given bird species on an island in a year before those data were included in our analysis.

All statistical analyses were performed with Systat for Windows version 5.02 (Wilkinson et al., 1992).

Results

The proportion of age-1 walleye pollock in the diets of four seabird species (black-legged kittiwake, red-legged kittiwake, common murre, and thick-billed murre) decreased from 1975–79 to 1985–89 (Fig. 3). For all four bird species combined, 14% of 1,494 pollock in samples collected in the 1970's were age 1, whereas in the 1980's, less than 1% of 3,355 pollock were age 1. Furthermore, fewer age-1 pollock were found in food samples of all four bird species in 1985–89 than in 1975–79 (Table 1). Although there was considerable interannual variation in the number of age-1 pollock taken by each seabird species in the 1970's (Fig. 3), in each case there appeared to be an overall decline in the use of age-1 pollock between 1975 and 1979. Note that the diets of surface-foraging kittiwakes and subsurface-foraging murres showed similar changes. Collections of food samples on the Pribilof Islands in 1992 and 1993 showed that age-1

Table 1

Change in the occurrence of walleye pollock in seabird food samples from the Pribilof Islands between 1975–1979 and 1985–1989. For all tests, df =1.

Species	# of samples with pollock in 1970's	Proportion of samples with age-1 pollock	# of samples with pollock in 1980's	Proportion of samples with age-1 pollock	χ^2	p
Black-legged kittiwake	108	0.61	58	0.09	42.47	<0.001
Red-legged kittiwake	35	0.34	11	0.00	5.10	0.024
Common murre	34	0.65	11	0.09	10.29	0.001
Thick-billed murre	72	0.34	68	0.06	17.71	<0.001

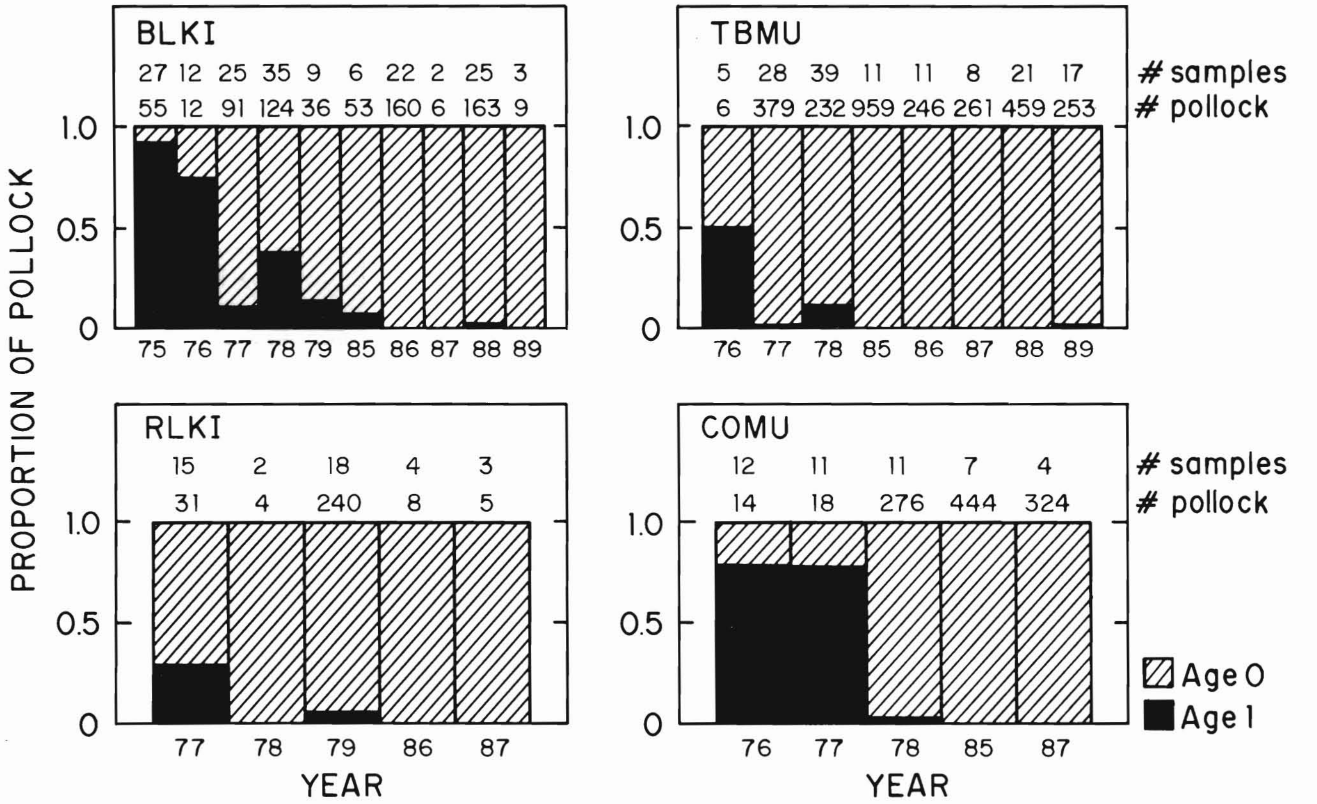

Figure 3

Proportions of age-0 and age-1 walleye pollock in the diets of four seabird species breeding on the Pribilof Islands. Data from birds from both islands are combined. For 1985 and 1986, counts are of otoliths, not fish. BLKI = black-legged kittiwake; RLKI = red-legged kittiwake; TBMU = thick-billed murre; COMU = common murre.

Table 2

Use of age-0 and age-1 walleye pollock by seabirds on the Pribilof Islands in the 1990's. Samples were collected between 24 June and 13 August.

Species	Year	# of samples with pollock	Percent of samples with age-1 pollock	# of pollock age 0 to 2 years	Percent of pollock that were age 1
Black-legged kittiwake	1992	6	0.50	35	0.11
	1993	8	0.37	23	0.15
Red-legged Kittiwake	1992	2	1.00	3	No data
	1993	6	0.17	19	0.26
Common murre	1992	14	1.00	103	0.91
Thick-billed murre	1992	42	0.64	404	0.17

walleye pollock had again become an important component of the diets of breeding seabirds (Table 2).

NMFS data on age-1 walleye pollock in the outer domain indicated dramatically reduced abundance beginning in 1982 in strata 611 and 612, and beginning in 1983 in stratum 50, when compared to earlier years (Fig. 4). In contrast, age-1 pollock did not decline in the northern strata of the outer domain (58° to 60°N, strata 613 to 615). In the vicinity of the Pribilof Islands (strata 32 and 42), age-1 pollock were relatively scarce by 1982, but showed no obvious trends in abundance in either the southern (stratum 31) or northern part (strata 41 and 43) of the middle domain (Fig. 5). Comparison of Figures 4 and 5 suggests that the pattern of change in age-1 pollock near the Pribilof Islands (strata 32, 42, 611, and 612) was more similar to the pattern in the southern outer domain (stratum 50) than it was to the patterns found elsewhere in the middle domain (strata 41, 43, and 31). There may have been a northward shift in the distribution of age-1 pollock in the immediate vicinity of the Pribilof Islands between the surveys conducted in 1975 and 1979, but the available number of trawl samples is small (Fig. 6). We have too few samples from birds in 1979 to determine if there was a parallel shift in the use of age-1 pollock between birds on St. George Island and birds on St. Paul Island.

We found that the sizes of age-0 walleye pollock taken by the four species of seabirds decreased between the 1970's ($\bar{x}$=69.4 mm) and the 1980's ($\bar{x}$=58.4 mm) (Table 3). Within the 1980's, there was considerable interannual variation in size of fish taken, with 1986 having the lowest values for any year in which there was an adequate sample. Growth rates of age-0 walleye pollock in August also showed considerable interannual variation (Table 4). But growth rates were not consistently lower in the 1980's than in the 1970's, as might have been expected if differences in growth rates were responsible for the observed interannual variation in size of age-0 pollock taken by seabirds. Of the years with strong year classes for which we have growth data, the 1978 year class was below average (0.70 mm/d vs. the 7-year average of 0.95 mm/d), whereas the 1988 year class was the median. We tested the hypothesis that growth rates of age-0 pollock in August were positively related to August sea-surface temperature, but the relation was not significant ($r=0.558$, $n=7$, $p=0.193$).

Table 3

Interannual variation in the size of age-0 walleye pollock as estimated from otoliths obtained from kittiwakes and murres at the Pribilof Islands, 10 to 18 August. The difference between the means for the 1970's and 1980's is statistically significant (Mann-Whitney $U=1111$, $N=72$, $p<0.001$).

Year	# samples for which mean fish length was estimated	Mean length (mm)	± standard deviation
1976	1	35.9	
1977	13	70.2	2.15
1978	12	71.3	2.04
Total 1970's	26	69.4	7.14
1986	9	45.3	2.14
1987	2	59.7	
1988	17	66.50	3.31
1989	18	57.3	3.35
Total 1980's	46	58.4	8.26

We hypothesized that either variations in ice cover over the eastern Bering Sea shelf or the number of adult pollock present in a stratum might influence the number of age-1 pollock present. We regressed the abundance of age-1 pollock in strata 50, 32, and 611 combined against the extent of ice along the 170°W meridian, but found no significant pattern (r=0.025; n=12; p=0.939). Likewise, we found no significant relation between the number of age-1 pollock in stratum 50, or in strata 32 and 42 combined, and the abundance of age-2 and older pollock in that stratum in the

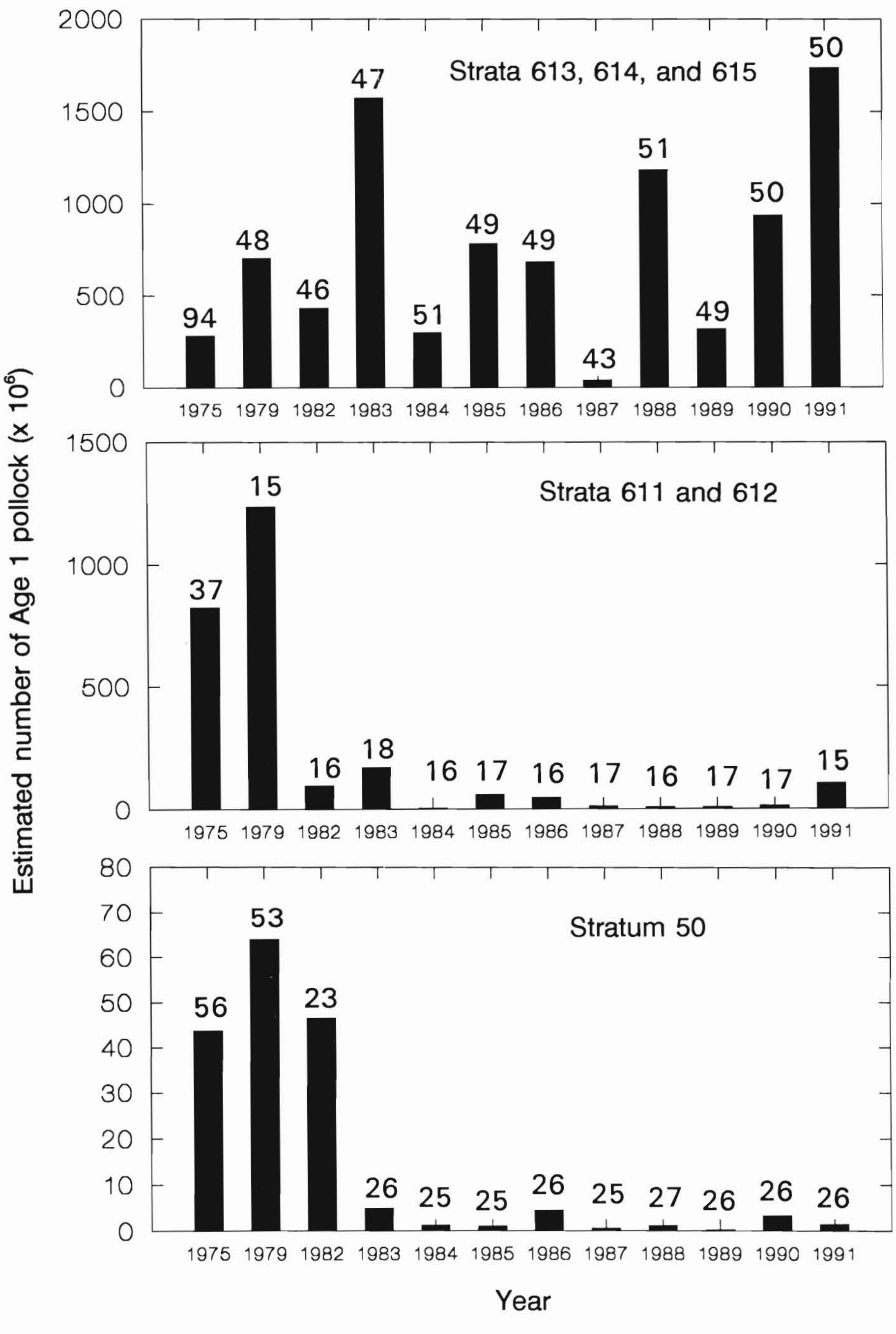

Figure 4
The abundance of age-1 walleye pollock in the outer domain of the eastern Bering Sea shelf, as estimated by the bottom trawl surveys of the National Marine Fisheries Service. Numbers at the tops of the bars are the numbers of trawls on which the estimates were based. See Figure 1 for locations of strata.

same year (stratum 50: $r=-0.019$; $n=12$; $p=0.954$; strata 32+42: $r=0.267$; $n=12$; $p=0.401$). Likewise, when the number of age-1 pollock was regressed against the number of age-2 and older pollock present in the previous year, there was no significant relation for either stratum 50 or for strata 32 and 42 combined.

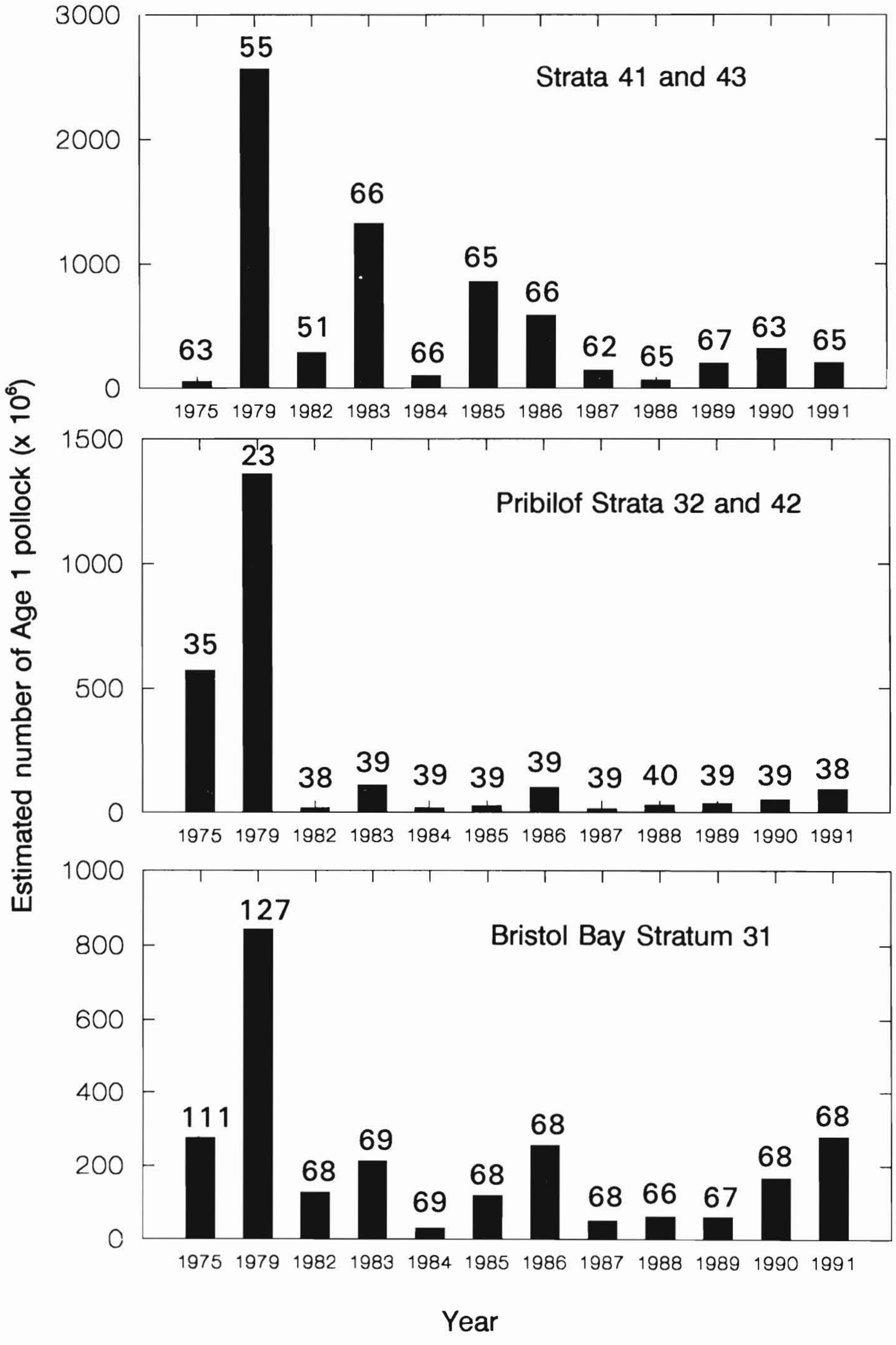

Figure 5

The abundance of age-1 walleye pollock in the middle domain of the eastern Bering Sea shelf, as estimated by bottom trawl surveys of the National Marine Fisheries Service. Numbers on the tops of bars are the number of trawls on which the estimate was based. See Figure 1 for locations of strata.

We examined the relation between the ratio of age-1 to age-0 pollock in the diets of the four species of seabirds in the period 20 July to 20 August and the breeding success of these species on each island (Fig.7). A test for homogeneity of slopes showed no significant interactions between bird species and age-1 pollock in the diet. An analysis of covariance performed on the data set as a whole showed no statistically significant relation between the percentage of age-1 pollock in bird diets and the number of chicks fledged per nest ($F_{2,1,17}$=0.183, p=0.675).

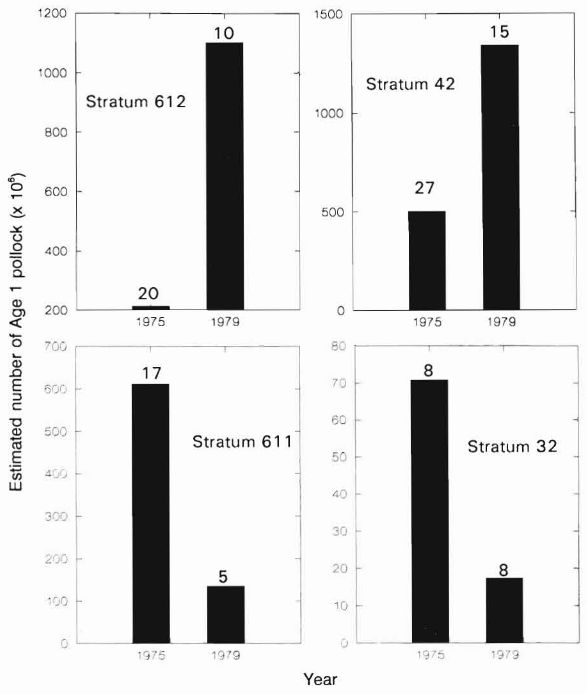

Figure 6

Abundance of age-1 walleye pollock in four strata in the vicinity of the Pribilof Islands in 1975 and 1979. Estimates of abundance are based on the bottom trawl surveys by the National Marine Fisheries Service. Numbers at the tops of bars are the number of trawls on which the estimates were based.

Discussion

Walleye pollock is one of the most important prey species for seabirds breeding in the eastern Bering Sea (Hunt et al., 1981a; Springer, 1991). At the Pribilof Islands, age-0 and age-1 pollock constituted the single most important prey taken by surface-foraging black-legged kittiwakes and subsurface-foraging common murres during the 1970's (Hunt et al., 1981b). Juvenile pollock were also important, but not quite so dominant, in the diets of red-legged kittiwakes and thick-billed murres. The proportion of age-1 pollock in the

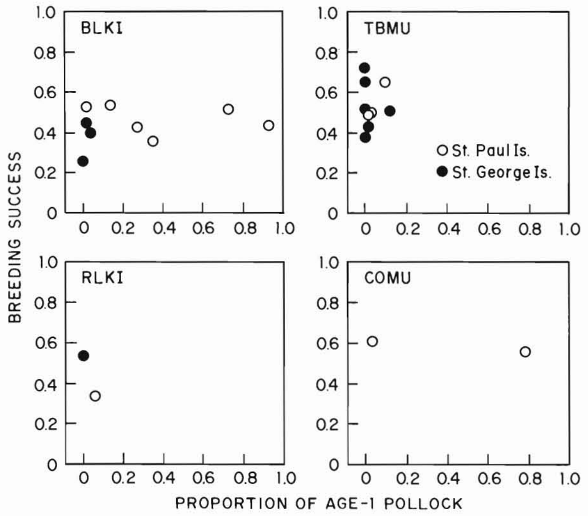

Figure 7

Relation between proportion of age-1 pollock in diets and breeding success of four species of seabirds at the Pribilof Islands between 1975 and 1989. BLKI = black-legged kittiwake; RLKI = red-legged kittiwake; TBMU = thick-billed murre; COMU = common murre.

Table 4

Growth rates of age-0 walleye pollock during August based on changes in modal size of otoliths obtained from seabird stomach contents at the Pribilof Islands. p = the significance level of the slope of the regression with respect to 0.0.

Year	1976	1977	1978	1979	1986	1987	1988
# days sampled	5	16	10	5	5	5	14
# fish sampled	8	109	285	101	321	536	186
Growth rate (mm/d)	1.04	0.77	0.70	1.57	0.32	1.33	0.93
p	0.052	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

diets of kittiwakes and murres breeding at the Pribilof Islands significantly decreased between 1979 and 1985, but increased again sometime after 1989.

The marked decrease in age-1 walleye pollock in the diets of seabirds coincided with reduced catches of age-1 pollock in NMFS bottom trawl surveys near the Pribilof Islands and along the outer shelf domain to the south and west of the islands. We assume that the bottom trawl samples provide valid indices of interannual variation in the horizontal distribution and abundance of age-1 pollock, rather than in their vertical distribution. Because age-1 pollock decreased in the diets of both surface- and subsurface-foraging birds capable of diving to 180 m (Croll et al., 1992), we interpret the combined data from seabirds and from bottom trawls as indicating a change in the horizontal distribution and abundance of age-1 pollock.

Numbers of age-1 pollock may have been declining in the eastern Bering Sea as early as 1973. Springer et al. (1986), Springer and Byrd (1989), and Springer (1991) developed estimates of the abundance of age-1 pollock based on both cohort analysis and bottom trawl surveys. They showed that, except for the 1978 year class, the abundance of age-1 pollock had a negative slope from 1973 through 1986. These estimates were for the eastern Bering Sea as a whole, and did not address the question of spatial heterogeneity in the distribution of these fish. Our analyses suggest that this decline was particularly severe in the southern and central portion of the outer domain (strata 50, 611, and 612) and in the vicinity of the Pribilof Islands (strata 32 and 42). A decline in the abundance of age-1 pollock in this region would be expected to adversely affect the breeding seabirds of the Pribilof Islands because it encompasses major portions of the foraging ranges of these birds (Hunt et al., 1981b; Schneider and Hunt, 1984). But despite the prominence of pollock in the diets of murres and kittiwakes, no species showed a significant positive correlation between the use of pollock and production of chicks, and the reproductive success of black-legged kittiwakes on St. George Island was negatively correlated with their use of juvenile pollock (Decker et al., 1995).

The decrease in age-1 pollock in the diets of seabirds is only one of a number of indications of changes in the marine environment near the Pribilof Islands. Decker et. al. (1995) documented a number of other dietary changes for Pribilof Island seabirds in the 1980's indicative of a regime change in the southeastern Bering Sea. This change apparently affected the availability of prey to seabirds. During the period encompassed by our study, Coyle and Cooney (1993) found interannual variation in water mass characteristics near the Pribilof Islands, as well as changes in chlorophyll levels and acoustically detected biomass. Evidence from other studies shows that the zooplankton community near the Pribilof Islands also varied on an interannual scale (Table 5). In some years *Calanus marshallae*, a middle-domain species (Cooney and Coyle, 1982; Smith and Vidal, 1984; Vidal and Smith, 1986), was an important component of the diets of least auklets, *Aethia pusilla*, nesting on the Pribilofs (e.g., 1975; Table 5). In other years, *C. marshallae* was scarce, and the outer-domain species *Neocalanus cristatus* and *N. plumchrus* (Cooney and Coyle, 1982; Smith and Vidal, 1984; Vidal and Smith, 1986) were most common in auklet diets (e.g., 1978; Table 5; and 1984; Roby and Brink, 1986). Euphausiids, *Thysanoessa raschii*, apparently increased in abundance near the Pribilofs between the late 1970's and the late 1980's, as evidenced by increased observations of feeding on euphausiids by whales (Baretta and Hunt, 1994) and short-tailed shearwaters, *Puffinus tenuirostris* (Hunt et al., 1996). The data of Coyle and Cooney (1993) and changes in the species composition of copepods taken by least auklets near the Pribilof Islands provide evidence for interannual variability in the characteristics and possibly the origin (middle vs. outer domain) of the water surrounding the Pribilof Islands.

It would be useful to know the cause of the decrease in age-1 pollock around the Pribilof Islands and in the

Table 5

Prey of least auklets on St. Paul Island by species. Numbers are percent whole equivalents, i.e., percentages of prey individuals, whether represented by whole organisms or their parts. Early = 1 May to 10 July; late = 15 July to 30 August. Data from 1975, 1976, and 1979 from G. Hunt, unpublished; data from 1989 from M. B. Decker, unpublished.

Year	1975 early	1975 late	1976 late	1978 early	1978 late	1989 late
Sample size	13	27	51	5	5	27
Prey type						
Calanus marshallae	85.3	73.4	21.2	0.0	4.1	0.6
Neocalanus cristatus	0.0	0.0	2.9	32.5	76.3	92.6
Neocalanus plumchrus	0.0	0.0	5.9	59.1	2.8	1.5
Parathemisto libellula	4.5	4.2	2.5	1.5	0.0	0.1

southern portion of the outer shelf. There may have been a change in the availability of their preferred foods. Euphausiids are an important component of the diet of age-1 walleye pollock in spring, whereas copepods dominate their diets in summer (Dwyer et al., 1987). In view of the observations of foraging shearwaters and whales mentioned above, it seems unlikely that a scarcity of euphausiids was responsible for the decline in age-1 pollock abundance during the 1980's. It is possible that copepod species composition changed or biomass declined between the decades. If such changes occurred, they could have profoundly influenced the density of energy available to juvenile walleye pollock in waters near the Pribilof Islands.

We briefly examined two other classes of non-mutually exclusive hypotheses. One group of hypotheses focuses on the possible role of cannibalism or competition in determining the distribution and abundance of juvenile pollock. Another group of hypotheses focuses on physical factors that might influence the location of young pollock during their first few months after hatching or during their second year of life.

Adult pollock are a major predator on juvenile pollock, particularly age-0 fish in the eastern Bering Sea (Dwyer et al., 1987; Bailey, 1989; Livingston, 1989; Livingston and Lang, 1996). This source of juvenile mortality is concentrated in the southeastern Bering Sea shelf and slope area and takes place primarily in autumn and winter (Dwyer et al., 1987). Bakkala (1989) found no correlation between the number of adult walleye pollock on the eastern Bering Sea shelf and the subsequent recruitment of age-1 pollock. Similarly, we found no significant relation between the abundance of age-2 and older pollock and the abundance of age-1 fish in the same or following year for either of the two strata surrounding the Pribilof Islands, or for stratum 50 along the outer shelf. Because age-1 fish move about, it may be inappropriate to try to explain local variations in their abundance by means of local estimates of pollock abundance. But cannibalism is not uniformly common throughout the Bering Sea (Dwyer et al., 1987), and there is no strong negative relation between the number of adult pollock and the abundance of age-1 pollock on the entire eastern Bering Sea shelf during the same period (Springer, 1992). Therefore, it may be useful to continue studying the possible population effects of cannibalism at smaller spatial scales.

Physical processes that influence the recruitment and distribution of juvenile pollock include variations in water temperature, which may affect spawning distributions, and ice cover and associated low water temperatures, which may affect growth rates and habitat selection by young fish. Addressing the possibility of physical influences on spawning location, Francis and Bailey (1983) suggested that during cold-water years spawning would be limited to the open ocean and outer shelf waters, from which eggs and larvae would drift to the northwest, away from the Pribilof Islands. In contrast, in warm-water years, spawning would occur on the southeastern shelf as far shoreward as the middle domain, and recruitment would be to midshelf waters southeast of the Pribilof Islands. Under this scenario, it is possible that age-0 pollock could have drifted toward the Pribilofs and that in the following year, age-1 pollock would be particularly abundant around the Pribilof Islands. The mid 1980's was a period of higher water temperatures (Royer, 1989; Decker et al., 1995), and one might expect that it would have been a period of high abundance of age-1 pollock around the Pribilof Islands. However, age-1 pollock were scarce near the Pribilof Islands during this period. We need better information on the source and numbers of age-0 pollock arriving at the Pribilof Islands, their subsequent survival, and their likelihood of remaining over the first winter. Without this information, it will be difficult to assess the importance of variation in spawning areas to the recruitment of age-1 pollock to the foraging grounds used by Pribilof Island seabirds.

Young pollock avoid cold water (Francis and Bailey, 1983), and age-1 fish may move to slope waters when there is extensive ice cover over the eastern Bering Sea shelf (Ohtani and Azumaya, 1995). We failed to find a significant correlation between the abundance of age-1 pollock in strata 50, 32, and 42 and the extent of ice cover along the 170°W meridian. Thus, although there may be a shift in the relative abundance of young pollock toward the shelf edge when water temperatures on the shelf are low (see also Wyllie-Echeverria, 1996), the absolute number of young pollock along the shelf edge may not vary as a function of ice cover. The abundance of young pollock there, which is more important to predators than is their relative abundance with respect to the middle domain, undoubtedly depends on a variety of factors, of which ice cover on the shelf is but one.

Low growth rates of juvenile fish may reduce their likelihood of survival because they remain vulnerable to predation for a longer period, or because, for a given age, they are in poorer condition (for a review, see Leggett and DeBlois, 1994). We found no evidence that age-0 fish grew more slowly during the 1980's than the 1970's. Our estimates of growth rates fell within or above the range of values found by Yoklavich and Bailey (1990) and Brown and Bailey (1992) for age-0 pollock in the western Gulf of Alaska. The variability in growth rates found in our study suggests that there was considerable interannual variability in conditions affecting growth, although we did not find this variability closely correlated with sea-surface temperature. Perhaps the roles of interannual variation in copepod species composition (as mentioned above) or abundance, as mediated by both the source of the water around the Pribilof Islands and water temperature, are worthy of investigation. Size-selective mortality could also influence apparent growth rates, as indicated by comparisons of modal size groups through time (Bailey[1]).

We had anticipated that age-1 pollock would be important to the reproductive success of seabirds breeding on the Pribilof Islands. Although there were no breeding failures when age-1 pollock constituted 10% or more of the birds' diets, variation in the ratio of age-1 to age-0 pollock in the diets did not significantly affect breeding success. This result parallels the finding of Decker et al. (1995) that from 1975 to 1989 there was no significant positive correlation between seabird reproductive success and the consumption of walleye pollock at the Pribilof Islands. We therefore conclude that variation in the abundance of juvenile walleye pollock near the Pribilof Islands is unlikely to be the principal cause of the interannual and interdecadal variations in seabird reproductive success that have been the focus of recent studies (e.g., Byrd, 1989; Springer, 1992; Decker et al., 1995). Rather, we interpret the changes in pollock use and age-1 pollock abundance near the Pribilof Islands as indicators of more general shifts in the marine environment which have affected the overall availability of prey to seabirds. The presence of relatively high proportions of age-1 pollock in the diets of Pribilof seabirds in 1992 and 1993, and a return of chick production to levels comparable to those in the 1970's (Climo, 1993; Dragoo and Sundseth, 1993; Byrd[2]) suggest that the marine ecosystem may be changing again. In the 1970's and the 1990's, elevated levels of seabird reproduction and use of age-1 pollock followed a period of below-average sea-surface temperatures (Decker et al., 1995). It is possible that cold surface temperatures indicate oceanographic conditions that promote population growth of prey or availability of prey to seabirds.

Seabirds are constrained to forage in the vicinity of their colonies when they are raising young. Although we were able to identify changes in the marine ecosystem near the Pribilof Islands that occurred at time scales of years to decades, we are unable to explain why age-1 pollock were largely absent from the birds' foraging grounds during the 1980's. We need to understand the causes of variation in prey availability within these foraging areas. Research designed to investigate fish population dynamics for the eastern Bering Sea as a whole may not provide sufficient resolution to answer these more local questions.

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Importance of Walleye Pollock, *Theragra chalcogramma*, in the Diet of Phocid Seals in the Bering Sea and Northwestern Pacific Ocean

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ABSTRACT

In the Bering Sea and northwestern Pacific Ocean all species of phocid seals feed on walleye pollock. Pollock has been one of the most important foods of harbor seals sampled at the Pribilof Islands, in Bristol Bay, and in the eastern Aleutian Islands. Ice-associated seals, particularly spotted and ribbon seals, feed on pollock in the winter and spring when they inhabit the drifting ice of the Bering Sea. In the Sea of Okhotsk pollock is a significant food for spotted and ribbon seals. The distribution of ringed seals is more coastal and northern, but they regularly feed on small gadid fishes and probably eat pollock when their ranges overlap. Bearded seals feed mostly on invertebrates and bottom fishes, but pollock have been found in their stomachs. Bearded seals consume more pollock in the southern part of the Sea of Okhotsk than in the north. In the eastern Bering Sea, harbor seals eat a wide range of sizes of pollock, but the other species eat mostly small pollock. Data from the Sea of Okhotsk suggest that younger seals eat mostly small pollock, whereas older seals also eat larger fishes. All species of seals also feed on other demersal and schooling fishes, and invertebrates. Overall, pollock is of most importance in the diets of harbor seals, spotted seals, and ribbon seals, and of little importance to bearded and ringed seals. Although some estimates have been made of the total amount of pollock consumed by seals, many of those estimates are based on old and incomplete data and are probably not reliable. Seal predation may affect pollock stocks, and pollock fishing may influence seal populations, but the possible interactions are complex and poorly understood.

Introduction

Five species of seals of the family Phocidae inhabit waters of the Bering Sea and northwestern Pacific Ocean: harbor seal, *Phoca vitulina*; spotted (or larga) seal, *P. largha*; ribbon seal, *P. fasciata*; ringed seal, *P. hispida*; and bearded seal, *Erignathus barbatus*. Harbor seals occur principally in coastal areas south of the normal extent of seasonal sea ice, including the Gulf of Alaska, Bristol Bay, the Aleutian Islands, the Pribilof Islands, the Commander Islands, the Kuril Islands, and the Sea of Japan (Bigg, 1981). Within this broad geographical range there may be two subspecies—*P. v. richardsi*, occurring along the coast of western North America, and *P. v. stejnegeri*, in eastern Asia (Shaughnessy and Fay, 1977). The closely related spotted seal spends summer months in more northern coastal waters, and moves to the drifting sea ice in winter and spring (Shaughnessy and Fay, 1977; Lowry et al., 1994). Ribbon seals also associate with drifting sea ice in spring, and are largely pelagic during other times of year (Burns, 1981a). Bearded seals and ringed seals are closely associated with sea ice throughout most of the year. During winter–spring, bearded seals occur principally in moving pack ice (Burns, 1981b) while ringed seals prefer stable, shorefast ice (Frost and Lowry, 1981a).

American, Russian, and Japanese investigators have devoted considerable research effort to the biology of these seal species in the North Pacific Ocean and the Bering Sea. Studies of natural history and biology often produced information on diet composition. The purpose of this paper is to review available information on the foods eaten by phocid seals in this region, with emphasis on the dietary importance of walleye pollock, *Theragra chalcogramma.*

Methods and Materials

Studies on foods of phocid seals in the region of concern have used a variety of sources for specimen material and various techniques for analyzing samples and data. Samples collected in Alaska have come principally from animals taken for subsistence by coastal Eskimos, and from animals collected for scientific research. Most of the samples in Russian and Japanese studies have come from scientific studies conducted in conjunction with commercial seal harvesting.

Diet has generally been analyzed by examining and identifying the material taken from stomachs or intestines. In cases where food was well digested, identifications have usually been based on characteristic hard parts. The sagittal otoliths of walleye pollock are relatively robust and easy to identify (Frost, 1981). Regression equations have been published and used to estimate the sizes of pollock consumed from otolith measurements (Frost and Lowry, 1986). For this paper, pollock lengths were estimated from otolith lengths by means of the formulas in Frost and Lowry (1981b) as follows:

$$\text{for otoliths} \leq 10 \text{ mm long, fish fork length (cm)} = 2.246 \text{ (otolith length [mm])} - 0.51$$

$$\text{for otoliths} > 10 \text{ mm long, fish fork length (cm)} = 3.175 \text{ (otolith length [mm])} - 9.77$$

There are many methods for quantifying diet composition (see review by Pierce and Boyle, 1991). The most straightforward are the apparent number of prey eaten (based on counts of whole items or unique parts) and the percent frequency of occurrence (number of samples in which a prey occurred, divided by the total number of samples examined, times 100). When stomachs with substantial contents are analyzed, the percent of total volume made up by a particular prey type can be calculated. All of these measures are biased because of differences in detectability and digestibility of prey. Various techniques have been used to correct for bias and produce more realistic estimates of the actual amounts of different prey species that were consumed (Pierce and Boyle, 1991). Most of the results presented in this paper will be given as number of prey eaten, percent frequency of occurrence, or percent volume.

Results and Discussion

Occurrence of Pollock in Seal Diets

Harbor Seals—The most comprehensive study of harbor seal foods was conducted in the Gulf of Alaska by Pitcher (1980), who examined 269 stomachs containing food. Overall, pollock was the most important prey, occurring in 21% of the samples and constituting 21% of the total volume. When analyzed by geographical subarea, pollock ranked number 1 in the northeastern gulf, Prince William Sound, and along the Kenai coast; number 2 along the Alaska Peninsula; and number 3 around Kodiak Island.

For other areas in the northwestern Pacific Ocean and Bering Sea, relatively few harbor seals have been collected and examined (see review in Lowry et al.[1]). In eight seals collected at Otter Island (central Bering Sea) during April 1979, fish made up 64% of the stomach contents; 44% of the identified fishes were pollock. Pollock have been recorded as prey in seals sampled at Port Moller and Port Heiden in Bristol Bay, and at Akun, Unalaska, and Amchitka Islands in the Aleutians, but sample sizes were too small to evaluate their relative importance. Harbor seals in the Commander and Kuril Islands have been reported to feed on cephalopods and bottom fishes, but the species of fishes were not identified (Burdin[2]).

Pollock were found in harbor seal stomach samples collected in southeast Hokkaido in 1982–83, but were not one of the top 20 foods in terms of volume or frequency of occurrence (Wada et al., 1992).

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[1] Lowry, L. F., K. J. Frost, D. G. Calkins, G. L. Swartzman, and S. Hills. 1982. Feeding habits, food requirements, and status of Bering Sea marine mammals. Council Doc. #19. North Pacific Fishery Management Council, Anchorage, AK, 292 p.

[2] Burdin, A. Kamchatka Institute of Ecology and Nature Management, Petropavlovsk-Kamchatsky, Russia. Unpubl. data.

Spotted Seals—Bukhtiyarov et al. (1984) presented data on foods of spotted seals collected in the Bering Sea in March–June 1972–78. Pollock were the most important prey in the central Bering Sea (88% of the identified fishes in 4 of 5 seals with stomach contents). Pollock occurred less frequently in seals from the southeastern Bering Sea (6 of 14) and the northern Bering Sea (1 of 12). Other studies (reviewed in Lowry et al.[1]) also indicate that pollock are not important in the diet of spotted seals in the northern Bering Sea. Lowry et al.[3] found pollock in all 12 spotted seals collected in the central Bering Sea in March 1985, and pollock made up 58% of all identified fishes. Lowry et al. also reported pollock in 1 of 3 seals collected in the western Bering Sea in April 1985.

Most of the information on foods of spotted seals in the western Bering Sea and Sea of Okhotsk comes from Russian studies that harvested seals from vessels operating in the pack ice during spring and early summer. In the western Bering Sea (Gulf of Anadyr and Karaginskiy Gulf) during the late 1960's, pollock occurred in 9% of the spotted seal stomachs examined, and octopus was the most commonly occurring food (Gol'tsev, 1971). Bukhtiyarov (1983) reported that pollock made up 5% of the diet in the Gulf of Anadyr. During the early 1980's, Trukhin et al. (1991), like Gol'tsev, found that octopus was the most important food in the Gulf of Anadyr and that saffron cod (*Eleginus gracilis*), followed by pollock, were the most commonly eaten fishes. In Karaginskiy Gulf, Trukhin et al. (1991) found that fish occurred in 75% of stomachs with food but that pollock were found in only 7%. Bukhtiyarov (1983) reported that pollock made up 35% of the overall spotted seal diet in Karaginskiy Gulf. Bukhtiyarov (1986) estimated that 24% of the diet of spotted seals in the Bering Sea consisted of pollock.

In the western Bering Sea, young seals beginning to feed independently ate mostly small pollock and other schooling fishes such as sand lance, *Ammodytes* sp., and saffron cod (Trukhin, 1986).

In the Sea of Okhotsk, pollock made up 83% of the total volume of stomach contents from 19 spotted seals collected in the pack ice off northern Hokkaido in April (Wilke, 1954). Pollock also occurred in spotted seal stomach samples collected in northeastern Hokkaido during the fall of 1992 and 1993, but was not one of the top 20 foods in terms of volume or frequency of occurrence (Wada et al., 1992).

In the southwestern Sea of Okhotsk, including the Gulfs of Aniva and Terpeniy near Sakhalin Island, Bukhtiyarov (1990) identified 24 species of prey in 222 stomachs with food collected during spring 1974–77. The most important foods were saffron cod and sand lance; pollock were found in only 5% of the stomachs. In the central and northern Sea of Okhotsk the most important food was pollock (65–91% frequency of occurrence). The measured amount of pollock in individual stomachs ranged from 100 to 4,000 g (Fedoseev and Bukhtiyarov, 1972; Popov and Bukhtiyarov, 1975).

In summer, stomachs were examined from spotted seals taken in scientific collections in coastal areas of the northern and eastern part of the Sea of Okhotsk, and the frequency of occurrence of pollock was 6–9% (Bukhtiyarov, 1984; Burkanov, 1990). Near the Kamchatka coast in the eastern part of the Sea of Okhotsk, the most important foods during summer were salmon, *Oncorhynchus* spp., and arctic char, *Salvelinus alpinus*. In the southeastern Sea of Okhotsk near the Kuril Islands, Panina (1966) found pollock in 10% of the stomachs she examined.

Information from the Sea of Okhotsk shows clear seasonal variation in the importance of pollock in the spotted seal diet. Pollock is most important in spring, particularly in the northern part. The picture is less clear for the southern Sea of Okhotsk, where pollock made up most of the contents in samples from the late 1940's and only a small portion of samples from the mid-1970's. In summer, pollock is much less important in the diet in the northern Sea of Okhotsk. In the southeastern area during summer, salmonids, rather than pollock, make up most of the spotted seal diet. Overall, Bukhtiyarov (1986) estimated that pollock made up 30% of the total mass of food eaten by spotted seals in the Sea of Okhotsk.

In the northern part of the Sea of Japan (Tartar Strait) the frequency of occurrence of pollock was 85% (Gol'tsev, 1971; Kosygin and Gol'tsev, 1971). In Peter the Great Gulf, pollock was not found in the spotted seal diet (Gol'tsev, 1971).

Ribbon Seals—Frost and Lowry (1980) reported on the diet of ribbon seals in the Bering Sea from samples collected during March–June 1976–79. Pollock was the most important prey item in the south central and central regions (89% of the total number of fishes and 50% of the total corrected weight, in 9 seal stomachs with food in the south central Bering Sea; 55% by number and 28% by weight, in 12 seals with food in the central Bering Sea). Pollock occurred in only one of seven seals with food collected in the northern Bering Sea. In contrast, Shustov (1965) did not find pollock to be an important food in the ribbon seals he examined from the central Bering Sea in 1961–63 (32 with food).

Trukhin et al. (1991) collected samples from ribbon seals in Karaginskiy Gulf during spring 1982 and found pollock in 4 of 18 stomachs with food. In the Gulf of

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[3] Lowry, L. F., K. J. Frost, and J. J. Burns. 1986. Assessment of marine mammal–fishery interactions in the western Gulf of Alaska and Bering Sea: consumption of commercially important fishes by Bering Sea pinnipeds. Final Rep. to NMFS, Contract NA-85-ABH-00029, 26 p.

Anadyr, pollock was reported to be the second most important food based on frequency of occurrence, but no figures were given. Overall, Bukhtiyarov (1986) estimated that pollock made up 13% of the total mass of food eaten by ribbon seals in the Bering Sea.

Arsen'ev (1941) examined stomachs with food from 54 ribbon seals collected in the ice of the southwestern Sea of Okhotsk during April–June and found that pollock was the major prey in all three months. Wilke (1954) reported that pollock made up 60% of the total volume of stomach contents in two ribbon seals he examined from the southern Sea of Okhotsk in April 1949. Bukhtiyarov (1990) examined stomachs of ribbon seals collected in the southern Sea of Okhotsk in 1974–77. Pollock was one of 13 identified species of prey and occurred in 12 of 50 stomachs with food. For young seals (1–2 years old) small pollock were the most important food.

Pollock was also a very important component in the diet of ribbon seals in the northern Sea of Okhotsk. In 1970–71, 42 of 48 stomachs examined contained pollock (Fedoseev and Bukhtiyarov, 1972) and in 1972–73 pollock occurred in 66 of 94 stomachs (Bukhtiyarov, 1978). Overall, Bukhtiyarov (1986) estimated that pollock made up 69% of the total mass of food eaten by ribbon seals in the Sea of Okhotsk.

Ringed Seals—Pollock have not been reported from stomachs of ringed seals collected in the Bering Sea (see review in Lowry et al.[1]). Other small gadids (saffron cod, and arctic cod, *Boreogadus saida*) are often very important in ringed seal diets (Lowry et al., 1980b), so pollock may be eaten in areas where their ranges overlap.

Pollock is not very important in the diet of ringed seals in the Sea of Okhotsk (Pikharev, 1946; Fedoseev, 1965; Kosygin et al., 1984; Trukhin et al., 1991). Bukhtiyarov (1984, 1990) examined the stomachs of more than 125 ringed seals collected in the Sea of Okhotsk in spring and found that pollock occurred at a frequency of about 1%. In summer and fall he examined 20 stomachs and found no pollock.

Bearded Seals—In general, bearded seals feed on invertebrates and benthic fishes (Lowry et al., 1980a). A few pollock were recorded in stomachs of 15 bearded seals taken north of the Pribilof Islands and near Nunivak Island in 1975–77.[1] Antonelis et al. (1994) found pollock in the stomachs of 7 of 74 bearded seals collected near St. Matthew Island in March–April 1981. In spring samples taken in the northern and eastern Bering Sea during 1963–65, Kosygin (1966, 1971) found pollock in only 1 of 152 stomachs examined. Lowry et al.[1] found no pollock in the stomachs of 173 bearded seals taken in the northern Bering Sea during 1975–79. Trukhin et al. (1991) found pollock in 3 of 31 bearded seals collected in April–May 1982 in Karaginskiy and Anadyr Gulfs. Trukhin et al. stated, however, that pollock play an important role in the diet of bearded seals in the western Bering Sea.

In the southern Sea of Okhotsk during spring 1974–77, Bukhtiyarov (1990) found pollock in 5% of the stomachs examined (*n*=63). He stated that pollock play a more important role in the bearded seal diet in the southern Sea of Okhotsk than they do in other regions. Pollock were not found in samples from the northern Sea of Okhotsk in spring (n=72) and summer (n=128) (Fedoseev and Bukhtiyarov, 1972; Bukhtiyarov, 1984).

Sizes of Pollock Consumed

Pitcher (1981) measured otoliths from stomachs of 94 harbor seals collected in the Gulf of Alaska during 1973–78 (Table 1). He reported that the average length of pollock eaten by harbor seals was 19.2 cm, and noted that this was significantly smaller than the pollock eaten by Steller sea lions, *Eumetopias jubatus*, collected in the same regions and years (mean 29.8 cm).

Information on sizes of pollock consumed by seals in other areas is based on relatively few otoliths retrieved from seal stomachs and intestines (Table 1). Frost and

Table 1

Sizes of pollock eaten by phocid seals in the Gulf of Alaska, Bering Sea, and Sea of Okhotsk.

Species	Location	Number of seals	Number of otoliths	Fork length (cm)		Source
				Mean	Range	
Harbor seal	Gulf of Alaska	94	2,030	19.2	4.2–53.2	Pitcher, 1981
	Bering Sea	5	35	24.5	8.2–56.3	Frost and Lowry, 1986
Ribbon seal	Bering Sea	19	468	11.2	6.5–34.4	Frost and Lowry, 1986
Spotted seal	Bering Sea	2	21	10.9	8.0–15.0	Frost and Lowry, 1986
	Sea of Okhotsk	10	26	15.9	2.0–39.1	Burkanov, unpubl. data
Bearded seal	Bering Sea	5	56	11.8	6.9–14.3	Antonelis et al., 1994

Lowry (1986) summarized available data on sizes of pollock eaten by pinnipeds in the Bering Sea. Their data showed that ribbon seals and spotted seals ate almost entirely small pollock, while harbor seals ate all sizes (Fig. 1–3). Data from spotted seals collected in the Okhotsk Sea (Fig. 2) showed a wider range in sizes of pollock eaten (Burkanov, unpubl. data). Antonelis et al. (1994) reported that bearded seals collected in the central Bering Sea had eaten only small pollock (mean length 11.8 cm). Bukhtiyarov (1984, 1990) stated that all the pollock found in ringed seals collected in the Sea of Okhotsk in spring were small.

This information suggests that most phocid seals eat predominantly small pollock. Harbor seals, which eat all sizes of pollock, are the principal exception. Because of the exponential relation between pollock length and weight, however, the few larger fishes that are eaten may be of considerable nutritional significance. We used the formula in Frost and Lowry (1981b) to estimate the weights of pollock eaten by harbor seals in the central Bering Sea in April 1979. Although only 11 of the 23 pollock eaten were estimated to be over 30 cm long, those fishes contributed 84% of the estimated biomass consumed.

Quantities of Pollock Consumed

Simple calculations of the amount of food consumed by pinnipeds are often based on estimates of population sizes and daily food consumption rates. More detailed studies may take into account the size structure of the pinniped population, metabolic requirements, and caloric values of various prey (e.g., Perez and McAlister, 1993). Information on diet composition can then be used to estimate the amount of a particular prey that is eaten annually.

The only estimate of the amount of pollock eaten by harbor seals in the Gulf of Alaska is that by Lowry et al. (1989), who estimated that 72,800 metric tons (t) were consumed annually. Their calculations were based on population size and diet data from the late 1970's provided in Calkins (1986) and Pitcher (1980), and may not reflect the current consumption level.

Ashwell-Erickson and Elsner (1981) used energy-flow models to estimate that harbor seals consumed 34,700 t of pollock in the Bering Sea each year, and that spotted seals consumed 46,900 t (Table 2). Frost and Lowry (1980) used diet composition, daily ration, and population size to estimate that ribbon seals could consume 55,000 t of pollock per year in the Bering Sea. Lowry et al. (1989) produced estimates of pollock consumed by ribbon seals that were much lower than Frost and Lowry's (1980) estimates, partly because Lowry et al. included only the eastern section of the Bering Sea.

Bukhtiyarov (1986) estimated that the average amount of pollock eaten by a ribbon seal each day in the Bering Sea was 1.1 kg, and in the Sea of Okhotsk 7.4 kg. Corresponding estimates for spotted seals were 4.2 and

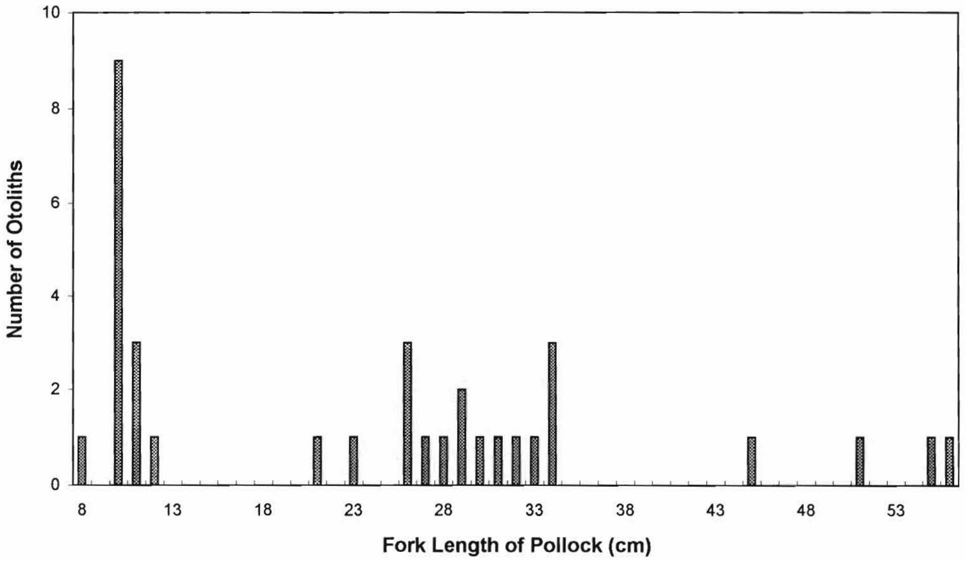

Figure 1
Fork lengths of walleye pollock eaten by harbor seals in the Bering Sea (from Frost and Lowry, 1986).

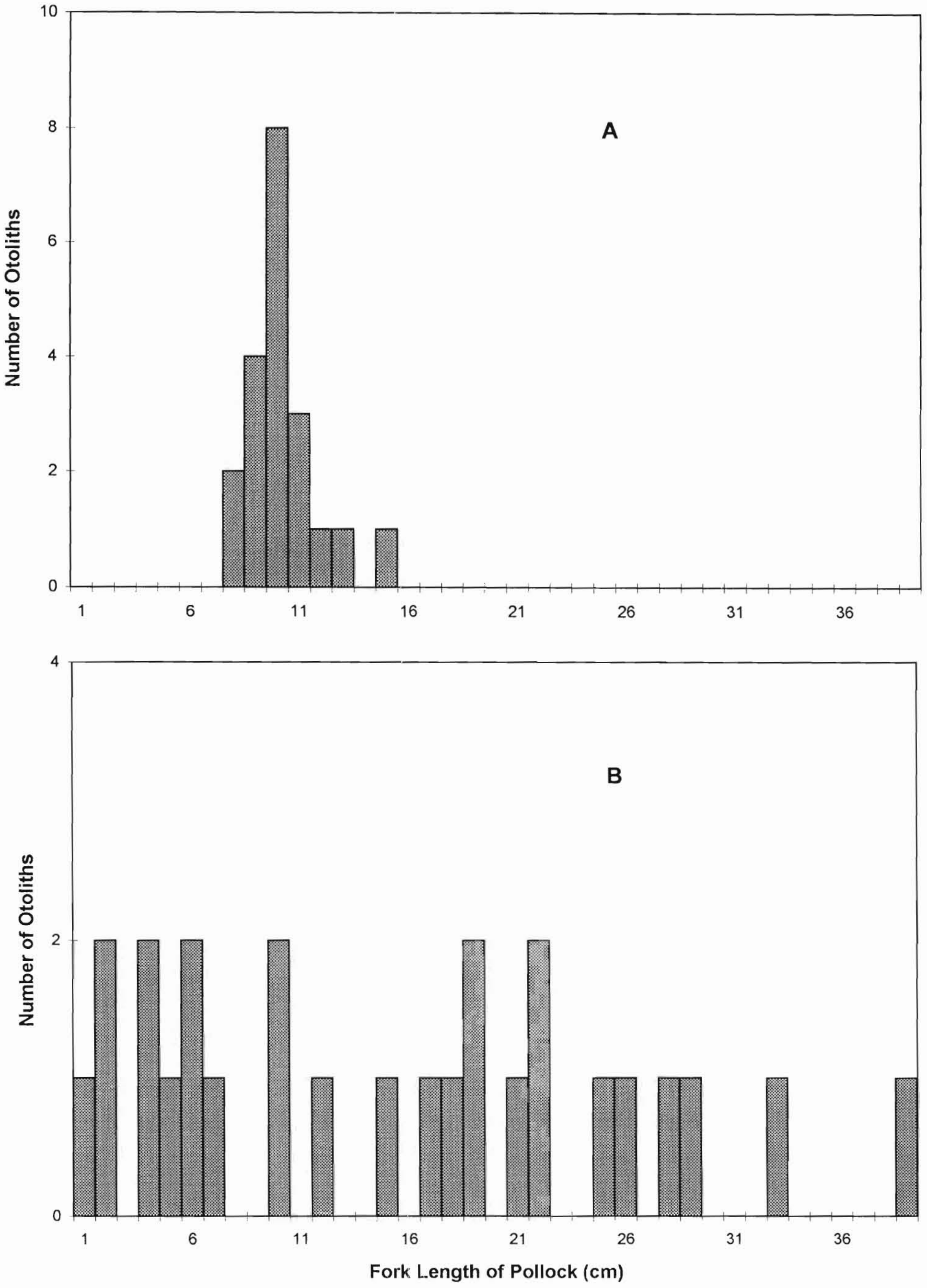

Figure 2

Fork lengths of walleye pollock eaten by spotted seals in (A) the Bering Sea and (B) the Sea of Okhotsk (from Frost and Lowry, 1986, and Burkanov, unpubl. data).

2.2 kg. These figures were used to extrapolate to the annual amounts eaten by the seal populations in each area (Table 2). For the Bering Sea his estimate for spotted seal consumption was nearly twice that derived by Ashwell-Erickson and Elsner (1981), while his ribbon seal estimate was less than that of Frost and Lowry (1980).

The consumption estimates made by Bukhtiyarov (1983) indicated that over 900,000 t of pollock were eaten by seals in the Sea of Okhotsk. Of this, 128,000 t was attributed to spotted seals and 772,000 t to ribbon seals. In another set of calculations, Bukhtiyarov (1990) estimated that during April–June ribbon seals in the

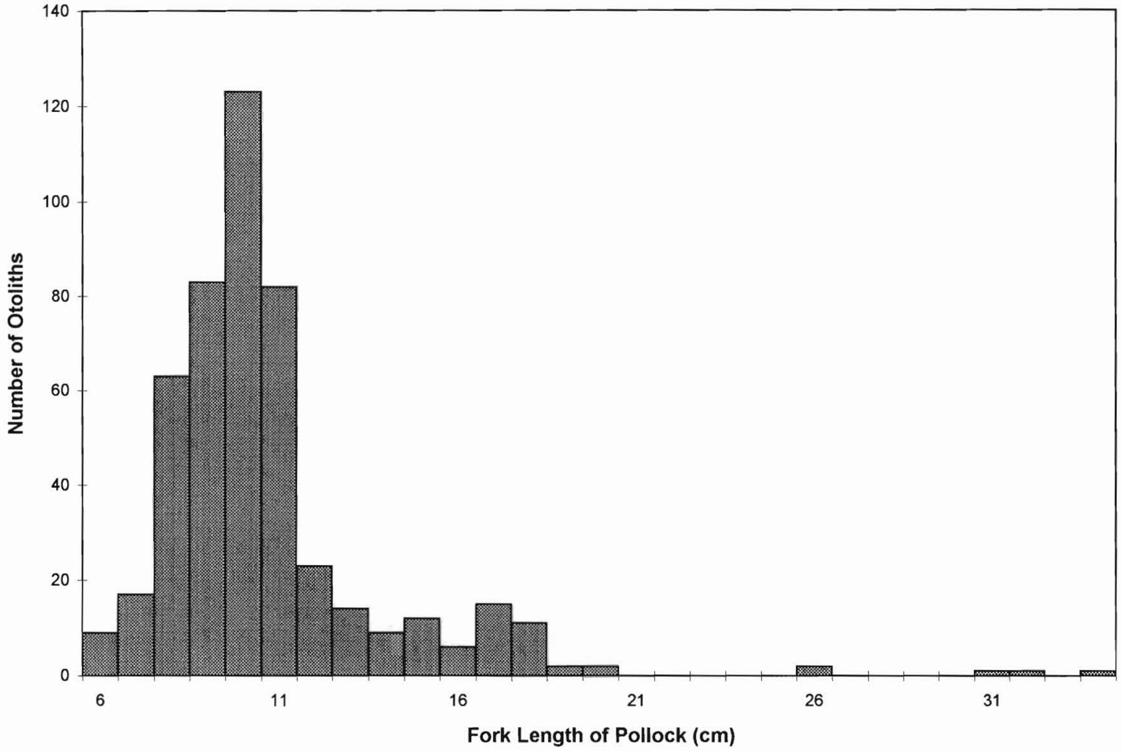

Figure 3
Fork lengths of walleye pollock eaten by ribbon seals in the Bering Sea (from Frost and Lowry, 1986).

Sea of Okhotsk would eat more than 100,000 t of pollock. Sobolevsky (1983) estimated the total amount of fish eaten each year in that region by spotted seals as 164,000 t and by ribbon seals as 171,000–239,000 t. These estimates are much less than would be expected from the pollock consumption calculated by Bukhtiyarov (1983). For ribbon seals, this may largely be due to the high value that Bukhtiyarov used for per capita food consumption. Applying his estimate of 7.4 kg pollock per day to a diet consisting of 69% pollock results in a total daily food intake of 10.7 kg. We do not consider this a realistic average consumption for a seal whose body weight averages less than 100 kg (Fedoseev, 1973; Burns, 1981a), because maintenance requirements for similar phocids are generally 3–6% of body weight per day (e.g., Markussen et al., 1990).

The variation in estimates of the amount of pollock consumed by phocid seals is largely due to differing assumptions about individual energy requirements, overall diet composition, and population sizes. From the information presented in previous sections it is evident that the dietary data available are fragmentary, and most come from samples collected before the mid-1980's. The situation is similar for population sizes. Most estimates are derived from information collected in the 1970's, and in nearly all cases the surveys they come from were not adequately designed or conducted (see reviews in Lowry et al.[1] and Lentfer, 1988). Rea-

Table 2
Estimates of the amount (metric tons × 1000) of pollock consumed by phocid seals in the Gulf of Alaska, the Sea of Okhotsk, and the Bering Sea.

Species	Gulf of Alaska	Sea of Okhotsk	Bering Sea	Source
Harbor seal			34.7	Ashwell-Erickson and Elsner, 1981
	72.8		5.3	Lowry et al., 1989*
Spotted seal		127.6	85.9	Bukhtiyarov, 1983
			46.9	Ashwell-Erickson and Elsner, 1981
			19.2	Lowry et al., 1989*
Ribbon seal		799.2	39.6	Bukhtiyarov, 1983
			55.0	Frost and Lowry, 1980
			11.4	Lowry et al., 1989*

*Estimates are for the eastern Bering Sea only.

sonably good information on relative numbers of harbor seals comes from counts of hauled-out animals (e.g., Pitcher, 1990; Loughlin[4]), but those figures are not population estimates because they do not account for animals not hauled out during surveys. Thus the data needed to generate current estimates of the quantities of pollock being consumed by phocid seals are not available, and we consider that previous estimates are of unknown reliability.

Potential Interactions with Pollock Fisheries

In the late 1970's, pollock was an important food for harbor seals in the Gulf of Alaska. The commercial trawl fishery targeting on pollock developed in the late 1970's, peaked in the early 1980's, and has declined since then. Harbor seal numbers at index areas at Tugidak Island and Prince William Sound have shown a major decline in the 1980's (Pitcher, 1990; Frost et al., 1994). It is not known whether the pollock fishery has been a factor in the harbor seal decline.

The 1993 estimate of the exploitable biomass of pollock in the Gulf of Alaska was 1,062,000 t (Hollowed et al.[5]). The estimate of pollock consumption by harbor seals in Lowry et al. (1989) would represent a significant fraction of that pollock stock. However, that consumption estimate was based on diet and population size data collected during the 1970's, and the amount currently consumed may be much less.

Estimates of the amount of pollock eaten by seals in the Bering Sea are also based on relatively old data on diets and population sizes (Lowry et al., 1989). Harbor seal numbers may be stable in that region,[4] and the population status of ribbon and spotted seals is not known. Nonetheless, if pinnipeds still consume about 150,000 t of pollock in the Bering Sea annually, that should have little impact on the pollock stock, which had an estimated 1993 exploitable biomass of about 6,700,000 t (Wespestad[6]).

In recent years, commercial fisheries have harvested approximately 4 million metric tons of pollock in the Bering Sea annually, and stock abundance has fluctuated largely as a result of variable year-class strengths (Springer, 1992). Because the phocid seals discussed in this paper eat principally small pollock, fisheries should not have a major effect on seal nutrition unless the fisheries affect recruitment or survival of young fishes.

Sobolevsky (1983) compared the amount of pollock eaten annually by all species of pinnipeds (including Steller sea lions and fur seals, *Callorhinus ursinus*) in the Sea of Okhotsk (240,000–280,000 t) to estimates of the biomass of pollock (4.0–4.5 million t) and concluded that pinnipeds ate about 6–7% of the total biomass. If the higher estimate of pollock consumption produced by Bukhtiyarov (1983) is used, this figure would be 21–23% for phocid seals alone.

In the Sea of Okhotsk, pollock are very important in the ribbon seal diet and are subject to major commercial fisheries. Nonetheless, during the period from 1981 to 1988 the ribbon seal population in the region is thought to have doubled from 250,000 to 500,000 (Bukhtiyarov, 1990).

Conclusions

Available data allow a general description of the foods eaten by phocid seals in most regions of the northwestern Pacific Ocean and Bering Sea (Table 3). Of the five species discussed in this paper, pollock are of greatest significance in the diets of harbor seals, spotted seals, and ribbon seals. Bearded seals feed mostly on benthic invertebrates and fishes, while ringed seals eat mostly Arctic cod, saffron cod, and crustaceans. For most species, our understanding of the diet is based on irregular and incomplete sampling. We have only limited information to evaluate seasonal, annual, geographical, or sex/age-related variation in pollock consumption.

Available samples make it evident that prerecruit pollock are eaten by all species of seals. Harbor seals and spotted seals also eat larger pollock, while ribbon seals, ringed seals, and bearded seals may eat only small pollock. For most species and areas, few otoliths have been measured, and quantitative data are very limited.

Estimates of the amount of pollock consumed by seals have been calculated with various techniques that have produced quite different results. The estimators mostly used data that are 10–20 years old, and the estimates therefore cannot be considered reliable measures of current pollock consumption.

Phocid seals (and other marine mammals) consume large amounts of prerecruit and older pollock in the northwestern Pacific Ocean and Bering Sea. It is not clear whether or how this predation may affect pollock stocks and their ability to withstand fishery harvests.

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[4] Loughlin, T. R. 1992. Abundance and distribution of harbor seals (*Phoca vitulina richardsi*) in Bristol Bay, Prince William Sound, and Copper River delta during 1991. Unpubl. Annu. Rep. NMFS Population Assessment Program, Nat'l. Marine Mammal Lab., Alaska Fish. Sci. Cent., NMFS/NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070, 26 p.

[5] Hollowed, A. B., B. A. Megrey, and E. Brown. 1993. Walleye pollock. *In* Stock assessment and fishery evaluation report for groundfish resources of the Gulf of Alaska as projected for 1994, p. 1–54. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[6] Wespestad, V. G. 1993. Walleye pollock. *In* Stock assessment and fishery evaluation report for groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1994, p. 1–26. North Pacific Fishery Management Council, Anchorage, AK.

Table 3

Principal foods of seals in the Gulf of Alaska, the Bering Sea, and the Sea of Okhotsk, listed in approximate order of overall importance. From Pitcher (1980), Lowry et al.,[1] Bukhtiyarov (1984, 1986, 1990), and Trukhin et al. (1991).

Species	Gulf of Alaska	Eastern Bering Sea	Western Bering Sea	Northern Bering Sea	Sea of Okhotsk
Harbor seal	Pollock Octopus Capelin Eulachon Herring	Pollock Octopus Pacific cod Sculpins Sand lance	Octopus Squid Rockfishes		
Spotted seal		Pollock Capelin Herring Eelpout Sculpins	Pollock Arctic cod Sand lance Saffron cod Herring	Arctic cod Capelin Saffron cod Sculpins Herring	Pollock Saffron cod Sand lance Shrimps Octopus
Ribbon seal		Pollock Eelpout Capelin Shrimp Flatfish	Pollock Squid Saffron cod Shrimp	Arctic cod Saffron cod Sculpins Pollock	Pollock Saffron cod Shrimps Squid
Ringed seal		Saffron cod Mysids Sculpins Shrimp	Capelin Sand lance Saffron cod Amphipods Shrimp	Arctic cod Saffron cod Shrimp Mysids Amphipods	Euphausiids Shrimp Saffron cod Pollock
Bearded seal		Shrimp Crabs Sculpins Isopods Pollock	Shrimp Crabs Octopus Clams Saffron cod	Shrimp Clams Crabs Sculpins Arctic cod	Crabs Shrimp Clams Saffron cod Pollock

Conversely, without a detailed understanding of how pollock fisheries affect the availability of pollock for foraging seals, it is not possible to assess whether fishing has had or may have an impact on seal populations.

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Importance of Juvenile Walleye Pollock, *Theragra chalcogramma*, in the Diet of Gulf of Alaska Steller Sea Lions, *Eumetopias jubatus*

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ABSTRACT

Walleye pollock, *Theragra chalcogramma*, were the most common prey of juvenile (≤4 years old) and adult Steller sea lions, *Eumetopias jubatus*, in virtually all seasons and areas of the Gulf of Alaska sampled during 1975–78 and 1985–86. Other fish prey (e.g., small forage fish) were consumed only on a seasonal basis. The proportion of sampled animals eating walleye pollock increased in the Kodiak Island area from the 1970's (49.2%) to the 1980's (68.7%). This increase resulted from a combination of seasonal increases (particularly for the May–August time period) and age-specific (particularly for juvenile sea lions) increases in the proportion of sea lions eating pollock, coupled with coincident declines in the consumption of small forage and demersal fish. Juvenile pollock were a major part of the sea lion diet in both the 1975–78 and 1985–86 sea lion collections; juvenile sea lions ate significantly smaller and relatively more juvenile pollock than adult sea lions. Juvenile pollock remained a major prey in 1985–86 despite a 48.1% decrease in abundance of age 2–3 juvenile pollock between 1975–78 and 1985–86. This paradox could be explained by the sea lion's preference for small fish, coupled with a disproportionate, simultaneous decrease in the abundance of alternative small fish prey. Generally low abundance of juvenile pollock and alternative prey throughout most of the 1980's, combined with reduced consumption of alternative prey, may have contributed to the sea lion population decline in the central Gulf of Alaska during the 1980's.

Introduction

Steller sea lion, *Eumetopias jubatus*, numbers in the central Gulf of Alaska (GOA) declined 20.5% from 1976 to 1985 (2.5% per year; Merrick et al., 1987). The cause for this decline appears related in part to the number of animals taken incidental to commercial fisheries (Perez and Loughlin, 1991). The rate of decline accelerated in 1985; the central GOA population declined by 55% between 1985 and 1989 (18.1% per year; Merrick et al., 1991). Central GOA sea lion declines have continued through 1991–92 at a similar rate (Sease et al., 1993).

One explanation for the ultimate cause of the recent (ca. 1985–93) decline of Steller sea lions is that the quantity or quality of their prey has declined (Braham et al., 1980; Merrick et al., 1987; Loughlin and Merrick, 1989; Alverson, 1991; Calkins and Goodwin[1]). Other proposed causes (e.g., emigration, disease, subsistence harvest, commercial pup harvests, pollution, predation) are either not supported by the data or could not ex-

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[1] Calkins, D., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpubl. rep. Alaska Dep. Fish and Game, 333 Raspberry Rd., Anchorage, AK 99502, 76 p.

plain declines in areas such as the central and western Aleutian Islands, where there is little human activity (e.g., fisheries). Such widespread declines (from Prince William Sound to the end of the Aleutian Islands) point toward an ecosystem-wide effect.

Circumstantial evidence supports the food-limitation explanation. Analysis of the proximate cause of the sea lion decline points toward reduced juvenile survival (Merrick et al., 1988; Loughlin and Merrick, 1989; York, 1994). Juvenile sea lions would be especially susceptible to increased mortality brought on by reduced food availability because young animals, especially newly weaned pups, are inexperienced foragers with limited range (Merrick and Loughlin[2]).

Sea lions in the GOA were significantly heavier from age 1 onward in the 1970's (predecline) than they were in the 1980's (during the decline).[1] There is also a suggestion in the 1980's collection that some animals were anemic.[1] Both smaller size and anemia would be expected in nutritionally stressed animals. A decline in prey abundance provides the most parsimonious explanation for GOA population declines of other piscivorous marine predators—harbor seal, *Phoca vitulina*, (Pitcher, 1990; Loughlin[3]) and sea birds (e.g., black-legged kittiwakes, *Rissa tridactyla*; Springer, 1993).

If the cause of the decline from the early 1980's to the present is food-related, then how has the diet or prey base changed? Because walleye pollock, *Theragra chalcogramma*, has been the most common prey of Steller sea lions in the GOA since the 1970's (Pitcher, 1981; Calkins and Goodwin[1]), an understanding of this prey's role in the sea lion's diet may provide the key to understanding the sea lion's decline in the GOA. But the importance of walleye pollock cannot be understood *in vacuo*; the whole diet must be considered. Thus we discuss the general Steller sea lion diet as determined from data collected in the GOA in 1975–78 (predecline) and 1985–86 (during the decline), and compare this with the limited data available on the abundance of various sea lion prey.

Methods

The information presented here is a reanalysis of data obtained from animals collected specifically for studies of food habits and related questions. We include only data from collections made in the GOA in 1975–78 and 1985–86 (Pitcher, 1981; Calkins and Goodwin[1]). These data form the only relatively complete data set available for analysis of temporal or area- specific trends in the diet of Steller sea lions. Earlier studies in the GOA used very small sample sizes (Imler and Sarber, 1947; Fiscus and Baines, 1966), focused on a single site in one season (Mathisen et al., 1962), or considered only territorial males (Thorsteinson and Lensink, 1962). The latter two studies also did not completely identify prey remains. We have generally not included data for animals incidentally caught in fisheries because the data may represent a biased sample of food habits. We do, however, present some of these data (Loughlin and Nelson, 1986) in our discussion of the importance of small fish.

Collections in 1975–78 were made in six areas where sea lion numbers were not declining (Merrick et al., 1987)—eastern GOA, Middleton Island, Prince William Sound, Kenai Peninsula, Kodiak Island, and western GOA (Fig. 1). In 1985–86, animals were collected only in southeast Alaska, Kodiak Island, and western GOA. At that time, sea lion numbers were declining in both the Kodiak Island area and the western GOA, but increasing in southeast Alaska (Merrick et al., 1987).

Seasonal coverage varied between the two collections (Table 1). Only in the Kodiak Island area were sea lions collected throughout the year in both the 1970's and 1980's. Consequently, most of the treatment of temporal differences in this analysis uses only Kodiak Island data.

A total of 408 animals were collected: 230 in 1975–78, and 178 in 1985–86. Of these animals, 263 had stomachs with contents: 178 in 1975–78, and 85 in 1985–86 (Table 1). Animals were collected and stomach contents processed as described in Pitcher (1981) and Calkins and Goodwin.[1] Prey identification was based on whole fish, fish otoliths, and cephalopod beaks. Estimates of the fork lengths (FL) and mass of walleye pollock consumed were calculated from a linear regression of otolith length to FL or mass (Frost and Lowry, 1981).

Individual species consumed are reported in Pitcher (1981) and Calkins and Goodwin.[1] The species identified were

1. Gadids—walleye pollock; Pacific cod, *Gadus macrocephalus*
2. Pacific salmon—*Oncorhynchus* spp.
3. Small forage fish—capelin, *Mallotus villosus*; Pacific herring, *Clupea harengus*; Pacific sand lance, *Ammodytes hexapterus*.
4. Flatfish—Pacific halibut, *Hippoglossus stenolepis*; arrowtooth flounder, *Atheresthes stomias*; rock sole, *Lepidopsetta bilineata*; other Pleuronectidae

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[2] Merrick, R. L., and T. R. Loughlin. 1993. Foraging behavior of adult female and young-of-year Steller sea lions in Alaskan waters. Abs. Tenth Biennial Conf. Biol. Mar. Mammal, November 11–15, 1993, Galveston, TX. (Avail. National Marine Mammal Laboratory library, 7600 Sand Point Way N.E., Seattle, WA 98115-0070).

[3] Loughlin, T. R. 1993. Abundance and distribution of harbor seals (*Phoca vitulina richardsi*) in the Gulf of Alaska and Prince William Sound in 1992. Ann. Rep., Mar. Mammal Protection Act Assess. Prog., Ofc. Protected Res., NMFS, NOAA.

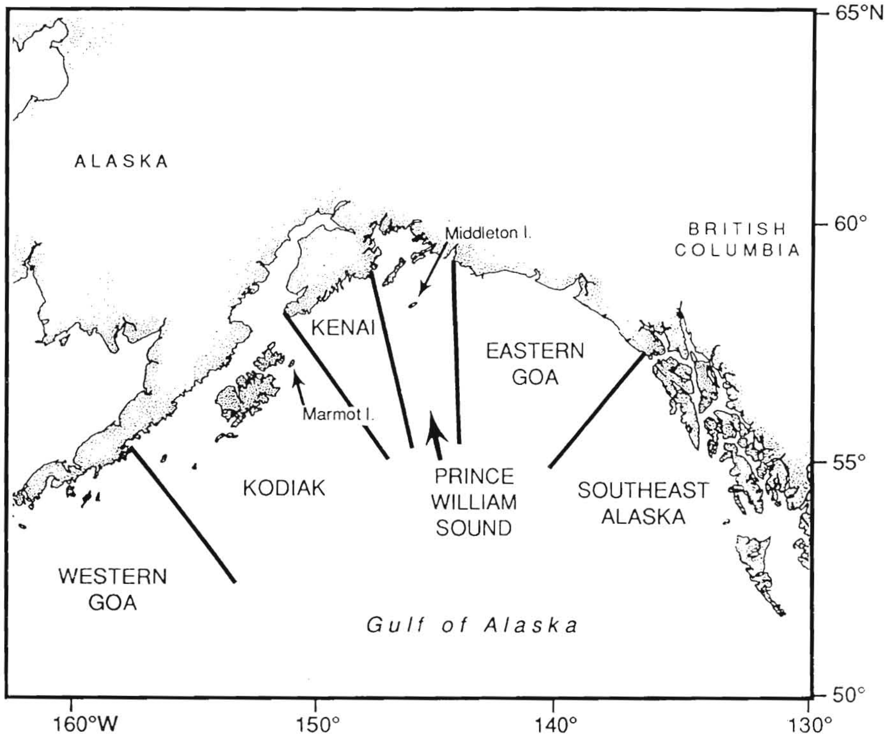

Figure 1
Collection areas for study of Steller sea lion diet.

5. Other demersal fish—sculpins, Cottidae; rockfish, *Sebastes* spp.; eelpout, *Lycodes* spp.; Pacific sandfish, *Trichodon trichodon*; poacher, Agonidae; skates, *Raja* spp.
6. Cephalopods—squid and octopus

In categorizing prey, we recognized that the traditional presentation of species data adds little to our understanding of how sea lions forage. It is presumed that sea lions select prey through a combination of their own foraging behavior and the prey's behavior. Differences in prey behavior (e.g., schooling, seasonal movements, diel vertical migration) lead to different daily or seasonal patterns of aggregation. Consequently, prey may be available only seasonally (e.g., capelin) or to those sea lions with a foraging ability (e.g., dive depths) that allows them to encounter the prey. For example, shallow-diving young-of-the-year sea lions may not be able to dive deep enough to reach most adult pollock. Our species groupings also account for the different caloric values of prey (Perez, 1994). For example, the "small forage fish" group is generally rich in fat, whereas the gadid group is low in fat but rich in protein. Finally, we also recognize that these taxa have exhibited similar trends in abundance since the late 1970's (Low, 1991; Bakkala, 1993; Fritz et al., 1993; Anderson et al., 1994; Hollowed et al.[4]).

Prey consumption was based on the proportion of animals found to consume a specific prey (i.e., frequency of occurrence of a prey group in sea lion stomachs). That is, if a prey was found in one-half of all stomachs with contents that were sampled, its frequency of occurrence was 50%. We have not presented data on the numbers of prey found in individual stomachs, largely because of a lack of data and specimens from the collections. Without these data, it is difficult to perform rigorous volumetric comparisons. Fortunately, most stomachs contained prey from only one group. The only prey species commonly found mixed with other taxa was walleye pollock. To clarify the frequency of consumption of pollock, we present the frequency of occurrence of pollock both as the number of stomachs containing pollock mixed with other prey and the number of stomachs containing only pollock.

We used Pearson's chi-square statistic for statistical comparisons of frequencies of occurrence. The level of significance was set at $\alpha = 0.05$.

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[4] Hollowed, A. B., B. A. Megrey, and E. S. Brown. 1993. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 1994 Gulf of Alaska groundfish fishery. Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council , P. O. Box 103136, Anchorage, AK 99510, 50 p.

Table 1

Collection of Steller sea lion stomachs with contents by period, area, sea-lion age class, and season.

			Season			
Period	Area	Age class	Spring	Summer	Fall	Total
1975–78	Southeast Alaska	Juvenile				
		Adult				
		Sum	0	0	0	0
	Eastern Gulf of Alaska	Juvenile	1	1		2
		Adult	2			2
		Sum	3	1	0	4
	Prince William Sound	Juvenile	15		18	33
		Adult	17		16	33
		Sum	32	0	34	66
	Kenai Peninsula	Juvenile	25	2	1	28
		Adult	10			10
		Sum	35	2	1	38
	Western Gulf of Alaska	Juvenile	0			
		Adult	2		1	3
		Sum	2	0	1	3
	Kodiak Island	Juvenile	9	14	10	33
		Adult	6	14	10	30
		Sum	15	28	20	63
	Middleton Island	Juvenile		2		2
		Adult		2		2
		Sum	0	4	0	4
	Total 1975–78	Juvenile	50	19	29	98
		Adult	35	18	27	80
		Sum	85	37	56	178
1985–86	Southeast Alaska	Juvenile		1		1
		Adult		13		13
		Sum	0	14	0	14
	Eastern Gulf of Alaska	Juvenile				
		Adult				
		Sum	0	0	0	0
	Prince William Sound	Juvenile				
		Adult				
		Sum	0	0	0	0
	Kenai Peninsula	Juvenile				
		Adult				
		Sum	0	0	0	0
	Western Gulf of Alaska	Juvenile		4		4
		Adult		0		0
		Sum	0	4	0	4
	Kodiak Island	Juvenile	5	6	5	16
		Adult	22	14	15	51
		Sum	27	20	20	67
	Middleton Island	Juvenile				
		Adult				
		Sum	0	0	0	0
	Total 1985–86	Juvenile	5	11	5	21
		Adult	22	27	15	64
		Sum	27	38	20	85

Results

Overall Diet

Fish were the primary prey of Steller sea lions in all areas in both the 1970's and 1980's (94.4% to 87.1% of all GOA stomachs with contents; Table 2). Consumption of cephalopods was common (29.2% to 36.5% of stomachs). However, few sea lions ate just squid and octopus; most consumers of these taxa also had fish remains in their stomachs. The cooccurrence of fish and cephalopod remains may indicate the accumulation of beaks in stomachs through successive feeding trips, which would lead to underrepresentation of those sea lions feeding only on fish.

Gadids (mostly walleye pollock) were the most common fish taxa consumed (70.8% to 72.9%) in all areas of the GOA (Table 2, 3). Small collections in the eastern GOA (*n*=4) and the western GOA (3 in the 1970's and 4 in the 1980's) also showed walleye pollock to be the most common prey. Pollock was generally the most common sea lion prey whether one considers all stomachs containing pollock or those containing only pollock (Table 3). The proportion of animals consuming pollock was greatest in the 1970's Prince William Sound and Kenai Peninsula collections (83.3% and 84.2% of stomachs, respectively). The lowest frequency was in the Kodiak Island area in the 1970's (49.2%), but the Kodiak Island area frequency of consumption increased to 68.7% in the 1980's. This was comparable to southeast Alaska in the 1980's (64.3%).

The only collections where walleye pollock was not the most common prey were made in the 1970's. In 1977–78, capelin alone was found in 25.0% of the Kodiak Island area stomachs (compared to 23.8% for pollock-only stomachs) and in all four stomachs of animals collected at Middleton Island in 1976.

Small forage fish were the second most common fish prey in the 1970's (23.0% of stomachs; Table 2), whereas flatfish were the second most common fish prey in the 1980's (15.3%). Pacific salmon was uncommon in all collections. Cephalopod consumption varied between areas and years from 15.8% to 42.4% of stomachs (Table 2). These prey items were generally octopus, except in Prince William Sound in the 1970's, when squid was consumed most frequently.

In 1975–78, there were two significant differences between the Kodiak Island area diet and the remainder of the GOA collection (Table 2, 3). Pollock was consumed less frequently in the Kodiak Island area ($P<0.01$), while salmon were consumed more frequently there ($P=0.01$). There were no significant differences in the frequency of occurrence of the various prey for the 1980's Kodiak Island and southeast Alaska collections.

Sizes of Pollock Consumed

Juvenile pollock constituted a major part of the pollock eaten in the Kodiak Island area in both the 1975–78 (*n*=2,080; mean=29.8 cm FL; sd=11.6; Pitcher, 1981) and 1985 (*n*=1,040; mean=25.1 cm FL; sd=10.3) sea lion

Table 2

Percentages of Steller sea lion stomachs containing various prey taxa from the Gulf of Alaska (GOA) subareas for the 1970's and 1980's. "Gadid" includes walleye pollock and Pacific cod; "Small forage fish" includes Pacific herring, capelin, and Pacific sand lance; and "Other demersal fish" includes rockfish, sculpins, etc. Gulfwide summary includes additional samples from the eastern GOA, Middleton Island, and the Alaska Peninsula.

			Percentage of stomachs with various prey							
Area	Period	*n*	Gadid	Salmon	Small forage fish	Flatfish	Other demersal fish	All fish	Squid and octopus	Fish and ceph.
Kodiak Island	1970's	63	52.4	7.9	28.6	7.9	11.1	88.9	22.2	12.7
	1980's	67	70.1	2.0	10.4	13.4	1.5	85.1	40.3	25.4
SE Alaska	1970's	0								
	1980's	14	85.7	7.1	14.3	28.6	0.0	92.9	28.6	21.4
Prince William Sound	1970's	66	83.3	0.0	24.2	0.0	10.6	98.5	42.4	40.9
	1980's	0								
Kenai Peninsula	1970's	38	86.8	0.0	7.9	5.3	15.8	94.7	15.8	13.2
	1980's	0								
Gulfwide	1970's	178	70.8	3.4	23.0	5.1	12.4	94.4	29.2	24.4
	1980's	85	72.9	4.7	11.8	15.3	1.2	87.1	36.5	23.5

Table 3

Percentage of adult and juvenile Steller sea lion stomachs with contents that included walleye pollock and those containing only walleye pollock from Gulf of Alaska (GOA) subareas for the 1970's and 1980's. Gulfwide summary includes additional samples from the eastern GOA, Middleton Island, and the Alaska Peninsula.

		1975–78			1985–86		
Area	Age	*n*	With pollock	Only pollock	*n*	With pollock	Only pollock
Kodiak Island	Juvenile	33	45.5	27.3	16	75.0	50.0
	Adult	30	53.3	20.0	51	66.7	29.4
	All	63	49.2	23.8	67	68.7	34.3
SE Alaska	Juvenile	0			1	0.0	0.0
	Adult	0			13	69.2	23.1
	All	0			14	64.3	21.4
Prince William Sound	Juvenile	33	84.8	39.4	0		
	Adult	33	81.8	12.1	0		
	All	66	83.3	25.8	0		
Kenai Peninsula	Juvenile	28	82.1	64.3	0		
	Adult	10	90.0	30.0	0		
	All	38	84.2	55.3	0		
Gulfwide	Juvenile	98	68.4	41.8	21	71.4	47.6
	Adult	80	70.0	18.8	64	67.2	28.1
	All	178	69.1	31.5	85	68.2	32.9

collections. This difference in mean fork length was significant (t=13.7, P<0.01). Over 74% of the fish in the 1985 sample were smaller than 30 cm FL. Mass of the average-size fish consumed by sea lions fell 37%, from 148 g in 1975–78 to 93 g in 1985.[1] The average number of pollock consumed by sea lions in a feeding trip may have increased between the two periods. Stomachs (n=20) examined from the 1975–78 collections contained remains of an average of 49 pollock, whereas 44 stomachs examined in 1985–86 contained an average of 72 pollocks' remains. Thus the mean mass of pollock consumed on the most recent feeding trip of these animals was around 7.3 kg in 1975–78 and 6.7 kg in 1985–86.

The length distribution of fish consumed in 1985 (Fig. 2) indicated a strong mode around 17–19 cm FL; these would have been 1-year-old fish (1984 year class). A second, weaker mode was apparent around 39–43 cm FL. This mimicked the GOA size distribution of pollock in 1985 (Fig. 2; Hollowed et al.[4]). Most (73.1%) of the fish consumed were smaller than 30 cm FL, but only 26.8% of the mass consumed came from pollock smaller than 30 cm FL.

Juvenile sea lions in 1985 consumed smaller pollock (n=344; mean=20.8 cm FL; sd=7.9; Fig. 3) than adult sea lions (n=720; mean=27.3 cm FL; sd=11.0; Fig. 3). The differences were significant (F=92.38; P<0.01). Juvenile sea lion diets included a significantly greater proportion of juvenile pollock than did adult diets (P<0.01). Of all pollock consumed by 7 juvenile sea lions, 93.2% were smaller than 30 cm FL, compared with 65.6% of pollock consumed by 18 adults.

The mean mass of individual pollock consumed in 1985–86 by juvenile sea lions (mean=86.8 g; sd=130.3) was also smaller than the mean mass consumed by adults (mean=173.0 g; sd=186.4). Slightly over half of the walleye pollock mass consumed by juvenile sea lions (50.7%) came from fish smaller than 30 cm in length, while only 21.1% of the mass consumed by adults was from juvenile pollock. Stomachs of 11 juveniles examined from 1985–86 contained the remains of an average of 80 pollock (sd=109.8), while 33 adults' stomachs contained remains from an average of 70 pollock (sd=101.8). The mean mass of a meal of pollock consumed by these animals was, consequently, 7.0 kg for juvenile sea lions and 12.0 kg for adults.

Seasonal and Annual Differences in Prey Consumption

During the 1970's there were significant (P<0.05) seasonal differences in the consumption of all prey taxa (Fig. 4). Walleye pollock was consumed most frequently in spring (January–April) and fall (September–December). Small forage fish and salmon were consumed almost exclusively in summer, whereas flatfish, other demersal fish, and cephalopods were consumed most

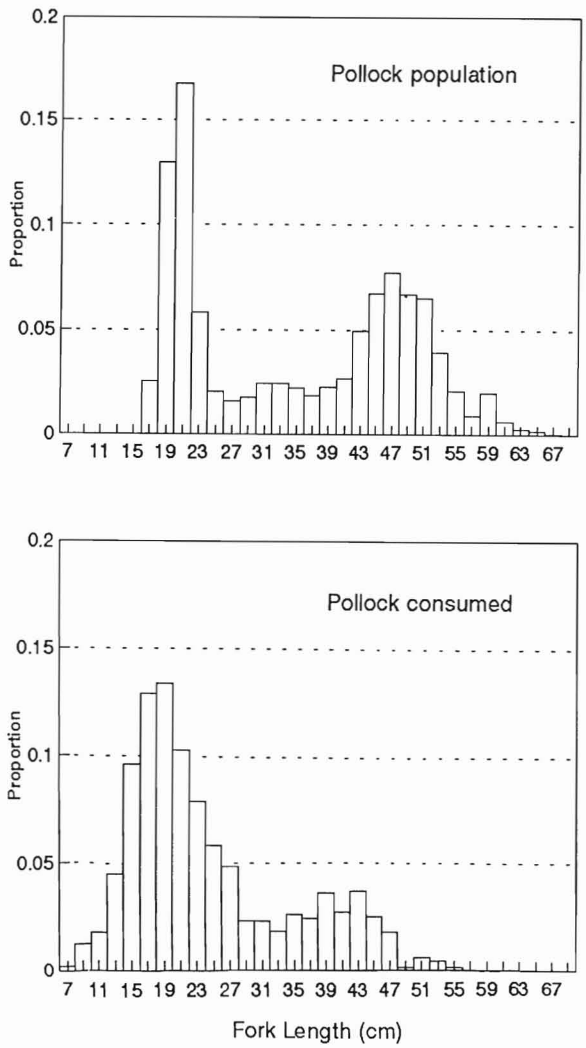

Figure 2
Size distributions (cm) of the walleye pollock population (upper) and walleye pollock consumed by Steller sea lions (lower) in the Kodiak Island area of the Gulf of Alaska in 1985.

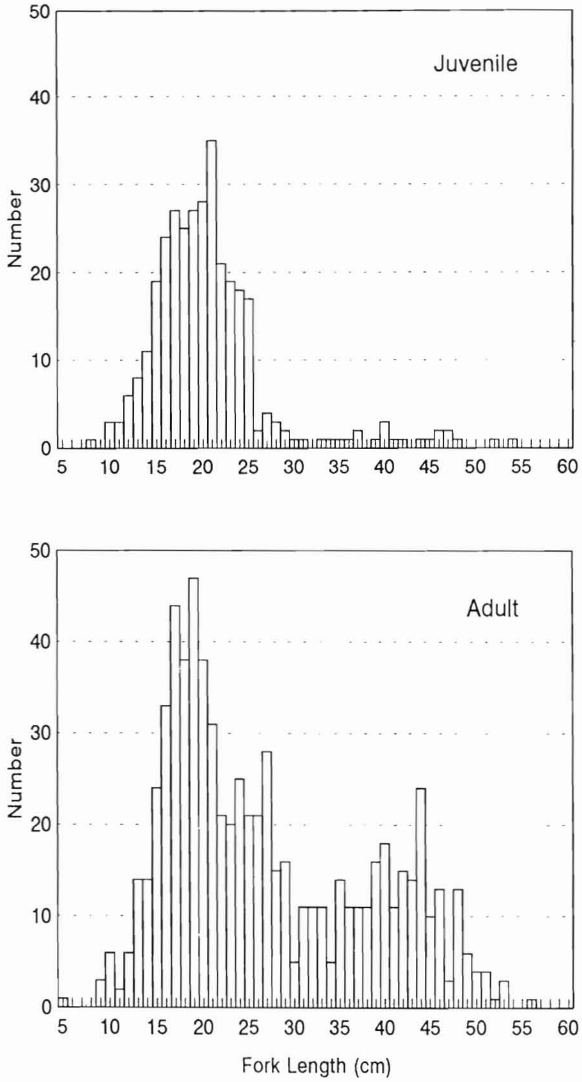

Figure 3
Size distributions (cm) of walleye pollock consumed by juvenile (upper) and adult (lower) Steller sea lions in the Kodiak Island area of the Gulf of Alaska in 1985.

frequently in spring or fall. No significant seasonal differences were found for any of the prey taxa from the 1985–86 collection.

Between 1975–78 and 1985–86, the proportion of animals consuming pollock and cephalopods increased significantly ($P<0.05$; Table 2, 3). The proportion consuming small forage fish and other demersal fish decreased significantly ($P<0.01$).

Walleye pollock was the fish prey most commonly consumed by sea lions collected in the Kodiak Island area for all seasons examined in the 1970's and 1980's, except for summer in the 1970's (Fig. 4). However, the proportion of animals consuming pollock increased significantly in summer between 1975–78 and 1985–86 (from 32.1% to 60.0%; $P=0.05$). A nonsignificant increase was observed in the spring (from 66.7% to 81.5% of stomachs; $P>0.05$), whereas fall consumption remained unchanged at 60%. Between the 1970's and 1980's, summertime consumption of small forage fish declined significantly ($P=0.01$) from 60.7% to 20.0%. Other demersal fish declined in the spring (from 26.7% to 3.7%; $P=0.03$) and fall (15.0% to 0.0%; $P=0.07$), the only times they were consumed.

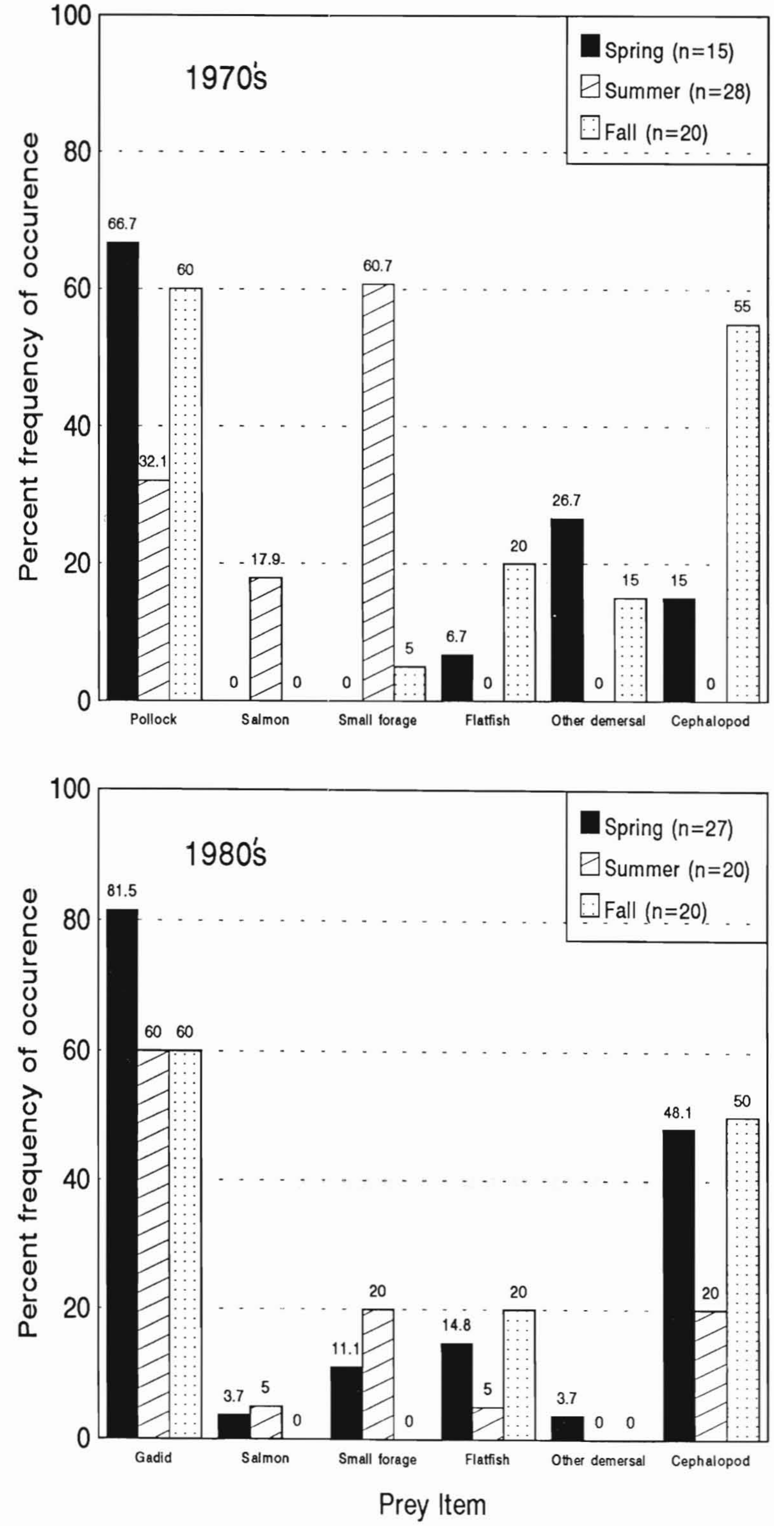

Figure 4

Frequency of occurrence of Steller sea lion prey items by season for the Kodiak Island area in 1975–78 and 1985–86. Spring includes January through April, summer includes May through August, and fall includes September through December.

Sea Lion Age Differences in Prey Consumption

Pollock was the most common prey for both sampled juvenile (≤4 years old) and adult sea lions. More juveniles than adults had only pollock in their stomachs in most areas and times sampled (Table 3). Kodiak Island area juveniles ate small forage fish more frequently than did adults (P=0.01; Fig. 5), whereas adults ate flatfish and cephalopods more frequently than did juveniles (P=0.01; Fig. 5). Salmon and other demersal fish were all consumed more frequently by adults, but the differences were not statistically significant. Similar dietary differences were observed for juveniles and adults in collections outside the Kodiak Island area, except that there was not a significant age difference in the consumption of small forage fish.

Between the 1970's and 1980's, the proportion of juvenile sea lions consuming pollock increased significantly, from 45.5% to 75.0% (P=0.05; Fig. 5). The proportion of adults consuming pollock increased from 53.3% to 66.7%, but the difference was not significant (P=0.23). The proportion of juveniles consuming pollock increased in the spring (from 66.7% in the 1970's to 80.0% in the 1980's), summer (from 21.4% to 50.0%), and fall (from 60.0% to 100.0%). Similar increases were observed for adults in the spring (from 66.7% to 81.8%) and summer (from 42.9% to 64.3%). Adult consumption in the fall fell from the 1970's to 1980's (from 60.0% to 46.7%).

In 1985–86, the only fish prey found in 16 Kodiak Island area juveniles' stomachs were walleye pollock, Pacific cod, Pacific herring, and Pacific sand lance. None contained salmon, flatfish, or other demersal fish.

Discussion

Walleye pollock was the most common prey of Steller sea lions in virtually all areas, seasons, and years sampled. This includes areas and times when the Steller sea lion population was either stable (the 1970's and the 1980's southeast Alaska collection) or decreasing (the 1980's Kodiak Island collection). Areas where the biomass of pollock was not large enough to support large fisheries for pollock (Prince William Sound and southeast Alaska) also had high pollock consumption.

The proportion of sampled animals consuming pollock increased in the Kodiak Island area from the 1970's to the 1980's, particularly during the summer. The overall proportion of animals consuming pollock was, however, somewhat affected by the uneven sampling of sea lions by age and season during the two collections (Table 1). An alternative approach to estimating the proportions consuming pollock would be to average within yearly periods the proportions from each sea lion age–season combination (e.g., juveniles in spring). This yields revised estimates of the proportion of Kodiak Island animals consuming pollock: 53.0% in the 1970's and 70.5% in the 1980's. Because these are not substantially different from the original estimates of 49.2% in the 1970's and 68.7% in the 1980's, it would appear that the decadal increase in Kodiak area pollock consumption by sampled animals was real.

Another important finding from these analyses is that small forage fish were consumed only seasonally. Capelin, sand lance, and herring were most commonly found in Kodiak Island area sea lion stomachs during May and July–August. In Prince William Sound, herring were generally consumed only in February (14 of 32 stomachs); only 2 of 34 stomachs from October through November contained forage fish. This seasonal pattern may be due to increased accessibility of these prey species at those times of year. These prey represent an ephemeral resource that is exploited when abundant (e.g., capelin during the spring spawning run). It remains a possibility, however, that these prey could play a significant role in the seasonal foraging ecology of sea lions (particularly juvenile sea lions). Nonetheless, the small fish prey most commonly consumed by sampled GOA sea lions on an annual basis was juvenile walleye pollock.

Diet Changes and Their Causes

The diet of Kodiak Island area sea lions appears to have changed between the 1970's and 1980's. The proportion of sea lions consuming pollock, flatfish, and cephalopod was greater in the 1980's than in the 1970's, while significant decreases occurred in the proportion of animals consuming small forage fish and other demersal fish. These changes were most apparent in juveniles. The proportion of juveniles consuming walleye pollock increased by 65%, while the proportion consuming forage fish decreased by 25%. None of the juveniles sampled in 1985–86 consumed salmon, flatfish, or other demersal fish.

The apparent change in diet of Kodiak Island area sea lions could represent

1. An artifact of the small sample size or of sampling locations
2. A change in prey preferences
3. Increased abundance of walleye pollock relative to the abundance of small forage fish and other demersal fish in the 1980's.

Effects of the sample sizes are difficult to discount—sample sizes were small, particularly if only juvenile

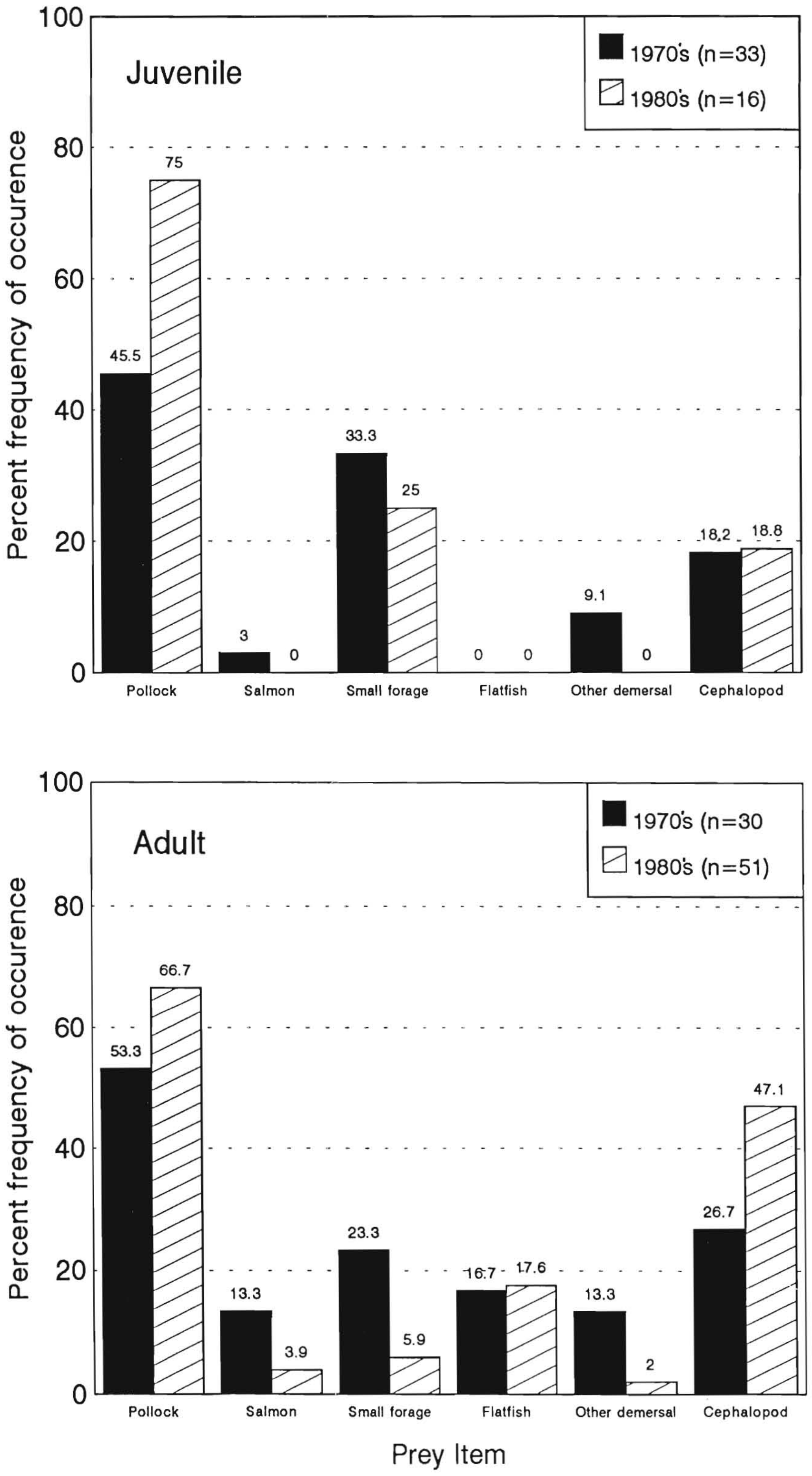

Figure 5

Frequency of occurrence of prey items in the diets of Kodiak Island area juvenile and adult Steller sea lions in 1975–78 and 1985–86.

animals are considered. The 1985–86 juvenile sample (compared to the 1975–78 sample) may have been too small to include less common prey. However, more adult sea lions were sampled from the Kodiak Island area in 1985–86 than in 1975–78, and adults still showed a reduced consumption of salmon, other demersal fish, and small forage fish.

This analysis was focused on Kodiak Island area collections partly to reduce bias due to sampling area. The Kodiak Island area samples include animals collected at the same general times and locations during the 1970's and 1980's. For example, during May 1977 most of the sea lions collected at the northeast end of the Kodiak Island Archipelago (e.g., Marmot and Sea Otter Islands) had consumed capelin. Animals were collected there in May 1985, and no capelin was found. The similarity of feeding habits of Kodiak Island area animals to those collected elsewhere in the 1970's and 1980's also suggests that the general dietary patterns found there are representative of gulfwide consumption patterns.

Increased consumption of pollock in the 1970's could have been due to an increased preference for this prey. No data exist to support or refute this hypothesis.

The differences in diet may reflect a change in relative prey abundance. Mean Gulf of Alaska walleye pollock spawner biomass was 0.995 million metric tons (t) in 1975–78 and increased 46.6% to 1.459 million t in 1985–86.[4] The number of adult fish (≥4 years old) was estimated to be the same in 1975–78 (2,099 billion fish) and 1985–86 (2,108 billion fish). The biomass increase was due to the number of large older fish (i.e., 7- and 8-year-old fish from the 1978 year class).

Total biomass of pollock ≥2 years old did, however, decrease from 1,925 t in 1976–78 to 1,686 t in 1985–86. This was due to low recruitment. Numbers of 2- and 3-year-old fish declined by 48.1% from an average of 2,851 billion fish in 1975–78 to 1,479 billion fish in 1985–86. Although estimates of the biomass of age-1 fish are not available, the numbers of age-2 fish the following year provide an index. These data suggest that the abundance of age-1 fish declined by at least 29% from 1975–78 to 1985–86.[4]

These trends in walleye pollock abundance could best explain increased pollock consumption if the mean size of pollock consumed increased. But the mean size appears to have remained small, implying continued reliance on small pollock, even with lower abundance. One explanation for this paradox could be that sea lions have a preference for small fish, and alternative small prey were less abundant (relative to juvenile pollock) in 1985–86 than in 1975–78.

Sea lions do commonly eat small fish. Ten of 13 food habits studies (Table 4) indicated that Steller sea lions consumed many small fish (mean fork length <30 cm). Juveniles ate smaller fish than adults in two of the three collections where juveniles were distinguished from adults (Table 4). In the Kodiak Island area, 74% of the pollock eaten by 25 sea lions sampled were under 30 cm FL. The data for the Kodiak Island area indicated that small schooling fish may be more important for younger, smaller sea lions (e.g., a significantly greater proportion of juvenile sea lions ate small forage fish, and the mean size of pollock eaten by juvenile sea lions was significantly smaller than the size consumed by adult sea lions).

Recent changes in the abundance of cephalopods, noncommercial fish (e.g., capelin), and even some commercial species (e.g., herring) are poorly understood. Commercial groundfish surveys generally do not include or do not adequately sample many of these potentially important prey species. The available data suggest that, in at least one area of the Gulf of Alaska, some of these species decreased in abundance after the late 1970's. Anderson et al.[5] found in an analysis of trawl data collected at Pavlof Bay (Alaska Peninsula) during 1972–92 that the species assemblage there had changed. Before 1978 the assemblage was dominated by Pandalid shrimps. During 1978–83 the assemblage shifted abruptly to one dominated by gadids, and then to flatfish during 1984–92. Large declines were observed in the abundance of shrimp and several small forage and demersal fishes (e.g., capelin, Pacific sandfish, and pricklebacks). The decreased abundance of shrimp, and the increased abundance of cod and flatfish in Pavlof Bay during 1978–92 seems to be a common characteristic of the western and central Gulf of Alaska (Albers and Anderson, 1985; Hollowed et al.[2]; Anderson et al.[5]; Wilderbuer and Brown[6]). Because shrimp, gadid, and flatfish abundance trends in the Gulf of Alaska are so similar to those of Pavlof Bay, it may be that forage fish abundance also decreased during the 1980's in areas outside of Pavlof Bay. This has been demonstrated from a preliminary analysis of Alaska Department of Fish and Game shrimp trawl data from other areas of the GOA (Anderson et al.[5]).

More data on the abundance of forage and other demersal fish prey is available from the Bering Sea. Capelin abundance was high in the 1970's but has since declined (Wespestad[7]). Analysis of the pattern of scale

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[5] Anderson, P. J., S. A . Payne, and B. A. Johnson. 1994. Long-term demersal community structure changes in Pavlof Bay, Alaska. Unpubl. manuscr. Kodiak Lab., Alaska Fish. Sci. Cent., P. O. Box 1638, Kodiak, AK 99615, 28 p.

[6] Wilderbuer, T. K., and E. S. Brown. 1992. Flatfish. *In* Stock assessment and fishery evaluation report for the 1993 Gulf of Alaska groundfish fishery. Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council , P. O. Box 103136, Anchorage, AK 99510, 25 p.

[7] Wespestad, V. G. 1994. Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle 98115-0070. Personal commun.

Table 4

Fork length (cm) of prey from stomachs of Steller sea lions collected in various areas during 1975–86 for all animals, for juveniles (age ≤4 years), and for adults.

Species	Area	Year	*n*	Mean FL (cm)	FL range (cm)
All ages					
Walleye pollock	Gulf of Alaska	1976–78	102	29.8	5.6–62.9
	Shelikof Strait	1983–84	36	40.9	30.0–52.0
	Kodiak Island	1985	25	25.1	7.9–54.2
	SE Alaska	1985	8	25.5	4.8–55.7
	Pribilof Islands	1976–79	2	46.9	
	Pribilof Islands	1986	2	33.5	20.8–44.5
	Central Bering Sea	1981	19	27.4	6.2–60.1
	Central Bering Sea	1985	10	21.8	10.5–51.6
	Western Bering Sea	1981	31	23.5	8.3–64.2
	Eastern Aleutian Islands	1981–82	4	29.9	1.7–42.7
Pacific cod	Pribilof Islands	1986	3	27.5	4.3–59.4
Pacific herring	Central Bering Sea	1985	6	27.5	25.0–31.1
Yellowfin sole	Pribilof Islands	1986	5	23.7	9.8–35.7
Juveniles					
Walleye pollock	Kodiak Island	1985	7	20.8	8.0–54.2
	Bering Sea	1981	20	22.4	9.6–56.9
Yellowfin sole	Pribilof Islands	1986	2	25	12.0–32.7
Adults					
Walleye pollock	Kodiak Island	1985	18	27.9	8.7–53.1
	Bering Sea	1981	30	26.9	8.5–63.3
Yellowfin sole	Pribilof Islands	1986	3	21.6	9.8–35.7

deposition in sediments at Skan Bay on the north side of Unalaska Island (eastern Aleutian Islands) indicates that some small forage fish (probably capelin) disappeared from the area in about 1978 (Francis[8]). Capelin also disappeared from seabird diets in the Pribilof Islands beginning around 1978 (Hunt[9]). Analysis of bycatch of eulachon, *Thaleichthys pacificus*, in the eastern Bering Sea indicated that its biomass appeared to have decreased by an order of magnitude from 1980–81 to 1985 (Fritz et al., 1993). Bering Sea biomass of some other demersal species consumed by sea lions (sculpins and eelpouts) appeared to decrease from the late 1970's to the mid-1980's (Bakkala, 1993).

It appears that small forage and other demersal fish species were decreasing at the time gadid and flatfish populations were increasing. The declines in the consumption of small forage and demersal fish observed in the sea lion diet could then have resulted from the decrease in availability of these fish. Increased consumption of flatfish and gadids (particularly walleye pollock in the summer) could then have resulted from their greater availability compared to small forage and other demersal fish.

Significance of the Change in Diet to the Steller Sea Lion Population Decline After 1985

Studies of other pinniped species have found a relationship between the stock sizes of pinnipeds and their prey. In Antarctic phocid populations, normal interannual fluctuations in prey biomass produce relatively small, short-term adjustments in pinniped population sizes due largely to fluctuations in juvenile survival or reproductive rates (Testa et al., 1991). But the declines in the Alaskan sea lion population have been more profound. Between 1985 and 1992, sea lion numbers in the central GOA fell by 70% (Sease et al., 1993). Such a change, if driven by a decline in prey abundance, would be similar to that observed only in acute environmental disturbances like the 1983 El Niño event. The effects of that event on prey availability appear to have resulted in near-total year-class failures for north-

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[8] Francis, R. 1994. Fisheries Research Inst., Box 357980, Univ. Washington, Seattle WA 98195. Personal commun.

[9] Hunt, G. L., Jr. Dep. Ecology and Evolutionary Biology, Univ. California, Irvine, CA 92717. Personal commun.

ern fur seals, *Callorhinus ursinus*, and California sea lions, *Zalophus californianus*, in southern California, the Galápagos Islands, and coastal Peru (Trillmich et al., 1991). In western Alaska, however, the effect has been chronic: central GOA declines that began in the early 1980's have continued at least through 1993.

By 1985, the most common prey of Steller sea lions in the Kodiak Island area was still juvenile walleye pollock, even though juvenile pollock abundance was reduced in the GOA below 1975–78 levels. Declines in abundance of alternative small prey may have led to increased consumption of pollock. Very low recruitment of pollock from the 1986–87 and 1989–91 year classes further reduced available forage. Average recruitment (as 2-year-old fish) for those five year classes was 291 million fish, 19.7% of that of the 1984–85 year class (1,479 million fish) and 10.2% of the 1975–78 mean (2,851 million fish[4]). The smaller mean size of fish consumed in the 1980's would also mean that sea lions had to forage longer or catch adult pollock to meet their energetic needs.[1] Juvenile sea lions may not, however, have been able to dive deeply enough to catch adult pollock. Dive studies of young-of-the-year Steller sea lions have indicated that these young animals rarely dive deeper than 50 m.[2] Whereas juvenile pollock are commonly found in the upper 50 m, adult pollock are found far deeper (commonly down to 200 m or more). Thus, lacking the ability to capture adult pollock, young sea lions would have been particularly vulnerable to declines in the biomass of small prey.

In summary, walleye pollock was generally the most common prey item for the Gulf of Alaska Steller sea lion population during 1975–78 and 1985–86 in all areas and seasons sampled. Consumption of walleye pollock in the Kodiak area increased during this period, particularly for juvenile sea lions. This increase occurred despite decreases in the abundance of small pollock. Consumption of alternative prey items (e.g., small forage fish) declined in the same period, perhaps because of a relatively greater decrease in the abundance of these prey. Continued low abundance of both small pollock and alternative small fish prey after 1986 would have reduced juvenile sea lion foraging success. This, in turn, would have reduced juvenile survival and could have produced the sea lion population decline observed in the Gulf of Alaska during the 1980's and early 1990's.

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Northern Fur Seal, *Callorhinus ursinus*, Predation on Juvenile Walleye Pollock, *Theragra chalcogramma*

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ABSTRACT

Juvenile walleye pollock, *Theragra chalcogramma*, is a primary prey species of adult female and juvenile northern fur seals, *Callorhinus ursinus*, during summer in the eastern Bering Sea. Variability in walleye pollock year-class strength is reflected by the size distribution of walleye pollock consumed by northern fur seals.

Prey were identified from the gastrointestinal contents of 73 northern fur seals collected in the eastern Bering Sea in 1981, 1982, and 1985, and from 847 fecal samples collected on St. Paul Island (Pribilof Islands, Bering Sea) from 1987 to 1990. Walleye pollock represented 79% of all prey for all years combined in gastrointestinal tracts, and 78% of the total prey in fecal samples. The frequency of occurrence of pollock in all years averaged 82% in gastrointestinal tracts and 76% in fecal samples.

Adult female and juvenile fur seals forage primarily on age-0 and age-1 pollock measuring from 3 cm to 20 cm, as determined by regression analysis of otolith length versus fish fork length, accounting for wear on otoliths from digestion. Older age groups of pollock occurred with greater frequency in gastrointestinal samples when very strong cohorts were followed by weak year classes, and probably in the absence of other prey resources.

The synchrony of trends in walleye pollock year-class strength with the number and size distribution of pollock observed in the gastrointestinal tracts of adult female and juvenile northern fur seals indicates that the variability of juvenile pollock recruitment directly influences the feeding habits of northern fur seals.

Introduction

The Pribilof Island population of northern fur seals, *Callorhinus ursinus*, is a significant component of the Bering Sea ecosystem in summer and fall. The herd contains approximately 980,000 animals, which is about 72% of the world's breeding population for the species (Loughlin et al., 1994). The population is pelagic throughout the northern Pacific Ocean from November to May. From June through October, the seals haul out on the Pribilof Islands (St. Paul and St. George) in the Bering Sea to give birth and to breed (Fig. 1). Adult males fast during the summer breeding season. Most adult females give birth in June and July, then conduct cyclic feeding trips throughout the summer; the cycles average 2.5 days onshore nursing pups and 5.9 days at sea feeding (Gentry et al., 1986; Loughlin et al., 1987). Juveniles are primarily pelagic for the first few years of life, returning to the islands intermittently during late summer or fall.

The decline of the Pribilof Island population of northern fur seals in the late 1970's to early 1980's (York and Hartley, 1981) and lack of growth through the early 1990's may be related to diet or food availability (Sinclair, 1988; Trites, 1992; Sinclair et al., 1994). This study examines patterns in consumption of walleye pollock, *Theragra chalcogramma*, by northern fur seals in the Bering Sea during the 1980's and early 1990's, including the age of walleye pollock eaten relative to pollock year-class strength.

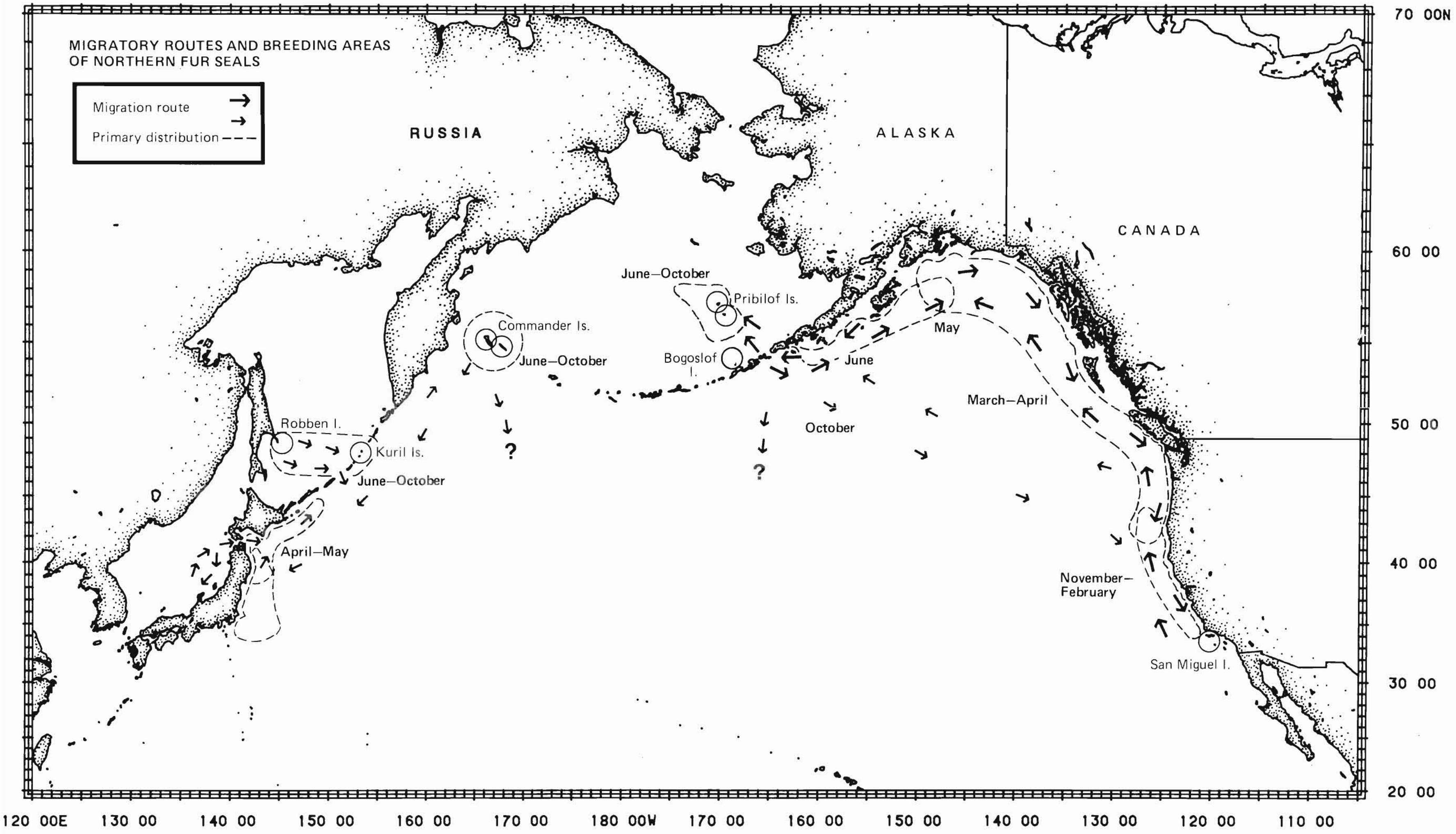

Figure 1

Breeding islands and migratory routes of northern fur seals, *Callorhinus ursinus* (adapted from Loughlin and Miller, 1989).

Methods

Information on the diet of northern fur seals from the eastern Bering Sea was collected from August to October between 1981 and 1990. Fresh (within 2 hours of death) stomach and intestinal (gastrointestinal, or GI, tract) contents were collected from 16 juveniles and 57 adult females shot at sea in the vicinity of the Pribilof Islands in 1981 (n=7), 1982 (n=23), and 1985 (n=43; Fig. 2). Most seals were collected in areas where water was shallower than 200 m and within the outer domain of the continental shelf (Kinder and Schumacher, 1981). The GI tract data presented here originally appeared in Sinclair (1988) and Sinclair et al. (1994).

Feces (scats) were collected on St. Paul Island beaches where adult female fur seals hauled out in 1987 (n=228), 1988 (n=85), 1989 (n=199), and 1990 (n=335). Gastrointestinal tracts and scats were stored frozen prior to analysis. In 1981 and 1982 prey material was gently flushed through a series of graded sieves, the smallest of which was 0.71 mm. After 1982, a 0.50-mm sieve was added to the series to further assure retrieval of all prey material. Otoliths were stored in 70% ethanol.

Prey were identified from remains of whole bodies or hard parts. The importance of a prey species in the northern fur seal diet was determined by examining values for percent number and percent occurrence. Percent number (PN) refers to the number of individuals representing a particular prey species as a percentage of the total number of all prey species in all samples. Percent occurrence (PO) refers to the number of seals that consumed a particular prey species, expressed as a percentage of all samples containing identifiable prey.

Before determining the size of walleye pollock eaten by seals, we assigned to quality categories otoliths recovered from GI tracts (Sinclair et al., 1994) to account for any potential loss of otolith length due to degradation by stomach acids. Quality categories were further defined for walleye pollock otoliths recovered from scats by calculation of and correction for the percent loss of length (Prime, 1979; North et al., 1983; Dellinger and Trillmich, 1988; Harvey[1]). Otoliths in fair or poor condition were counted but not measured. Otoliths in good or excellent condition were measured to the nearest .05 mm with vernier calipers or an ocular micrometer. Walleye pollock fork lengths (FL) were estimated based on Frost and Lowry's (1981) otolith-to-body-length regression formulae for pollock in the Bering Sea:

otoliths >10.0 mm:

$$Y \text{ (FL in cm)} = 3.175X - 9.770 \quad (r=0.968)$$

otoliths ≤10.0 mm:

$$Y \text{ (FL in cm)} = 2.246X - 0.510 \quad (r=0.981)$$

Ages were then assigned based on length–age relationships described by Smith (1981) and Walline (1983) for pollock from the Bering Sea. The GI and scat data sets were kept separate during analysis.

Results

Both PN and PO values indicated that walleye pollock was the dominant prey item for all years in GI tracts and scats (Fig. 3, 4). The similarity of walleye pollock PN and PO values in six of the seven sampling years gives a strong indication of the importance of walleye pollock in the diet of northern fur seals, as well as the comparative reliability of both collection methods (Fig. 5).

Juvenile walleye pollock (3–20 cm FL; ages 0 and 1) were the most numerous and frequently occurring prey in all years (within sample type) combined (Fig. 6). In GI tract samples, 72% of prey pollock were from the age-0 group (3–13 cm FL) and 24% were age 1 (13–20 cm FL). Four percent of prey pollock from the GI tracts were age 2+ (≥20 cm FL). In fecal samples, 73% of prey pollock were from the age-0 group, 22% were age 1, and the remaining 5% were age 2+.

Although age-0 pollock were the dominant prey of seals overall, there were marked differences between years in the GI tract collections (Fig. 7). In 1981, few walleye pollock remains were found in GI tracts compared to all other years, and most were from 3- and 4-year-old fish. In 1982, GI tracts contained primarily age-0 pollock; in 1985 they contained primarily age-1 pollock. The age–frequency distribution of walleye pollock in the scats, however, was similar from 1987 to 1990 and was dominated by age-0 juveniles (Fig. 8).

Discussion

The size distribution of walleye pollock in the GI contents of adult female and juvenile northern fur seals collected in the early 1980's reflected annual year-class strength estimates for walleye pollock (Fig. 9; Sinclair, 1988; Sinclair et al., 1994). The 1978 year class (age 3 in 1981) was the strongest ever recorded; the 1980 year class (age 1 in 1981) was about one-half the estimated average year-class size; and the 1981 year class (age 0 in 1981) was the weakest observed before 1983. The 1982 and 1984 year classes were strong, but the 1985 year class was considered below average (Fig. 9a; Wespestad and Dawson[2]). Similarly, seals ate primarily 3- and

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[1] James Harvey, Moss Landing Marine Laboratory, P.O. Box 450, Moss Landing, CA 95039-0450. Unpubl. data.

[2] Wespestad, V. G., and P. Dawson. 1992. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1993, p.1-2 to 1-32. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

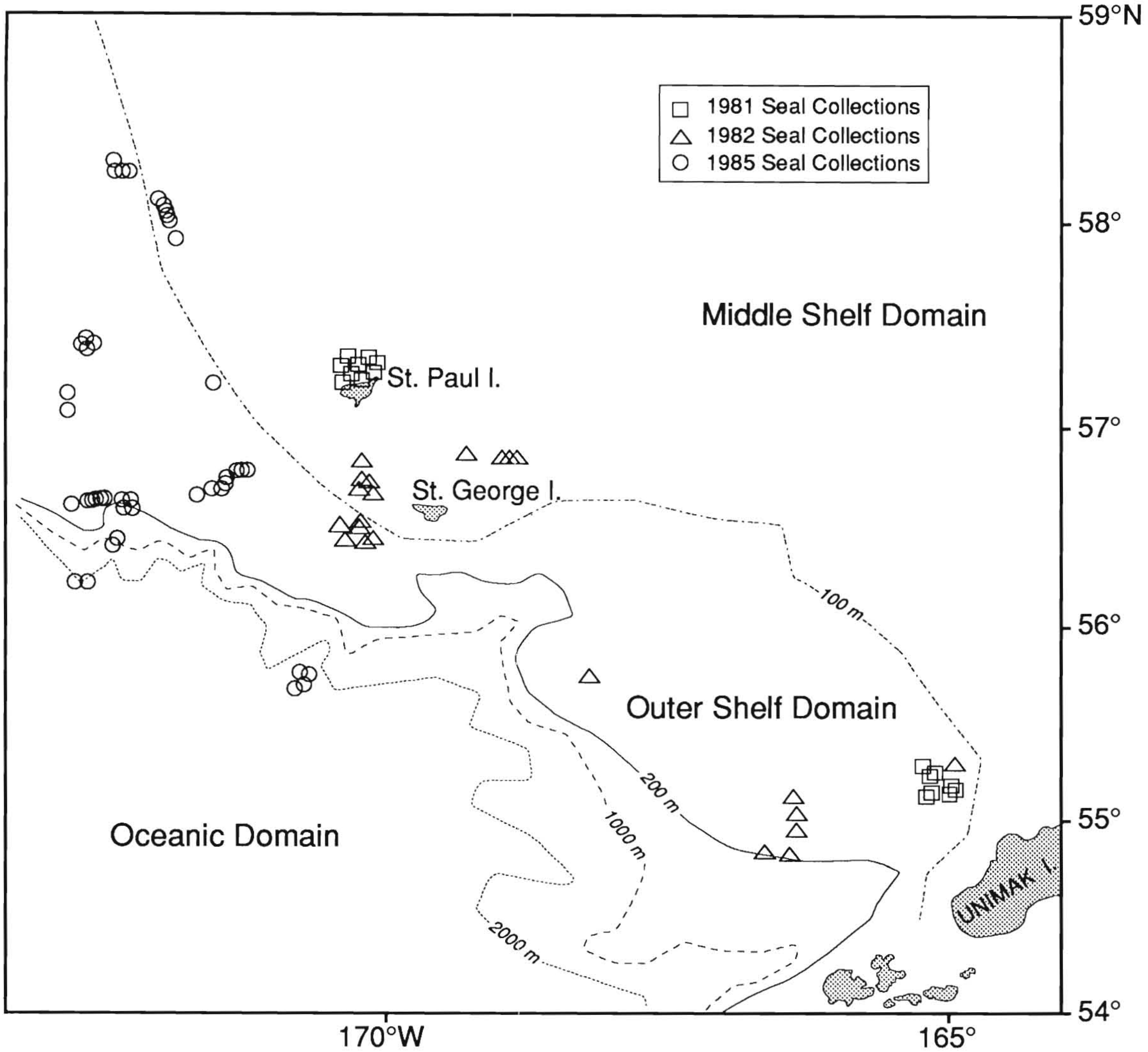

Figure 2

The study area showing locations of northern fur seal collections (adapted from Sinclair et al., 1994). Oceanic domains are shown as defined by Kinder and Schumacher (1981). Stomachs collected in 1981 off St. Paul Island were empty and not included in the final analysis.

4-year old pollock in 1981 (from the 1977 and 1978 year classes), age-0 pollock in 1982 (from the 1982 year class), and age-1 pollock in 1985 (from the 1984 year class; Fig. 9b). Lacking discrete annual distribution data on juvenile walleye pollock, we cannot be certain how much differences in sampling location may have influenced the relative yearly abundance of walleye pollock and walleye pollock age groups in northern fur seal GI contents. However, the variable recruitment patterns of walleye pollock were reflected in the GI contents of northern fur seals.

Scat analysis indicated a less direct association (relative to analysis of GI tract samples) between pollock year-class strength and seals' consumption of pollock. Analysis of the 1987–1990 samples indicated that seals ate primarily age-0 walleye pollock despite weak to average pollock year-class strength relative to the early 1980's (Fig. 9, 10). Fishery surveys and commercial catch data indicate that pollock year-class size in the late 1980's may actually have been much larger than the projections presented here[2] but revised estimates are not yet available. If the present estimates prove accurate, we speculate that seal consumption of age-0 walleye pollock as primary prey in the late 1980's may be due to the absence of alternate prey resources (Sinclair et al., 1994), strong localized abundances of age-0 fish, or the potential for a skewed concentration of remains of younger fish in the colons of northern fur seals (Sinclair and Antonelis, unpubl. data).

The largest series of studies of northern fur seal diet in the eastern Bering Sea was based on the analysis of

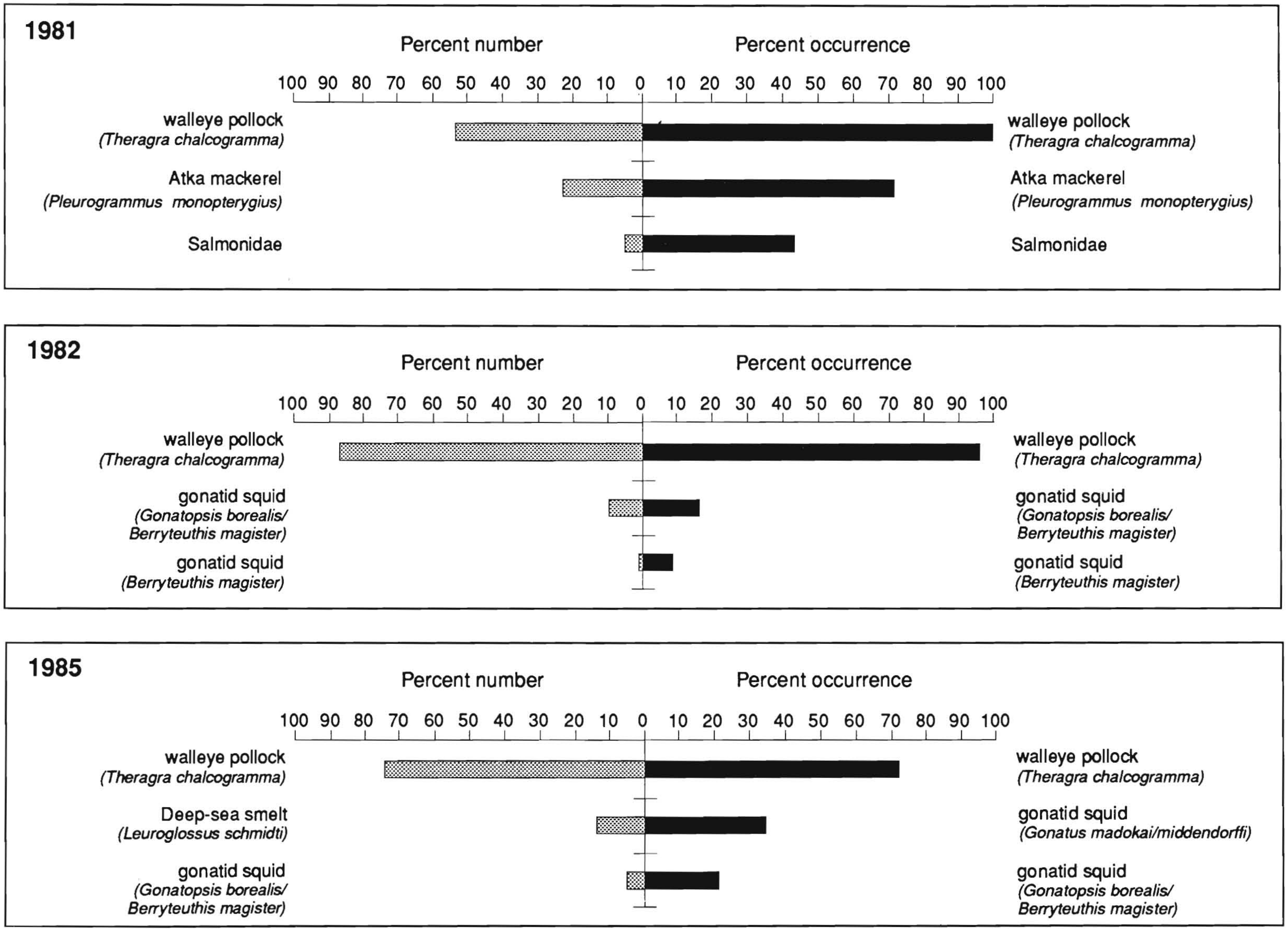

Figure 3

Percent number (PN) and percent occurrence (PO) values for the three dominant prey species identified in northern fur seal gastrointestinal tracts collected in 1981, 1982, and 1985 (data originally presented in Sinclair, 1988 and Sinclair et al., 1994).

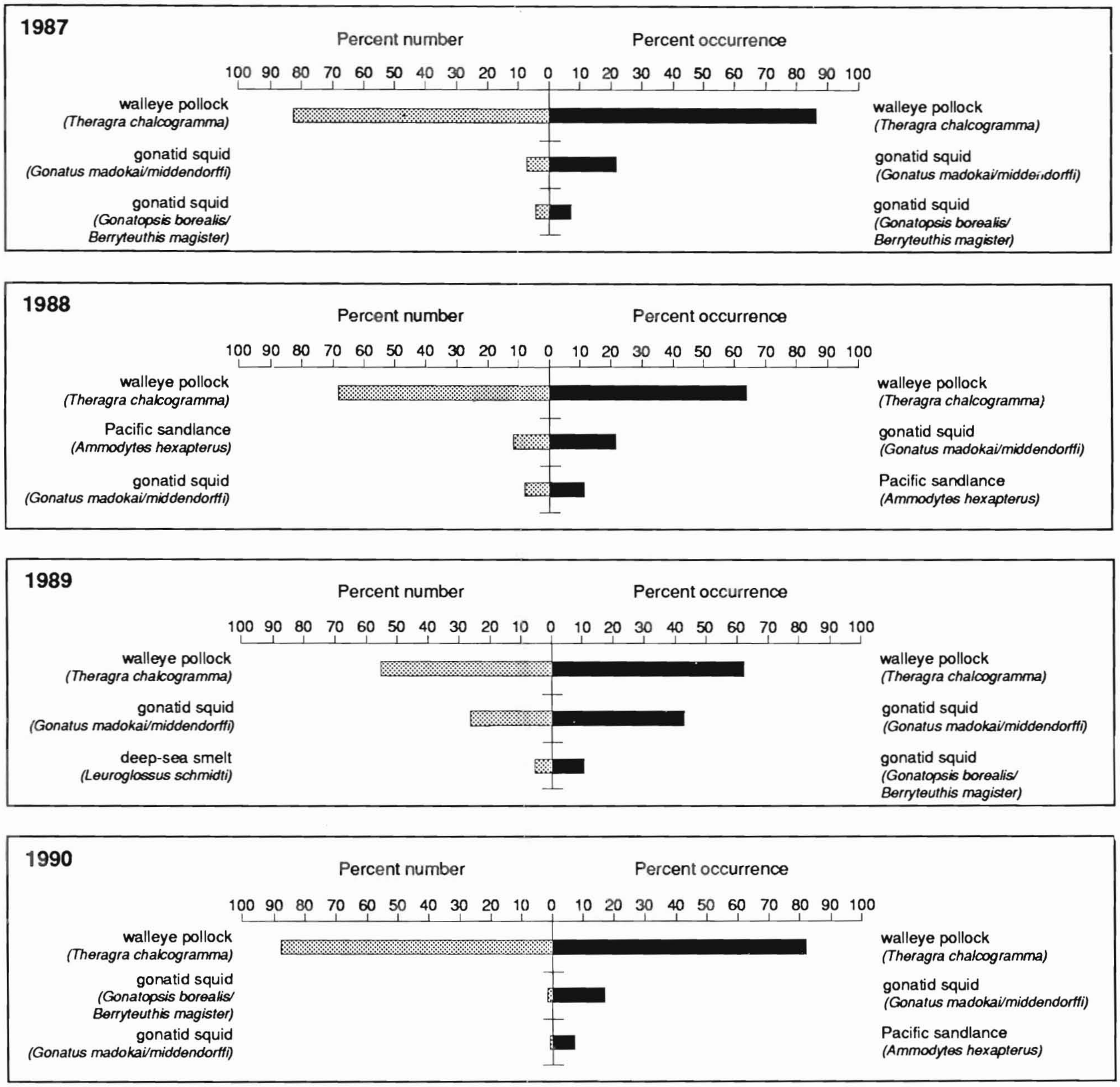

Figure 4

Percent number (PN) and percent occurrence (PO) values for the three dominant prey species identified in northern fur seal scats collected in 1987–90.

stomach contents of 1,800 animals collected pelagically from June to October in 1960, 1962–64, 1968, 1973, and 1974 (Kajimura, 1985; Perez and Bigg, 1986). Walleye pollock was the principal prey species for all years combined in the pelagic studies, yet it ranked less than 25% PO, compared with PO values of 79% for all years combined in the 1980's studies. Capelin, *Mallotus villosus*, was absent both in this study and in Sinclair et al. (1994), yet it ranked from first to third most important prey identified in northern fur seal stomachs from the earlier pelagic collections (Kajimura, 1985). The absence of capelin in all 7 years of this study is noteworthy, since samples were collected in the same region and season as in the pelagic studies. Herring, *Clupea pallasi*, was also a principal prey species of northern fur seals in the pelagic studies (Kajimura, 1985). Yet her-

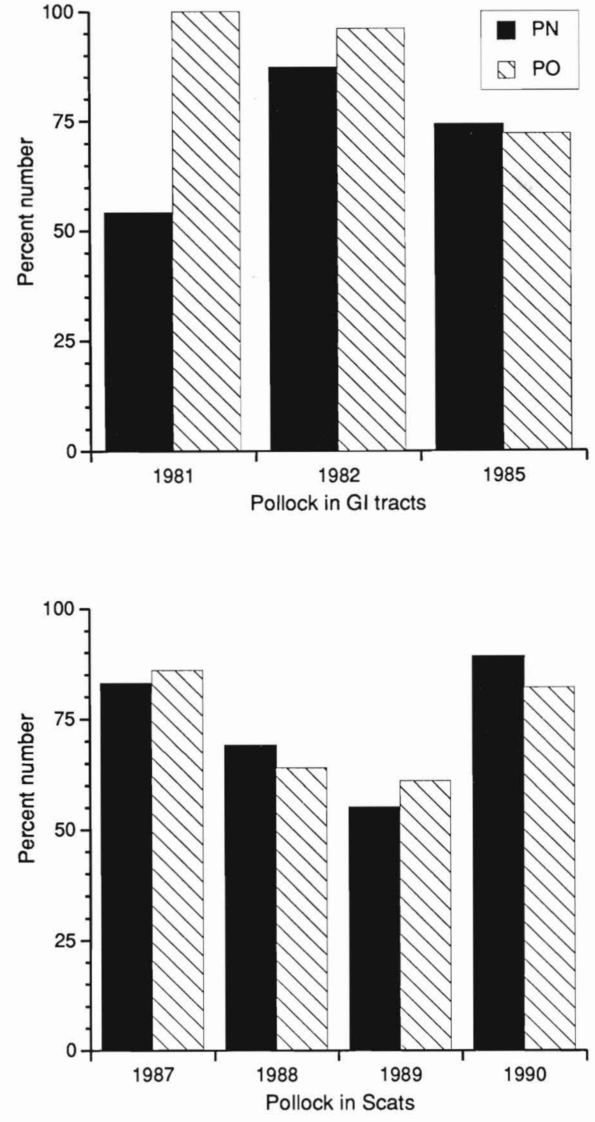

Figure 5

Percent number (PN) and percent occurrence (PO) values for walleye pollock, *Theragra chalcogramma*, in gastrointestinal tracts and scats of northern fur seals, 1981–90.

ring was present in only one GI tract and 3% of the scats in this study. Such changes in the consumption of fish probably reflect the dynamics of the Bering Sea ecosystem over the last 20 years. The composition of potential fur seal prey changed from being dominated by herring and capelin through the early 1970's, to a pollock-dominated system more recently (NMFS[3]).

The size of Bering Sea walleye pollock (Smith, 1981) and the size of pollock consumed by northern fur seals

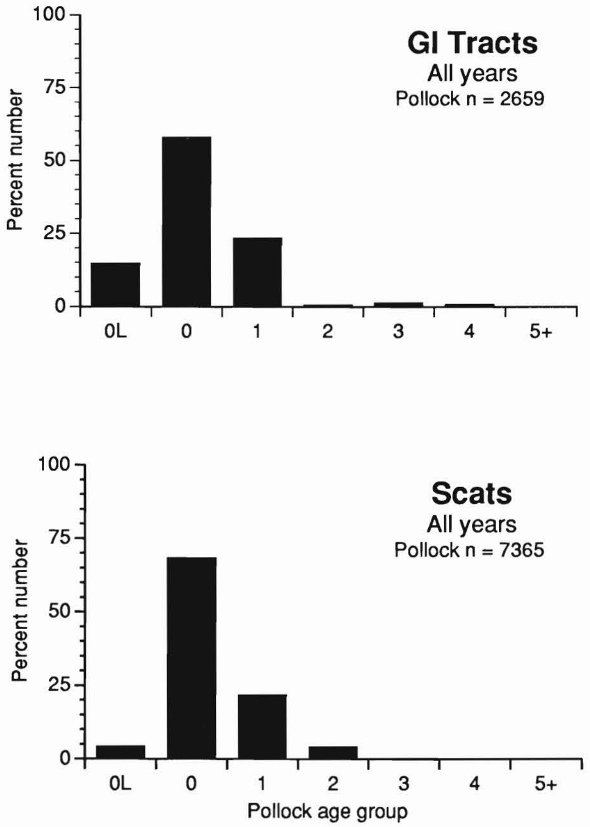

Figure 6

Percent number by age group of prey pollock from the gastrointestinal tracts (1981, 1982, and 1985) and scats (1987–90) of northern fur seals. The abbreviation OL represents larval-size walleye pollock (less than 5 cm in body length). The OL group is considered part of the age-0 group in PO and PN calculations.

(Swartzman and Haar, 1983) may have decreased during the 1970's. Swartzman and Haar further suggest that more small pollock became available in the Bering Sea ecosystem during the 1970's. A "juvenation" (Swartzman and Haar, 1983) of walleye pollock in the Bering Sea cannot be confirmed by northern fur seal diet studies because prey size was not consistently recorded before the 1980's. If such a size reduction has occurred, it may explain the high occurrence of juvenile pollock in fur seal diets in the 1980's and 1990's and the marked reduction of other small schooling

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[3] NMFS. National Marine Fisheries Service. 1993. Final conservation plan for the northern fur seal (*Callorhinus ursinus*). Prepared by the National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, and the Office of Protected Resources, National Marine Fisheries Service, Silver Spring, MD. 80 p.

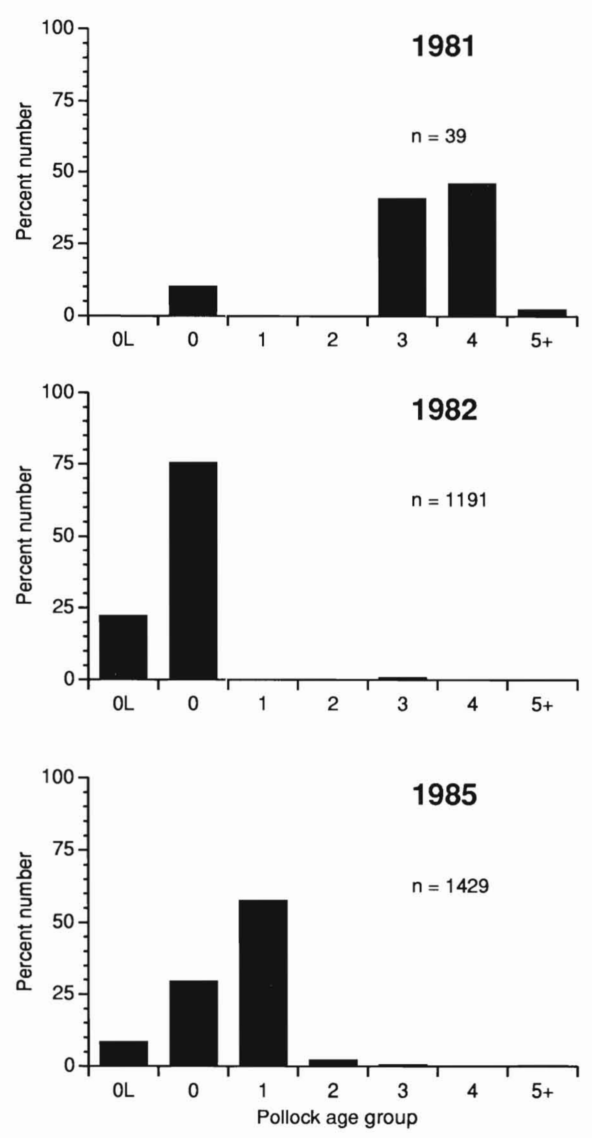

Figure 7
Interannual variation in the percent number by age group of prey pollock from the gastrointestinal tracts of northern fur seals (data originally presented in Sinclair, 1988 and Sinclair et al., 1994).

prey. Seals may have found a newly abundant but unreliable resource in walleye pollock because of its variable recruitment rates (Smith, 1981) and because it may have expanded at the expense of other prey species, such as Pacific herring (Wespestad and Barton, 1981; Bakkala et al., 1987). During years of low abundance or availability of juvenile pollock, fur seals can switch to other prey (capelin and herring). In spite of this capability, their food resources may be limited if these alternate prey species are displaced or depleted (Sinclair, 1988; Sinclair et al., 1994).

Summary

Our analysis indicates a marked shift in northern fur seal diet in the eastern Bering Sea since the 1970's; this shift includes increased consumption of pollock, de-

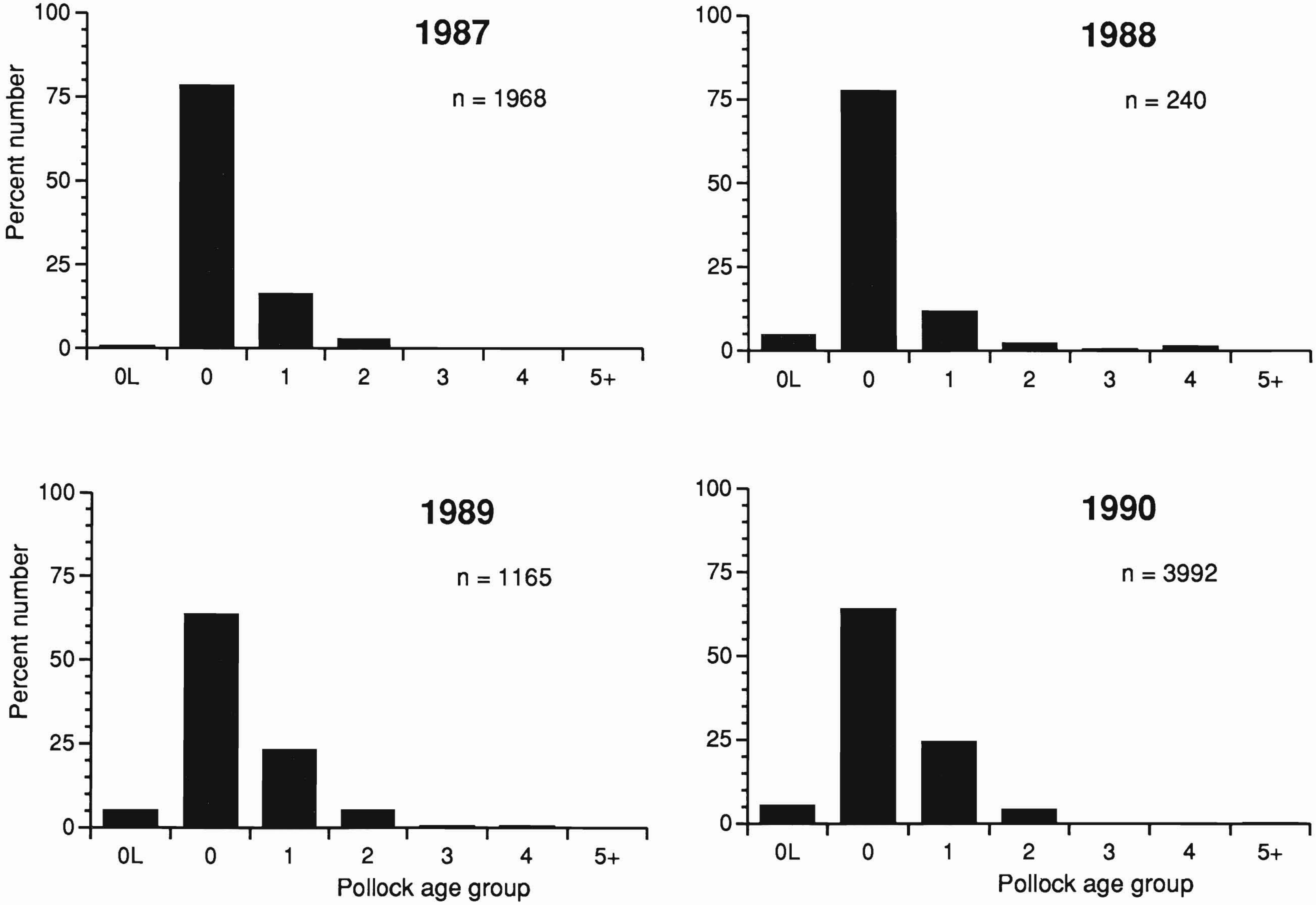

Figure 8

Interannual patterns in the percent number by age group of prey pollock from the scats of northern fur seals.

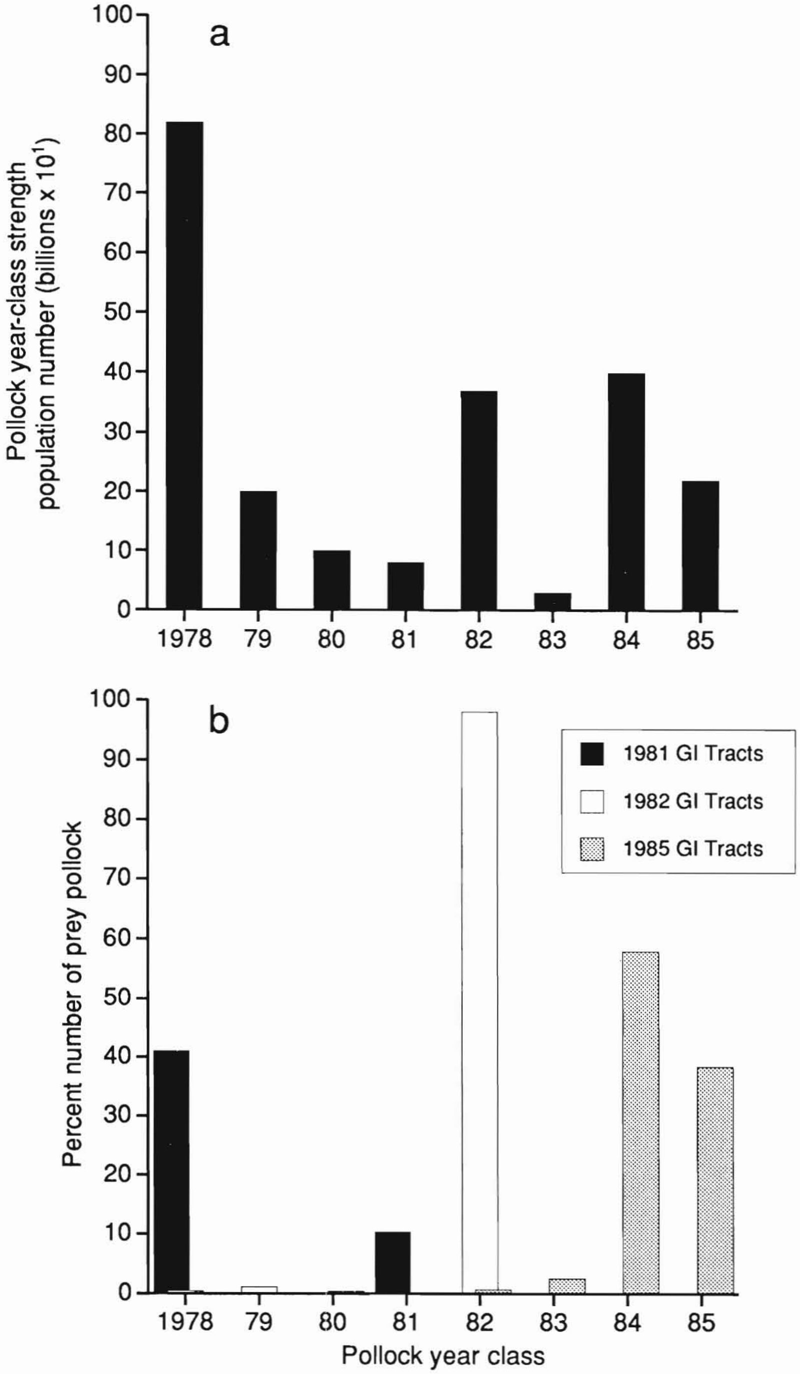

Figure 9

(a) Estimates of walleye pollock year-class strength, 1978–85, based on midwater acoustic and bottom trawl surveys of walleye pollock at age 1 (Wespestad and Dawson[2]); compared to (b) the estimated abundance of specific pollock year classes in northern fur seal gastrointestinal tracts collected in 1981, 1982, and 1985. Adapted from Sinclair et al. (1994).

creased consumption of other small schooling prey, and perhaps a decrease in the size of prey pollock. This study demonstrates the dominance of age-0 and age-1 pollock in adult female and juvenile fur seal diets over a 7-year period, and the strong influence of pollock year-class strength on the age frequency of pollock in GI tract samples collected in the early 1980's. For undetermined reasons, pollock year-class strength played a less important role in the age frequency of pollock in seal scat samples collected in the late 1980's relative to all

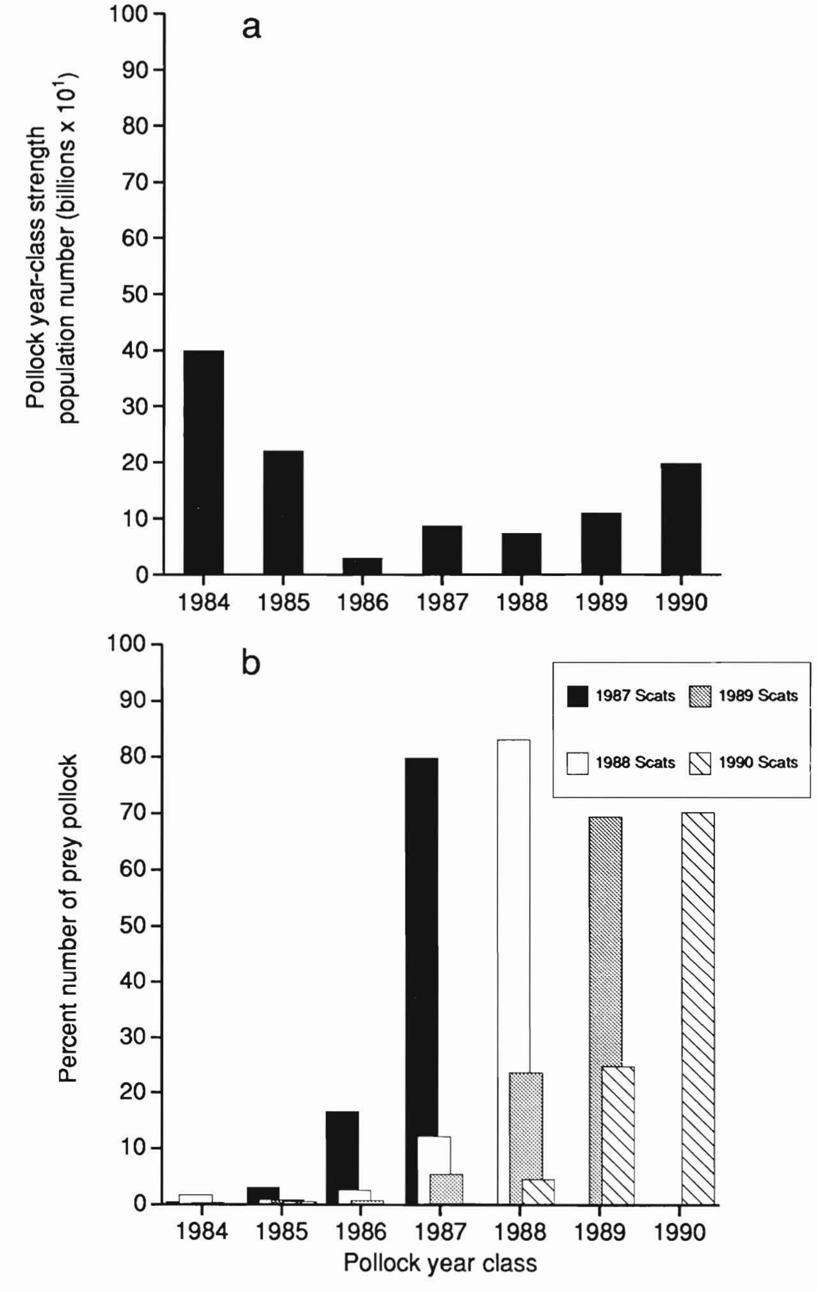

Figure 10

(a) Estimates of walleye pollock year-class strength, 1984–90, based on midwater acoustic and bottom trawl surveys of walleye pollock at age 1 (Wespestad and Dawson[2]); compared to (b) the estimated abundance of specific pollock year classes in northern fur seal scats collected in 1987–90.

other sample years. In order to fully evaluate patterns in consumption of walleye pollock by northern fur seals, we need more refined estimates of pollock year-class strength and movements of juvenile and adult walleye pollock, as well as estimates of the abundance and availability of noncommercial fish and squid.

Acknowledgments

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Juvenile Walleye Pollock, *Theragra chalcogramma*, Bycatch in Commercial Groundfish Fisheries in Alaskan Waters

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ABSTRACT

Juvenile walleye pollock, *Theragra chalcogramma*, (<30 cm total length) caught incidentally in trawl fisheries for groundfish off Alaska are generally discarded because they are too small to be processed into surimi or fillets. Catch rates of 20–29-cm pollock (ages 2–3) have varied greatly over time and area, but these fish account only for 1.8% of the Gulf of Alaska (GOA) pollock and 4.5% of the eastern Bering Sea (EBS) pollock measured by observers during 1977–92. Few pollock smaller than 20 cm are caught by groundfish fisheries. Most juvenile pollock are caught by pollock fisheries in both the GOA (98%) and EBS (96%). Bycatch rates of pollock <30 cm by pollock fisheries are similar for midwater and bottom pollock fisheries. However, annual average rates (1977–92) in the EBS (4.8% for both trawl types) have been double those in the GOA (2.0% for midwater and 1.8% for bottom trawls).

Bycatches of juvenile pollock varied depending on the age structure of the pollock population, season, locations fished, and, to some extent, the behavior of the fishery. Comparison of catch-at-age and population estimates between 1964 and 1991 suggest that catches of young pollock generally varied directly with their abundance. In the GOA, exploitation rates of 2–3-year-old pollock averaged about 1%, with levels as high as 3% from 1982 to 1984. In the EBS, exploitation rates on 2–3-year-olds averaged about 2% from 1964 to 1972 and 1980 to 1990 (maximum of 4%), but ranged between 11% and 21% from 1973 to 1979, apparently because the foreign fishery was targeting on small fish at the time.

Juvenile pollock in the GOA were generally found in embayments on the Kodiak Archipelago and along the Alaska Peninsula. Pollock trawl fisheries along the edge of the GOA continental shelf, especially in the western GOA, took fewer juvenile pollock than those located closer to shore. In the EBS, juvenile pollock were more commonly found along the mid to outer continental shelf northwest of the Pribilof Islands than southeast of the islands.

Introduction

Juvenile walleye pollock, *Theragra chalcogramma*, is an important component of the diets of many marine mammals, birds, and fish in the North Pacific Ocean and Bering Sea (e.g., Hunt et al., 1981; Lowry et al., 1988; Livingston, 1993), and adult pollock support one of the largest commercial fisheries in the world (Megrey and Wespestad, 1990). It has been speculated that commercial harvests of pollock, including bycatches of juveniles, have contributed to recent declines in many marine mammal and bird populations in the North Pacific and Bering Sea. In this paper, I describe the bycatch of juvenile pollock by federally managed groundfish fisheries in the eastern Bering Sea (EBS) and Gulf of Alaska (GOA). Conclusions about whether the described levels of juvenile pollock bycatch contribute to the marine mammal and bird population declines, however, are left to the reader.

Juvenile pollock are defined as fish <30 cm in total length (TL), which corresponds to 0–2-year-old and some 3-year-old fish (Hollowed et al.[1]; Wespestad and

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[1] Hollowed, A. B., B. A. Megrey, and W. Karp. 1992. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1993, p. 1-1–1-69. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

Dawson[2]). Wespestad and Dawson[2] reported that 3-year-old pollock in the EBS averaged 34.5 cm in length, and that 29% were mature. In the GOA, 3-year-old pollock averaged between 29 and 38 cm in length (Hollowed[3]) and approximately 20% were mature (Hollowed and Megrey[4]). In this paper, I address the following questions. 1) Which groundfish fisheries catch juvenile pollock, when, and where? 2) Has the juvenile pollock bycatch varied over time, and how does this relate to the age structure of the population? 3) Does the bycatch of juvenile pollock differ between the Gulf of Alaska and the eastern Bering Sea?

Methods

Observers aboard commercial fishing vessels in the North Pacific have collected data on species and size composition of catches since the mid-1970's (see Nelson et al., 1981 for a discussion of sampling methodology). For this study, pollock length-frequency data collected between 1977 and 1992 in the EBS (International North Pacific Fisheries Commission [INPFC] statistical areas 51 and 52) and the GOA (INPFC statistical areas 61–64) were tabulated by three seasons and various target fisheries. Seasons were defined as January–April (approximately the current Bering Sea/Aleutian Islands "A," or pollock-roe season); May–July (early "B," or non-roe season); and August–December (late "B" season). Only data collected aboard trawl vessels were used. Longlines and pots are not used in the directed pollock fisheries, and in other fisheries these gear generally account for less than 0.2% of the pollock catch in the Gulf of Alaska and Bering Sea each year. Observers collect and report length-frequency data from a sample of the entire catch, which consists of both retained and discarded species and sizes. However, no data were available that describe the length-frequency of just the discarded portion of the catch.

Pollock length frequencies were assigned to target fisheries based on a series of hierarchical catch-composition criteria of individual hauls (Berger[5]; Table 1). Under the criteria in Table 1, a single haul may satisfy the definition of more than one target species, but is assigned to the last fishery in the list for which it meets the criteria. For example, if a haul from the GOA comprised 21% deepwater flatfish, Pleuronectidae; 40% sablefish, *Anoplopoma fimbria*; and 37% rockfish, *Sebastes* spp., it would be defined as a rockfish haul despite meeting the criteria for both deepwater flatfish and sablefish fisheries. These hierarchical definitions and criteria were developed with considerable attention to what data (hauls) were included and excluded, in order to best capture the distribution and catch of fisheries as a whole.

Catch-at-age and numbers-at-age data for both the EBS and GOA pollock populations were obtained from recent assessments of the two stocks. Assessments of the EBS pollock population[2] and the GOA populations[1] were sources of data on catches and numbers of pollock at age.

Data on numbers of pollock caught and discarded by EBS fisheries from 1990 to 1992 were obtained from Michael Guttormsen, NMFS/AFSC. He combined weekly processor reports (retained and discarded weights of each species supplied by fish processors) and observers' estimates of catches to yield retained and discarded catches of all species, by time and fishery. Estimates of discarded and total pollock catch for each GOA fishery in 1990–92 were obtained from Hollowed et al.[6]

Results and Discussion

Catch of Pollock by Fishery

Target pollock fisheries in the GOA accounted for more than 85% of the pollock caught by weight in the GOA (with the Pacific cod, *Gadus macrocephalus*, trawl fishery contributing 10%), while pollock fisheries in the EBS accounted for more than 95% of the total pollock catch there in 1990–92 (Table 2). All fisheries generally discard pollock <30 cm long (Wespestad and Dawson, 1992). Fisheries other than the directed pollock fishery may keep pollock if the pollock fishery is open, but otherwise must discard all pollock bycatch. Consequently, size distributions of discarded pollock may vary considerably among fisheries and at various times.

Discard data have been collected for Alaskan groundfish fisheries since 1990 (Table 2). Estimates of pollock

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[2] Wespestad, V., and P. Dawson. 1992. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1993, p. 1-1–1-32. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[3] Hollowed, A. B., 1994. Alaska Fisheries Science Center, NMFS, NOAA. 7600 Sand Point Way N.E., Seattle 98115-0070. Personal commun.

[4] Hollowed, A. B., and B. A. Megrey. 1990. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1991, p. 22–89. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[5] Berger, J. D. 1992. NMFS Observer Program, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv. NOAA, 7600 Sand Point Way N.E., Seattle WA 98115-0070. Personal commun.

[6] Hollowed, A. B., B. A. Megrey, and E. Brown. 1993. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1994, p. 1-1–1-54. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

Table 1

Hierarchical catch-composition criteria for individual hauls used to assign pollock length-frequency data to target fisheries. Fisheries are listed from least to most restrictive; each haul was assigned to the most restrictive fishery possible.

Trawl fishery	Criteria
Eastern Bering Sea	
1. Other	Does not meet any of the following criteria
2. Atka mackerel	Atka mackerel ≥ 20% of retained groundfish[1]
3. Sablefish	Sablefish ≥ 20% of retained groundfish
4. Rockfish	Rockfish ≥ 35% of retained groundfish
5. Pollock (bottom[2])	Pollock ≥ 20% of retained groundfish
6. Flatfish	All flatfish except Greenland turbot and Pacific halibut ≥ 40% of retained groundfish
7. Pacific cod	Pacific cod ≥ 40% of retained groundfish
8. Greenland turbot	Greenland turbot ≥ 35% of retained groundfish
9. Pollock (midwater[2])	Pollock ≥ 95% of total catch
Gulf of Alaska	
1. Other	Does not meet any of the following criteria
2. Shallow flatfish[3]	Shallow flatfish ≥ 20% of retained groundfish
3. Deep flatfish[4]	Deep flatfish ≥ 20% of retained groundfish
4. Sablefish	Sablefish ≥ 20% of retained groundfish
5. Pollock (bottom[2])	Pollock ≥ 20% of retained groundfish
6. Rockfish	Rockfish ≥ 35% of retained groundfish
7. Pacific cod	Pacific cod ≥ 40% of retained groundfish
8. Pollock (midwater[2])	Pollock ≥ 95% of total catch

[1] Retained groundfish defined as catches of allocated groundfish species. Includes pollock, Pacific cod, Atka mackerel, sablefish, flatfish (except Pacific halibut), and rockfish in the Bering Sea and Gulf of Alaska.

[2] Data from both groups in each area were pooled and then separated on the basis of trawl type (bottom or midwater/pelagic trawl).

[3] Shallow flatfish = rock sole, Alaska plaice, English sole, butter sole, slender sole, sand sole, yellowfin sole, and starry flounder.

[4] Deep flatfish = Greenland turbot, flathead sole, rex sole, Dover sole, deepsea sole, and arrowtooth flounder.

Table 2

Total and discarded catch (metric tons) of pollock by trawl fisheries in the Gulf of Alaska and eastern Bering Sea, 1990–92. Annual fishery percentages by region are listed in parentheses.

	Total catch			Discards		
Fishery	1990	1991	1992	1990	1991	1992
Gulf of Alaska						
Midwater pollock	53,505 (63)	80,497 (75)	62,116 (66)	4,621 (27)	2,468 (15)	4,998 (32)
Bottom pollock	20,038 (24)	13,965 (13)	20,846 (22)	3,184 (19)	2,062 (13)	1,628 (10)
Pacific cod	8,482 (10)	9,330 (9)	7,985 (8)	6,548 (38)	8,676 (54)	6,886 (44)
Rockfish	1,950 (2)	1,390 (1)	545 (<1)	1,666 (10)	1,237 (8)	406 (2)
Deepwater flatfish	492 (<1)	1,666 (2)	1,404 (1)	299 (2)	1,208 (8)	1,086 (7)
Others	119 (<1)	657 (<1)	1,008 (1)	666 (4)	382 (2)	665 (4)
All	84,586	107,505	93,904	16,984	16,033	15,669
Eastern Bering Sea						
Midwater pollock	1,238,470 (94)	1,128,431 (74)	1,243,584 (90)	71,690 (62)	72,371 (45)	94,297 (69)
Bottom pollock	40,910 (3)	325,800 (21)	96,330 (7)	6,787 (6)	24,181 (15)	5,835 (4)
Pacific cod	25,730 (2)	43,610 (3)	19,590 (1)	25,649 (22)	34,914 (22)	14,131 (10)
Rock sole	6,300 (<1)	20,040 (1)	10,301 (1)	6,325 (6)	18,066 (11)	9,018 (7)
Yellowfin sole	1,870 (<1)	8,060 (<1)	12,865 (1)	1,871 (2)	7,154 (4)	12,014 (9)
Others	2,090 (<1)	4,113 (<1)	1,690 (<1)	2,653 (2)	3,574 (2)	1,407 (1)
All	1,315,370	1,530,054	1,384,360	114,975	160,260	136,702

discards by pollock fisheries ranged between 4,500 and 7,800 metric tons (t) in the GOA in 1990–92 (or between 5% and 10% of all pollock caught by weight), and between 78,000 and 100,000 t in the EBS (between 5% and 8% of all pollock caught by weight). The difference in magnitude of pollock discards between the two regions reflects the fact that pollock catches were 12–15 times greater in the EBS than in the GOA between 1990 and 1992. In the GOA, Pacific cod trawl fisheries discarded the most pollock from 1990 to 1992 (ranging between 6,500 and 8,600 t per year), followed by midwater (2,500–5,000 t per year) and bottom pollock (1,600–3,200 t per year) fisheries. In the EBS, midwater pollock fisheries discarded the most pollock (between 72,000 and 94,000 t per year, or 45%–69% of the total EBS pollock discarded annually between 1990 and 1992), followed by bottom trawl fisheries for Pacific cod (14,000–35,000 t per year) and pollock (6,000–24,000 t per year).

Fisheries observers measured more than 11 million pollock from the GOA and EBS between 1977 and 1992 (Table 3). These data represent the length-frequency distribution of the total catch. From 1977 to 1992, average catch rates of juvenile pollock (<30 cm TL) by trawl fisheries were more than twice as high in the EBS (slightly less than 5% of all pollock measured) than in the GOA (approximately 2% of all pollock measured). In the GOA, pollock <20 cm were rarely caught by any trawl fishery (<0.08% of all pollock measured) and 99% of the pollock <30 cm were caught by either midwater or bottom trawl pollock vessels; juvenile pollock made up only 1% or less of the catches of all other trawl fisheries. In the EBS, pollock trawl fisheries accounted for 96% of the juvenile pollock measured by observers. Only about 2% of the pollock caught by the EBS Pacific cod trawl fishery between 1977 and 1992 were <30 cm, while juvenile pollock made up over 13% of the pollock caught by EBS flatfish fisheries.

Annual Variability

Comparison of annual (Fig. 1, 2, 3) and aggregate (Table 3) length-frequency distributions of pollock caught by midwater and bottom trawl pollock fisheries (Fig. 1, 2) and Pacific cod trawl fisheries (Fig. 3) in the GOA and EBS between 1977 and 1992 suggest that 1) catch rates of pollock <30 cm TL have been similar for

Table 3

Numbers (and percentages) of walleye pollock, by length, measured by observers aboard foreign, joint venture, and domestic trawl vessels participating in various fisheries in the Gulf of Alaska and eastern Bering Sea from 1977 to 1992.

Gulf of Alaska fisheries

Pollock length	Midwater pollock		Bottom pollock		Rockfish		Pacific cod		All trawl fisheries	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1–9 cm	7	<0.01	1	<0.01	0	0.00	0	0.00	9	<0.01
10–19	741	0.06	295	0.07	16	0.05	6	0.02	1,089	0.07
20–29	21,596	1.97	7,552	1.73	115	0.35	251	0.98	29,630	1.86
30–39	167,879	15.33	57,293	13.12	5,791	17.42	3,993	15.62	237,043	14.86
40+	904,993	82.63	371,432	85.08	27,316	82.18	21,319	83.38	1,327,325	83.21
All	1,095,216		436,573		33,238		25,569		1,595,096	

Eastern Bering Sea fisheries

Pollock length	Midwater pollock		Bottom pollock		Pacific cod		Flatfish		All trawl fisheries	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1–9 cm	67	<0.01	207	<0.01	0	0.00	124	0.12	398	<0.01
10–19	17,059	0.25	11,094	0.43	268	0.20	3,524	3.36	31,951	0.33
20–29	306,467	4.55	109,365	4.32	2,821	2.07	10,228	9.76	429,290	4.49
30–39	1,841,797	27.33	462,831	18.27	20,907	15.31	7,904	7.55	2,342,754	24.49
40+	4,572,722	67.86	1,949,396	76.96	112,547	82.43	82,971	79.21	6,760,703	70.68
All	6,738,112		2,532,893		136,543		104,751		9,565,096	

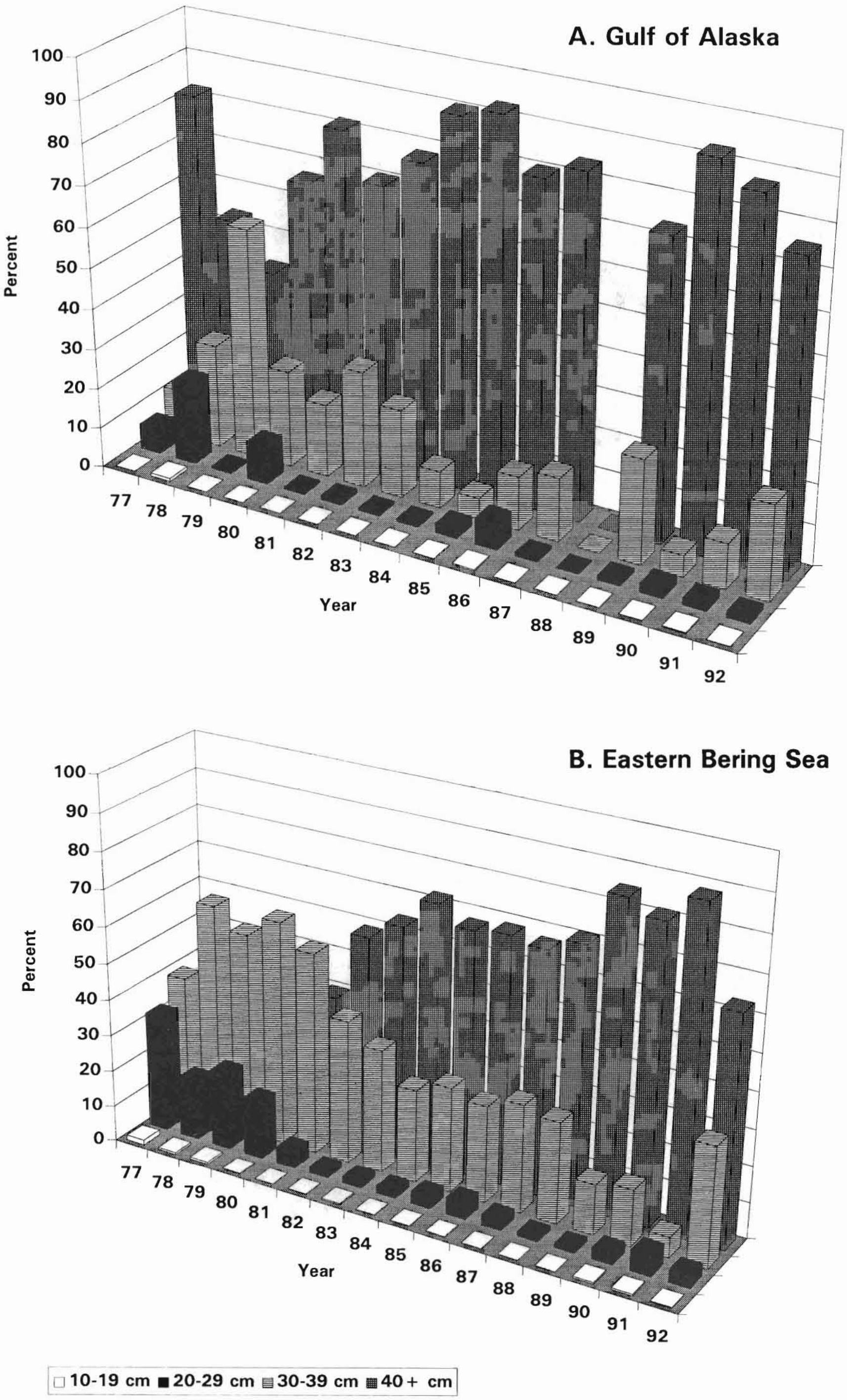
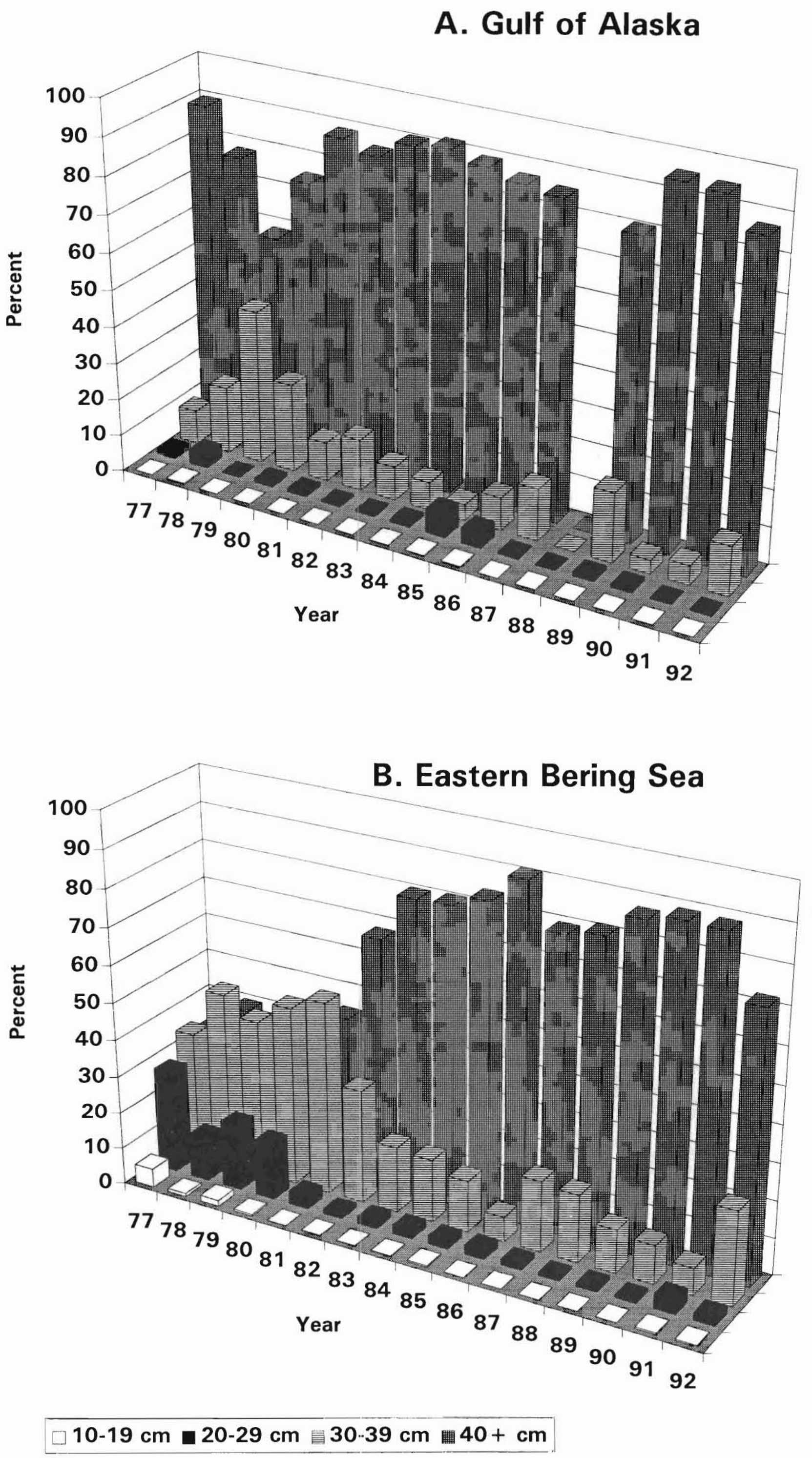


Figure 1

Percent length frequency of walleye pollock caught by midwater pollock fisheries in (A) the Gulf of Alaska and (B) the eastern Bering Sea by 10-cm length ranges. Numbers of pollock measured each year ranged from 5,591 to 265,678 (median = 38,408) in the Gulf of Alaska, and from 66,655 to 757,861 (median = 408,498) in the eastern Bering Sea. Data from the Gulf of Alaska in 1988 were not used because of small sample size.



A. Gulf of Alaska

B. Eastern Bering Sea

Figure 2

Percent length frequency of walleye pollock caught by bottom pollock fisheries in (A) the Gulf of Alaska and (B) the eastern Bering Sea by 10-cm length ranges. Numbers of pollock measured each year ranged from 916 to 76,418 (median = 20,712) in the Gulf of Alaska, and from 42,660 to 272,505 (median = 100,542) in the eastern Bering Sea. Data from the Gulf of Alaska in 1988 were not used because of small sample size.

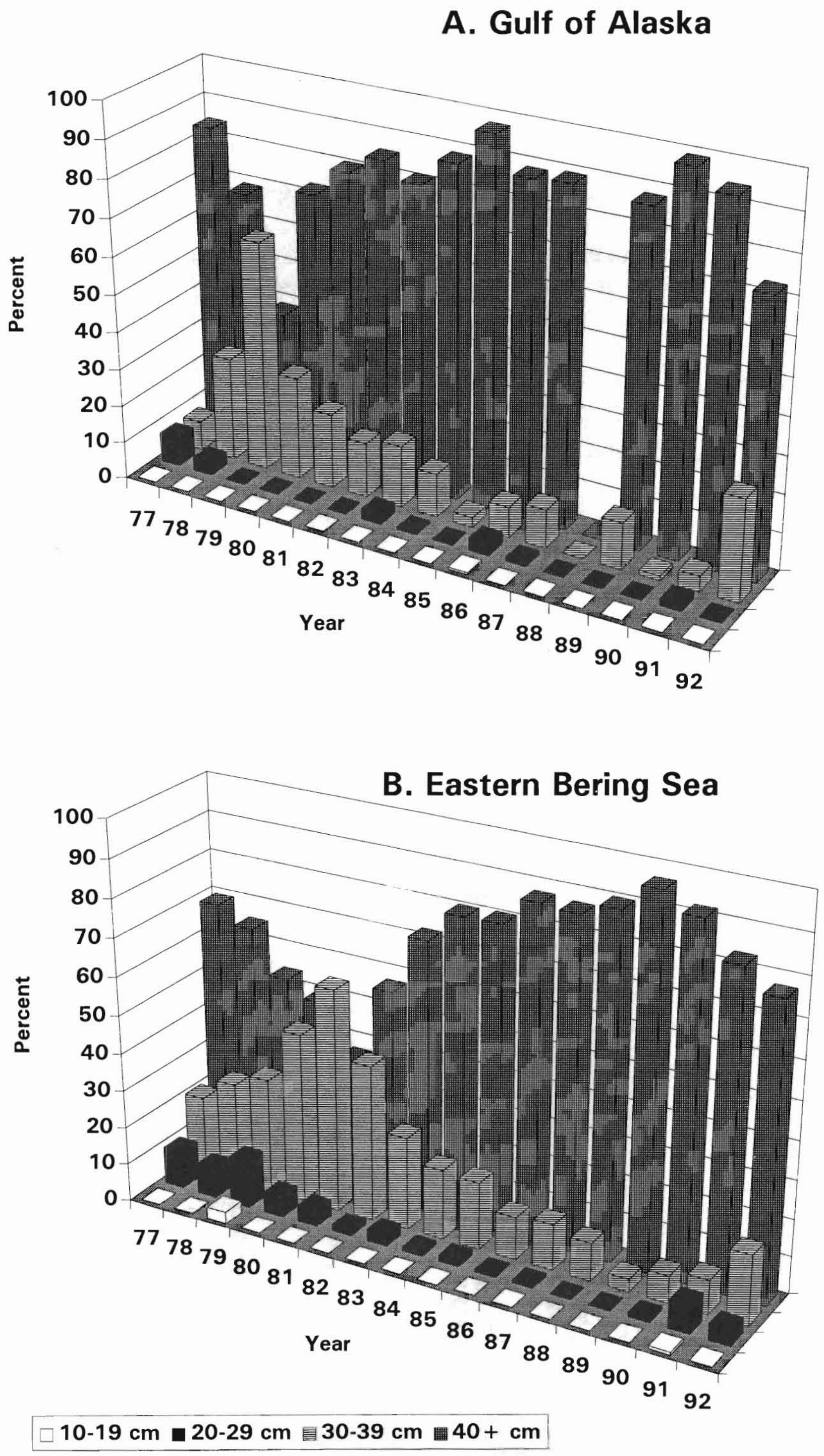


Figure 3

Percent length frequency of walleye pollock caught by Pacific cod trawl fisheries in (A) the Gulf of Alaska and (B) the eastern Bering Sea by 10-cm length ranges. Numbers of pollock measured each year ranged from 151 to 11,040 (median = 626) in the Gulf of Alaska, and from 468 to 24,760 (median = 7,714) in the eastern Bering Sea. Data from the Gulf of Alaska in 1988 were not used because of small sample size.

midwater and bottom trawl pollock fisheries in each region; 2) midwater pollock fisheries have had higher catch rates of pollock 30–39 cm TL than bottom trawl fisheries; and 3) there has been considerable annual variability in the catch rates of juvenile pollock. In the GOA, juvenile pollock were most commonly caught in 1977–78, 1980, 1985–86, and 1990–91 by the midwater pollock fishery (Fig. 1A); in 1978 and 1985–86 by the bottom pollock fishery (Fig. 2A); and in 1977–78, 1983, 1986, and 1991 by the Pacific cod trawl fishery (Fig. 3A). In the EBS, juvenile pollock were most commonly caught in 1977–80, 1985–86, and 1990–92 by the midwater (Fig. 1B) and bottom (Fig. 2B) pollock fisheries and the Pacific cod trawl fishery (Fig. 3B).

One possible explanation for this pattern of bycatch rates is variability in the size of pollock year classes in each region (Fig. 4). Since 1975, strong year classes were spawned in the GOA in 1975–79, 1984–85, and 1988; in the EBS, 1978, 1982, 1984–85, and 1989–90 produced strong year classes. Years with high juvenile

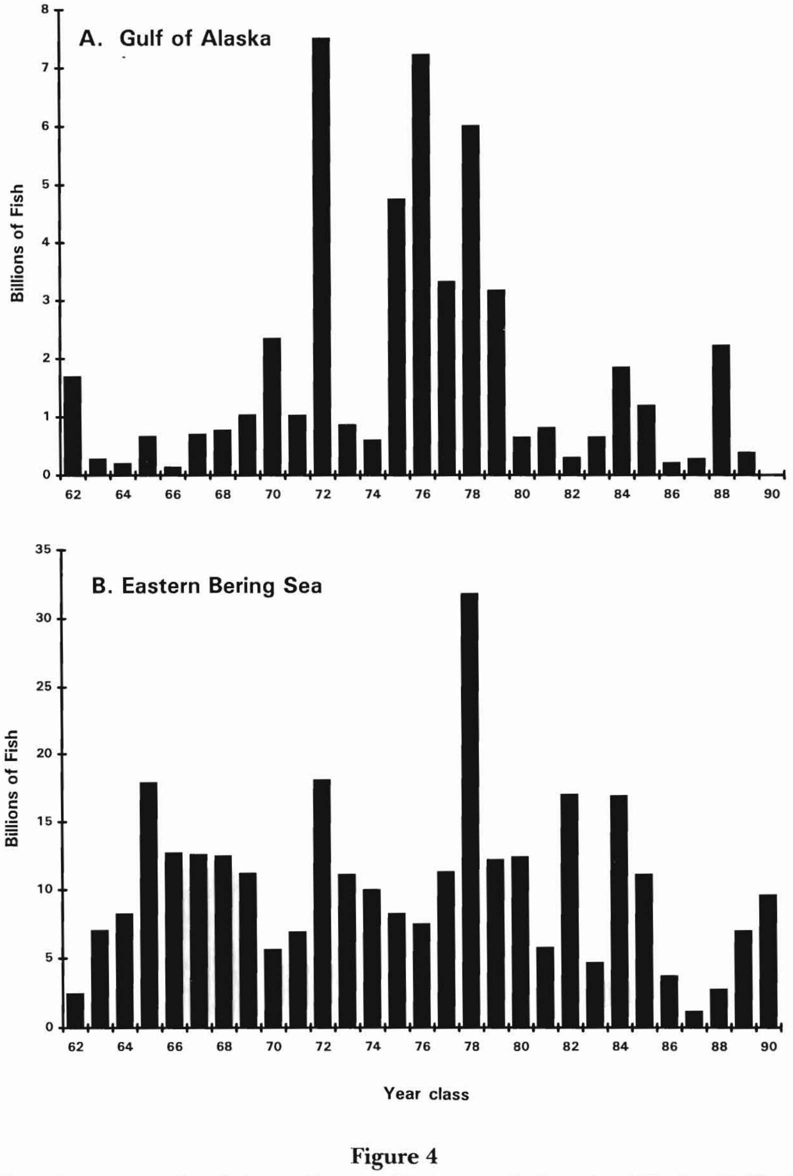


Figure 4
Year-class strength of the walleye pollock populations in (A) the Gulf of Alaska and (B) the eastern Bering Sea, assessed as 2-year-olds. Data from age-structured population assessments conducted by Hollowed et al.[1] and Wespestad and Dawson.[2]

pollock bycatch in each region follow (allowing for growth) years when strong year classes were spawned, suggesting that catch rates of juveniles by trawl fisheries vary directly with their abundance.

The relation between catches and numbers of 2–3-year-old pollock in the GOA and EBS from 1964 to 1990 are shown in Figures 5 and 6. In both regions, catches of juveniles increased directly with their abundance. The slope of the regression line in Figure 5A was 0.009 (F=22.00, P<0.001), suggesting that on the average, fisheries in the GOA took about 1% of the 2–3-year-old pollock each year from 1964 to 1991. The scarcity of pollock <20 cm TL (<0.08% of all pollock measured in observer samples; Table 3) suggests that catch rates of 0–1-year-old pollock in the GOA are very low.

From 1973 to 1979 in the EBS, catch rates of 2–3-year-old pollock were higher than during the combined 1964–72 and 1980–90 periods (Fig. 5B, 6B). During the "low" catch period, an average of 2.18% of the 2–3 year-old pollock were caught each year, and catches increased directly with abundance (lower regression line in Figure 5B: F=17.93, P<0.001). During the "high" catch period from 1973 to 1979, trawl fisheries caught between 11% and 21% of the 2–3-year-old pollock (F=43.82, P=0.001). Exploitation rates of pollock 4 years and older in the EBS were also higher from 1973 to 1979 (4 of 7 years had rates >20%) than from 1964 to 1972 or from 1980 to 1990 (all years but 1990 <15%). The length-frequency distributions, however, indicate that the foreign fishery active from 1973 to 1979 either

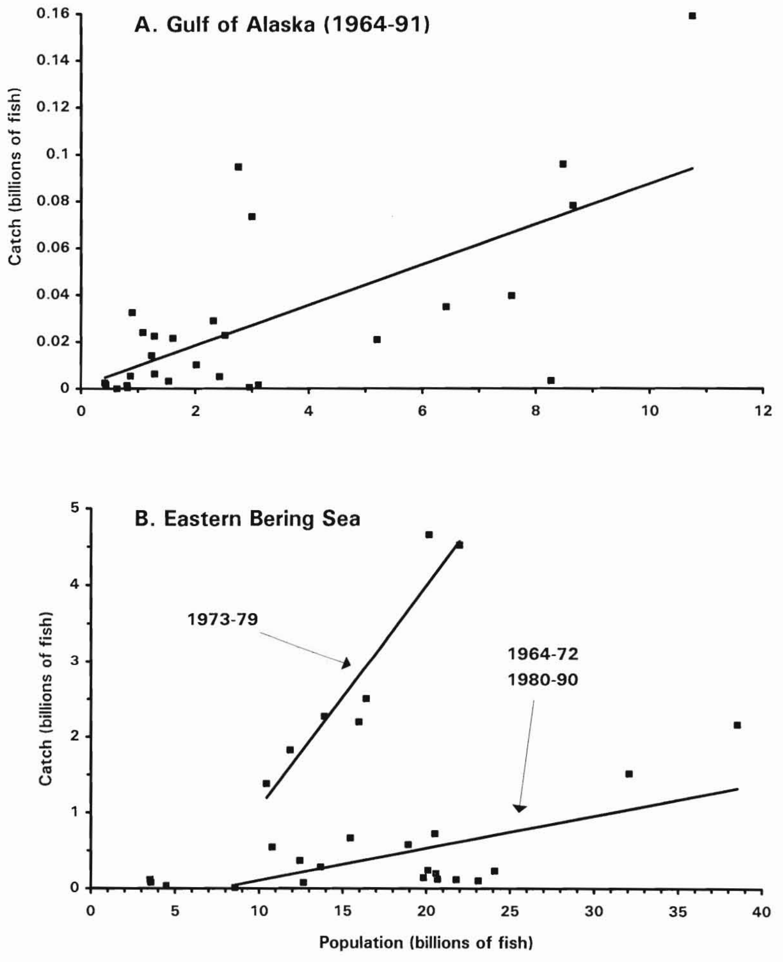


Figure 5

Fishery catches and populations of 2- and 3-year-old walleye pollock in (A) the Gulf of Alaska and the (B) eastern Bering Sea assessed as 2-year-olds. Data from age-structured population assessments conducted by Hollowed et al.[1] and Wespestad and Dawson.[2]

targeted small fish, possibly of the 1972 year class, or could not separate them from the mix of older year classes spawned from 1965 to 1969. The data in Figure 6B suggest that the fishery since 1980 has been more successful at avoiding small fish, because catch rates of 2–3-year-olds have been less than 5% (mostly less than 3%). Furthermore, catch rates 2–3 years after the large year classes spawned in 1978, 1982, and 1984–85 did not approach the "high" rates observed in 1973–79. Even though pollock <20 cm were about four times

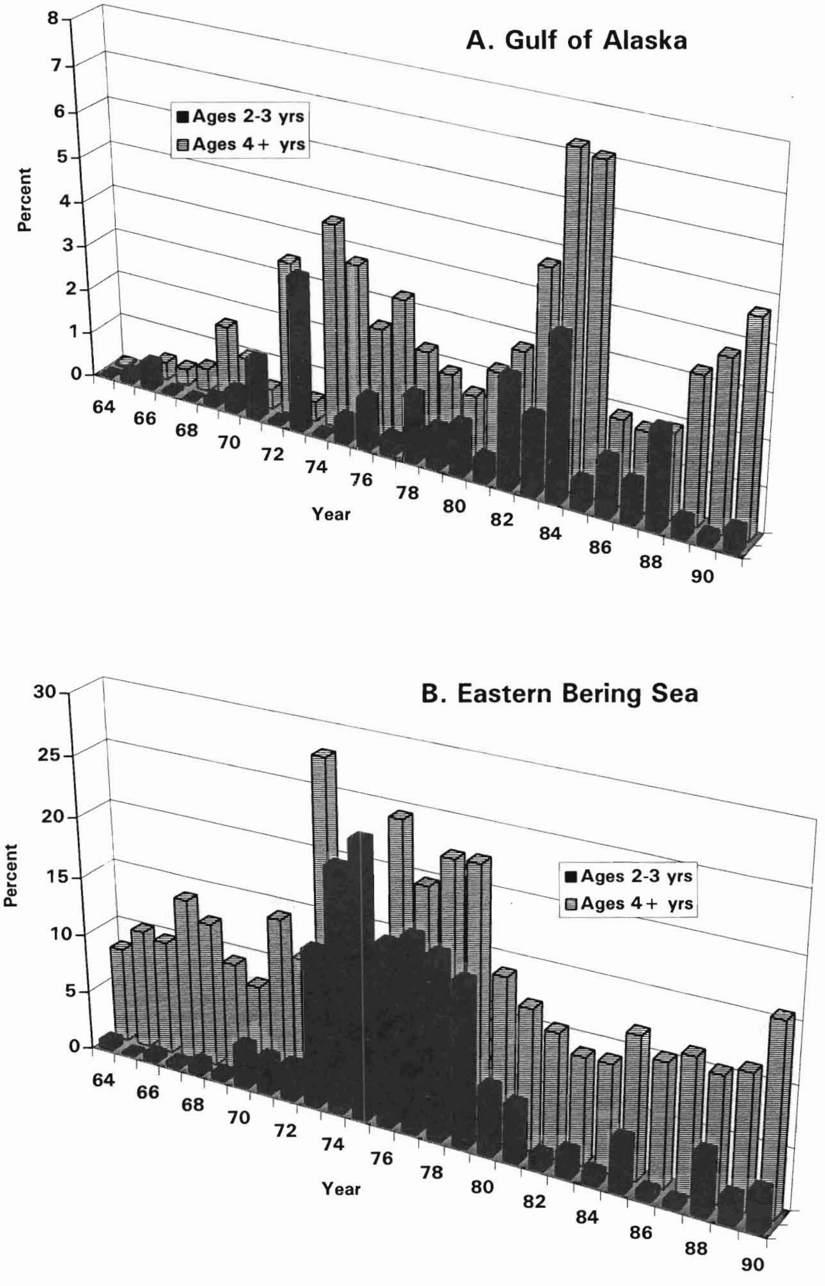


Figure 6

Percentage of the populations of 2–3-year-olds and 4+ year-old walleye pollock caught by fisheries in (A) the Gulf of Alaska and (B) the eastern Bering Sea. Data from age-structured population assessments conducted by Hollowed et al.[1] and Wespestad and Dawson.[2]

more common in the EBS length-frequency samples (<0.34% of all pollock measured; Table 3) than in the GOA, their scarcity suggests that catch rates of 0–1-year-olds in the EBS are also low.

Average catch rates of 2–3-year-old pollock in the GOA from 1964 to 1991 (0.94%) were less than one-half of those during the EBS "low" periods (1964–1972 and 1980–90; 2.18%) and only 5%–10% of those during the EBS "high" period (1973–79; 11%–21%). Two factors contribute to these regional differences in juvenile pollock bycatch rates. First, pollock year-class strength has varied less in the EBS than in the GOA (Fig. 4). In the EBS, about one-half (14 of 29, or 48%) of the year classes spawned during 1962–90 were larger than the long-term mean of 10.194 billion fish (at age 2), whereas only 5 classes (17%) were smaller than half the mean. In contrast, only about one-fourth of the year classes (8 of 28, or 28%) spawned in the GOA from 1962 to 1989 were greater than the long-term mean of 2.205 billion fish (at age 2), whereas more than one-half (17 of 28, or 61%) were less than half this size. Thus, 2–3-year-old pollock were more commonly encountered and caught in the EBS than in the GOA, reflecting the relation between abundance and catch shown in Figure 5. Second, the average (1964–90) exploitation rate for all pollock 2 years of age and older was five times higher in the EBS (9.20%) than in the GOA (1.83%).

Livingston (1993) compared estimates of pollock removals (by size in 1985) by groundfish, marine mammals, marine birds, and the commercial fishery in the EBS. She reported that the 1985 commercial fishery accounted for almost all removals (by weight) of pollock >40 cm, and most removals of fish >25 cm. Pollock cannibalism far exceeded all other removals of age-0 (<10 cm) pollock both in terms of numbers and biomass. Biomass removals of age-1 (10–19 cm) pollock were evenly distributed between groundfish (principally arrowtooth flounder, *Atheresthes stomias*; walleye pollock; and Pacific cod), marine mammals (predominately northern fur seals, *Callorhinus ursinus*), and marine birds, and far exceeded removals by the fishery. This pattern of removals by the fishery and other predators of pollock <20 cm has probably been the same for the entire 1977–92 period (Fig. 1–3). When the fishery has caught pollock <30 cm in great numbers (1977–80, 1991), the fish have primarily ranged from 20 to 29 cm (2-year-olds).

Seasonal Variability

Bycatch rates of juvenile pollock vary not only annually because of changes in pollock age structure and in the fishery, but also seasonally as the fish grow and recruit to the gear. Pollock are spawning during most of the January–April period in the Bering Sea, and they aggregate along the shelf edge or over deep basin waters where they tend to segregate by size, allowing the fishery to target large, mature, roe-bearing females.[2] Small fish between 25 and 45 cm dominated the catches during this period in the late 1970's (Fig. 7A). Since 1984, however, few pollock smaller than 30 cm have been caught in January–April (except for 1986, because of the large 1984 year class, and 1992, because of the 1989 and 1990 year classes), and most pollock caught measured 45–55 cm (see also Fig. 1B). Large, recently recruited (3-year-old) year classes are evidenced by modes in the mid-30-cm range, such as the 1984, 1985, and 1989 year classes in the respective 1987, 1988, and 1992 January–April length-frequency data.

By early summer, spawning aggregations have dispersed and pollock tend to be less segregated by size. This results in a greater bycatch of small fish in May–July compared to January–April (Fig. 7B). Large year classes of 2-year-old pollock are often unavoidable by the fishery, as evidenced by large catches of the 1978 year class in 1980 and the 1989 year class in 1991 (modes in the mid-20-cm range). In 1992, the 1989 year class appeared again as the large mode in the mid-30-cm range.

During August–December (Fig. 7C), modal lengths were greater, and fewer years had significant numbers of pollock <30 cm than in May–July, as the 2–3-year-old recent recruits grew during the year. The January–April pattern of modal lengths increasing from the late 1970's through the mid-1980's and stabilizing through 1991 was also evident in the August–December data. Between 1991 and 1992, however, the modal length declined 10 cm because of the large number of 1989 year-class fish and the relative scarcity of older year classes—particularly those spawned in 1978, 1982, and 1984—that sustained the fishery during the 1980's.

Spatial Variability

In the EBS, there are spatial as well as temporal components to the patterns of juvenile pollock bycatch. NMFS surveys conducted during the summer in the EBS have found that most juvenile pollock are north and west of the Pribilof Islands (57°N, 170°W). Four combined bottom and midwater trawl surveys conducted in the past 12 years found that 60%-90% of the 1- and 2-year-old pollock were northwest of the Pribilof Islands. Fisheries have also caught more juvenile fish there than in the southeastern portion of the EBS shelf between Unimak Pass (54°30'N, 165°W) and the Pribilof Islands.

Locations fished seasonally by the pollock fishery have changed considerably between 1977 and 1992

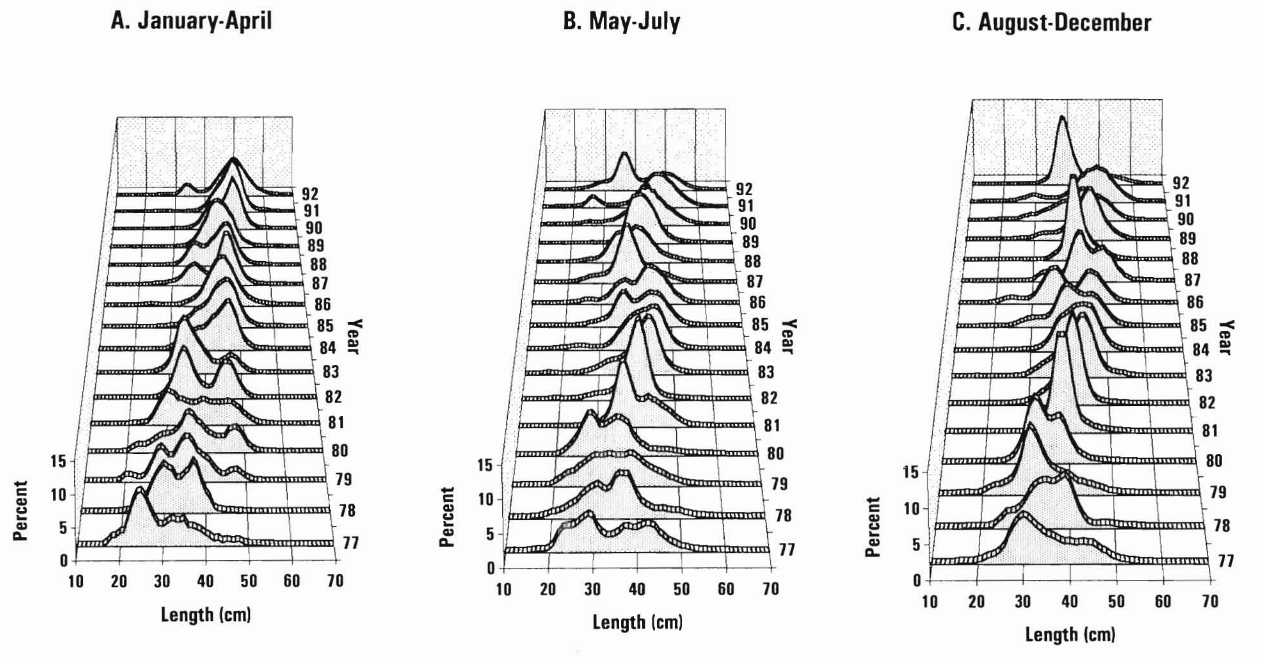


Figure 7
Percent length frequency of walleye pollock caught by midwater pollock fisheries in the eastern Bering Sea in (A) January–April, (B) May–July, and (C) August–December.

(Fritz[7]). In the late 1970's, pollock fisheries in January–April were located predominately on the edge of the continental shelf northwest of the Pribilof Islands (Fig. 8A), and pollock <20 cm were present throughout this area (Fig. 8B). Since the discovery of the spawning concentration of pollock near Bogoslof Island (54°N, 168°W) in 1986, the fishery has increasingly moved to locations in the eastern Aleutian Basin and on the southeastern Bering Sea shelf (Fig. 9A). The Bogoslof Island pollock roe fishery is represented by the concentrated fishing grounds north of Umnak Island (53°15'N,168°30'W), southwest of the trawl locations on the shelf. No fish smaller than 20 cm were caught in the deep waters of the eastern Aleutian Basin, and only small numbers were found near the shelf break to the northeast in 1991 (Fig. 9B). Therefore, the shift in fishing locations in the late 1980's,[7] changes in pollock age structure (Fig. 4), and changes in the fishery (targeting on spawning concentrations of large fish) all contributed to the January–April decline in juvenile bycatch observed since 1977. In 1992, the Bogoslof Island district (NMFS statistical area 518) was closed to directed pollock fishing. As a result, the fleet redirected its "A" season effort onto the EBS shelf, where juvenile pollock bycatch can be higher than over deep basin waters (as evidenced by catches of the 1989 year class, or the mode in the 30-cm range; Fig. 7A).

Locations fished have also contributed to the higher bycatch of smaller pollock in summer, compared with January–April, since 1977. In summer, the pollock fishery typically works the entire outer shelf area from Unimak Pass to Zhenchug Canyon (58°N,175°W; Fig.10A). However, small fish were caught more frequently northwest of the Pribilof Islands than on the southeastern shelf (Fig. 10B).

In the GOA, the pollock fishery since 1990 has fished predominantly in the gullies on the south and east sides of Kodiak Island, along the southern side of Shelikof Strait, in Shelikof Gully extending southwest of Kodiak Island, and—to a lesser extent—in the western GOA along the shelf break (Fig. 11A). The few pollock <20 cm caught by the fishery from 1990 to 1992, however, were caught around Kodiak Island, and none were caught in the western GOA on the shelf break (Fig. 11B). These results agree with surveys that found small pollock primarily in embayments along the Alaska Pen-

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[7] Fritz, L. W. 1993. Trawl locations of walleye pollock and Atka mackerel fisheries in the Bering Sea, Aleutian Islands, and Gulf of Alaska from 1977–92. AFSC Proc. Rep. 93-08, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.

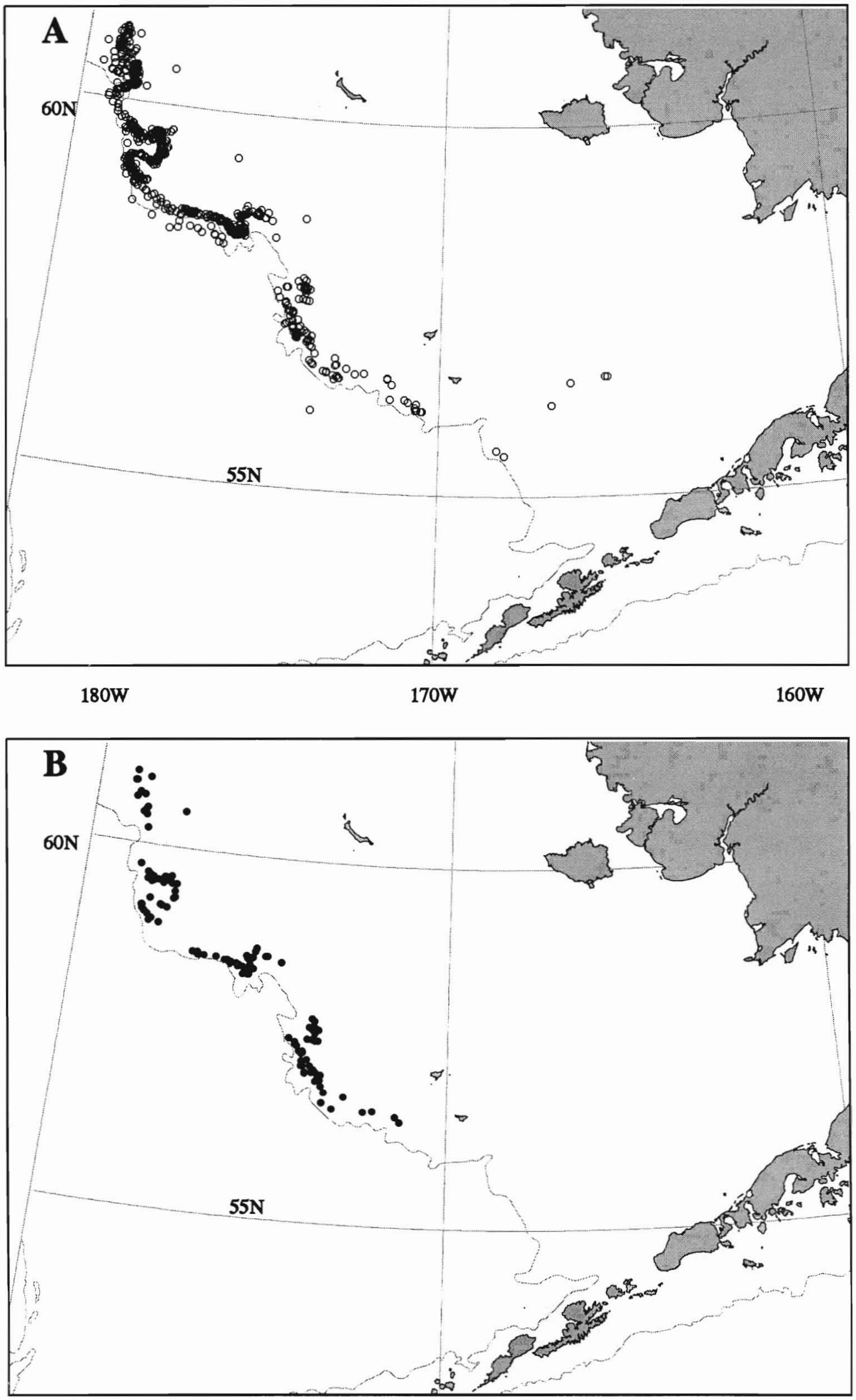

Figure 8

Trawl locations of the walleye pollock fishery in the eastern Bering Sea in January–April 1979 where (A) length-frequency data were collected (circles) and (B) pollock <20 cm were caught (dots). The 1,000-m isobath is shown.

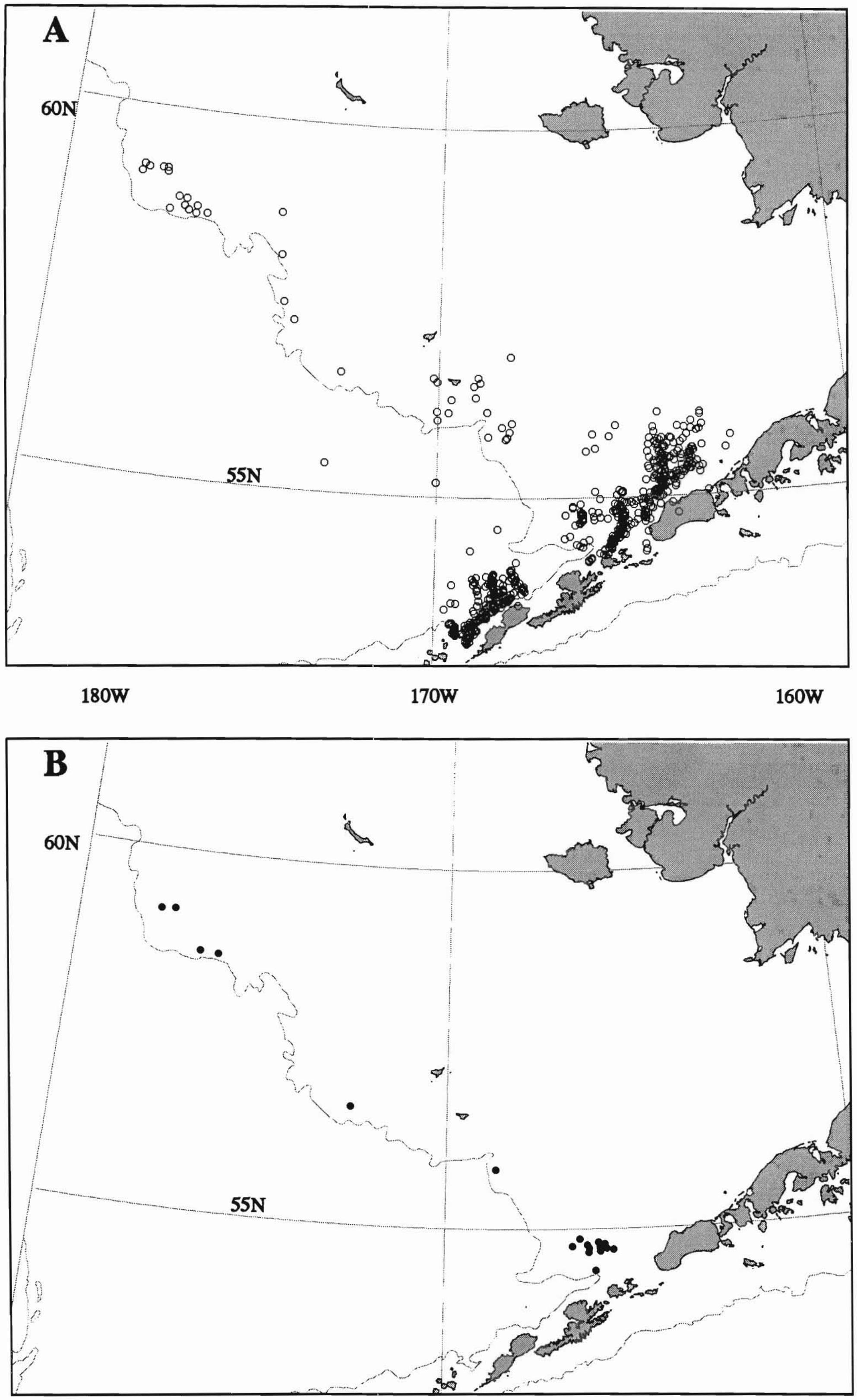

Figure 9

Trawl locations of the midwater walleye pollock fishery in the eastern Bering Sea in January–April 1991 where (A) length-frequency data were collected (circles), and (B) pollock <20 cm were caught (dots). The 1,000-m isobath is shown.

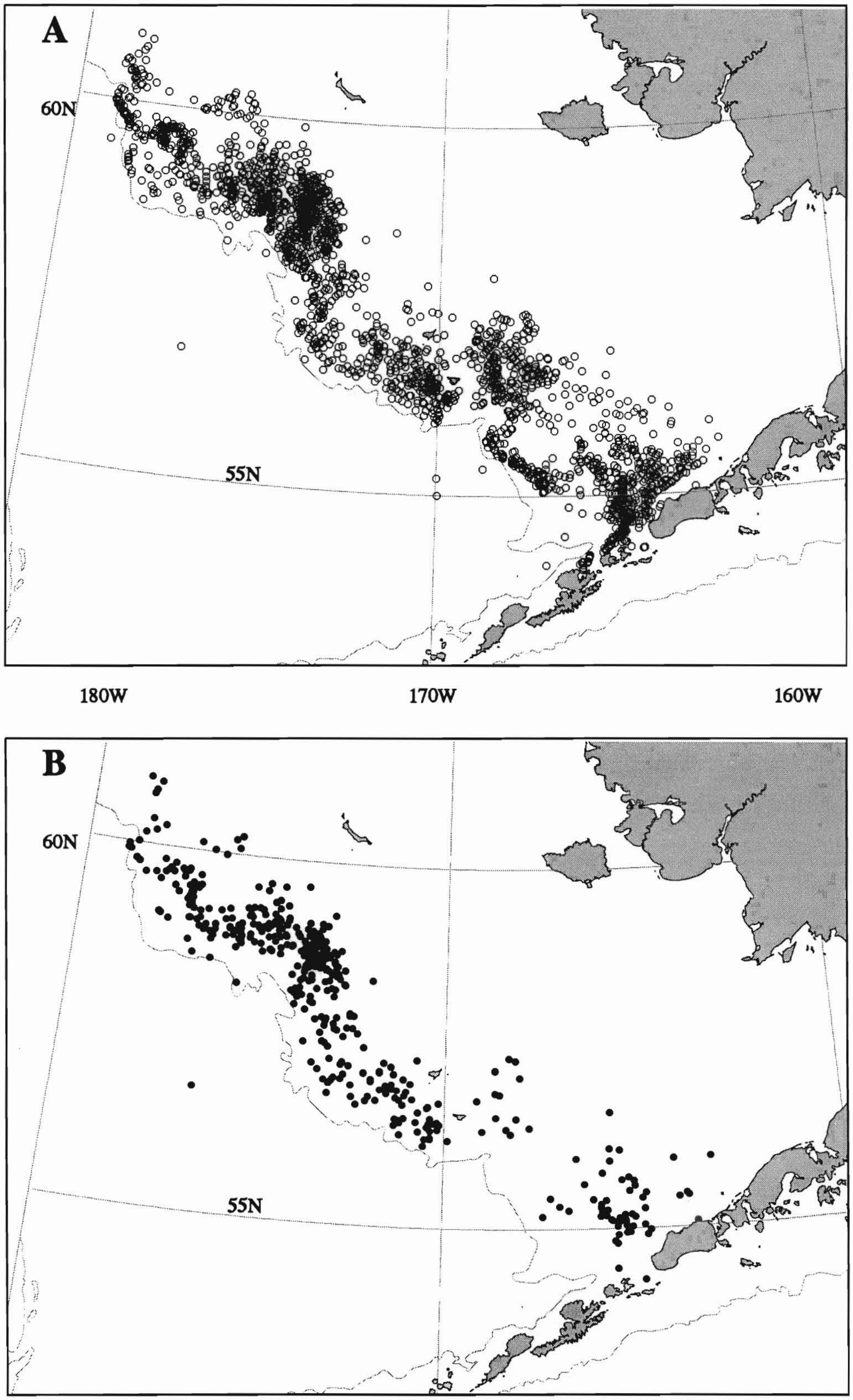

Figure 10

Trawl locations of the midwater walleye pollock fishery in the eastern Bering Sea in June–September 1991 where (A) length-frequency data were collected (circles) and (B) pollock <20 cm were caught (dots). The 1,000-m isobath is shown.

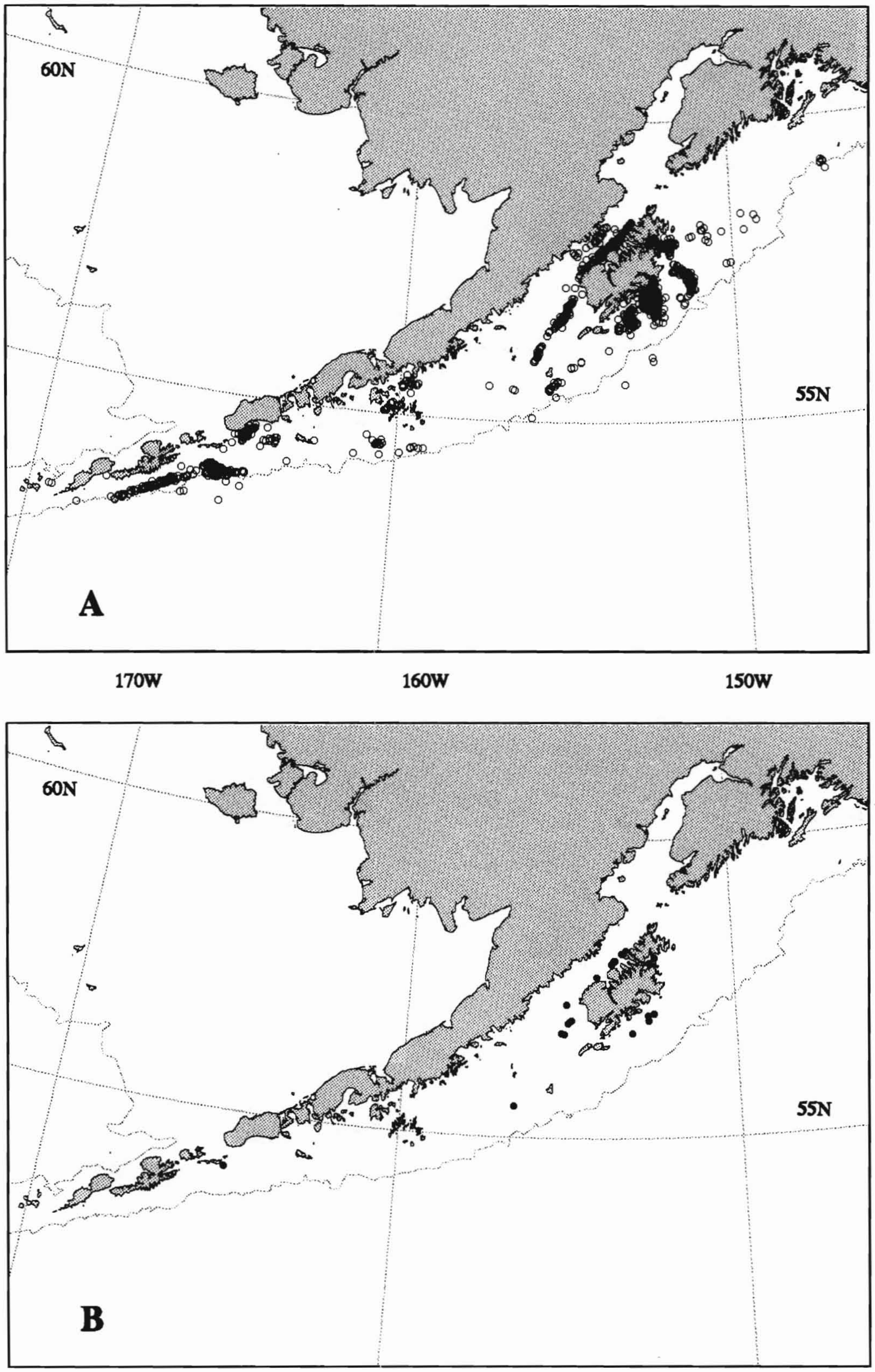

Figure 11

Trawl locations of the midwater walleye pollock fishery in the Gulf of Alaska in 1990–92 where (A) length-frequency data were collected (circles), and (B) pollock <20 cm were caught (dots). The 1,000-m isobath is shown.

insula and on Kodiak Island, not along the shelf break (Smith et al., 1984; Walters et al., 1985; Shippen[8]; Spring and Bailey[9]).

For two reasons, the rates discussed in this paper could be considered minimal estimates of the catch of juvenile pollock by trawl groundfish fisheries. First, only 30% of the trips made by vessels shorter than 125 ft carry observers. While this could lead to underestimates of the true rates in both the EBS and GOA, GOA rates may be affected more since small vessels catch a larger proportion of the pollock in the GOA than in the EBS.[1] Second, observers do not sample every haul, nor can they sample hauls that are not brought on board. It has been reported that codends full of fish have been dumped rather than brought on board. The number of times this has occurred and the size composition of the catches are unknown, but the underreporting problem this would create would exist even if 100% of vessels carried observers. The magnitude of underreporting of juvenile pollock catches probably increases when the population is dominated by young fish.

Acknowledgments

I thank the organizers of the juvenile pollock symposium for asking me to prepare this paper for presentation, as well as J. Berger, G. Duker, R. Marasco, R. Merrick, R. Methot, and V. Wespestad, whose comments improved the manuscript.

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Walleye Pollock, *Theragra chalcogramma*, in the Western Pacific Ocean and Bering Sea Ecosystems

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Because of its high abundance, walleye pollock, *Theragra chalcogramma*, is one of the key nekton species in both the pelagic and demersal communities of many far eastern Russian ecosystems. It is a main competitor of other plankton-eating fishes and invertebrates and a predator on small nekton. At the same time, it is an important food source for many higher-level predators. In the 1980's, the proportion of total fish biomass made up by walleye pollock was 35%–40% in the western Bering Sea (80%–90% of the epipelagic biomass), 40% in the Sea of Okhotsk (75%–85% of epipelagic biomass), 50% in the Pacific waters off Kamchatka (90% of epipelagic biomass), 20% (summer) to 55% (winter) near the Kuril Islands, and 35%–40% in the Sea of Japan.

During the 1980's, many thousands of pollock stomachs were examined by TINRO personnel. The annual ration of walleye pollock was determined to be 12.6 times its body weight. The average annual food consumed by walleye pollock in the western Bering Sea in the 1980's was estimated to be 189–252 × 10^6 t in the following proportions: copepods (45%), euphausiids (30%), amphipods (5%), chaetognaths (2%), fishes (8%), squid (3%), and other prey (7%). In the Sea of Okhotsk, an estimated 126–189 × 10^6 t were consumed: euphausiids (45%), copepods (15%), amphipods (10%), chaetognaths (5%), squids (3%), fishes (8%), and other taxa (14%). The total annual consumption for the Sea of Japan was estimated to be 50–88 × 10^6 t.

For the epipelagic communities in which walleye pollock occur, the adult pollock share was 80%–90% of the total annual fish consumption. Consequently, changes in the abundance of walleye pollock affect the food supply of other species in the pelagic nekton community. During the 1980's, walleye pollock annually consumed 4.5 × 10^6 t of squid and 12 × 10^6 t of small fishes in the Sea of Okhotsk. In the western Bering Sea, the corresponding consumption of squid and fish is 5.6 and 17.6 × 10^6 t. We estimate that less than 5% of the total fish consumed on an annual basis were juvenile pollock. The biomass of juvenile pollock lost to cannibalism was estimated to be approximately 0.6 × 10^6 t in the Sea of Okhotsk and 0.9 × 10^6 in the western Bering Sea. Thus, although cannibalism may be an important source of mortality for juvenile pollock, the adult pollock stocks probably inflict a greater proportional mortality on other forage fishes and crustaceans.

Table 1 shows the importance of juvenile walleye pollock as prey for other fishes in the Sea of Okhotsk and the western Bering Sea. These data show that the consumption by predators in both ecosystems exceeded the amount taken by intensive commercial fisheries. The complex interactions among the trophic levels in these regions, including self-regulation of abundance by adult pollock, have important implications for the rational management of these ecosystems.

Table 1

Annual mean consumption and production of juvenile walleye pollock (in million metric tons) in the Sea of Okhotsk and the western Bering Sea during the 1980's.

Source	Sea of Okhotsk	Bering Sea
Adult pollock (cannibalism)	0.6	0.9
Other predatory fishes	2.2	4.5
Marine mammals, birds	0.4	1.5
Total predation	3.2	6.0
Fisheries catch	1.8	2.0[1]
Walleye pollock production	5.0–7.5	10.0–12.5

[1] Mean value excluding a maximum catch of 3.8 × 10^6 t in one year.

Juvenile Walleye Pollock, *Theragra chalcogramma*, as Food for Teleosts in the Gulf of Alaska Ecosystem

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Analysis of stomach contents of groundfish collected during the summer of 1990 in the Gulf of Alaska showed that juvenile walleye pollock, *Theragra chalcogramma*, was eaten by arrowtooth flounder, *Atheresthes stomias*; Pacific halibut, *Hippoglossus stenolepis*; sablefish, *Anoplopoma fimbria*; Pacific cod, *Gadus macrocephalus*; and adult walleye pollock. Arrowtooth flounder and Pacific halibut ate the most walleye pollock by weight (66% and 57% of their diet, respectively). Juvenile pollock was a large component in the diet of arrowtooth flounder and Pacific halibut at most of the stations sampled. Consumption of age-0, age-1, and age-2 pollock by these two groundfish was also spread throughout the area, indicating a broad distribution and availability of all age groups of juvenile pollock to predators.

Additional stomach samples of potential predators were collected from March through May and in September to examine predation on juvenile pollock during other times of the year. Adult pollock collected during the spring were mostly in spawning condition, and predation on juveniles was not observed. In September, juvenile pollock were eaten by eight different taxa; adult pollock, arrowtooth flounder, and Pacific sandfish, *Trichodon trichodon*, had the highest incidences of age-0 juvenile pollock in their diets. Pacific cod and Pacific halibut consumed older age groups of pollock. The size distribution of age-0 pollock in predator guts was similar to that from a concurrent juvenile trawl survey.

Estimates of the total amount of walleye pollock consumed by groundfish predators in the Gulf of Alaska were produced using diet composition and predator biomass estimates from the 1990 Gulf of Alaska bottom trawl survey. A 9-month feeding season was assumed in these estimates, and daily rations were calculated from estimates of annual growth increments and assumptions about gross conversion efficiency. Although Pacific halibut consumed the most pollock in terms of biomass, most pollock they ate were adults. Arrowtooth flounder was the most important groundfish predator on juvenile pollock in terms of biomass and number consumed. Most of the pollock biomass consumed by arrowtooth flounder consisted of age-1 and age-2 fish. Age-0 pollock were eaten by arrowtooth flounder and walleye pollock.

Prerecruit Walleye Pollock, *Theragra chalcogramma*, in Seabird Food Webs of the Bering Sea

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Prerecruit walleye pollock, *Theragra chalcogramma,* are important prey of seabirds during the nesting season at St. Matthew Island, the Pribilof Islands, and Bogoslof Island in the eastern Aleutian Islands (Fig. 1). Limited data suggest that they might also be important to thick-billed murres, *Uria lomvia,* on the Near Islands in the western Aleutian Islands. Elsewhere, juvenile pollock are common, if not important, in seabird diets at Cape Peirce and Cape Newenham in Bristol Bay. They are probably common prey at Karaginskii Island and Verkhoturov Island in the western Bering Sea and at other colonies in the Aleutian Islands, but no data are available on diets at those locations.

Juvenile pollock were common prey of murres caught during summer in commercial gill nets offshore in the southeastern and northwestern Bering Sea (Fig. 2). Ages 1+ and 2+ pollock are apparently important prey of seabirds at the ice edge in winter, having been found in 60%–100% of five species of seabirds sampled in March–April 1976. As indicated by otolith lengths, the fish from the ice edge ranged in size from about 125–250 mm (about 15–130 g).

The occurrence of pollock in the diets of black-legged kittiwakes, *Rissa tridactyla,* on the Pribilof Islands tends to be inversely proportional to the occurrence of Pacific sand lance, *Ammodytes hexapterus* (Fig. 3). Years when sand lance were common in diets were probably years when sand lance were highly abundant, and the birds probably shifted from pollock. Pollock may also have been less available at the surface where kittiwakes fed in those years.

The proportion of juvenile pollock in diets of black-legged kittiwakes on St. Paul Island has been generally proportional to modeled estimates of pollock abundance based on survey information (r^2=0.38 for age 0+, and 0.47 for age 1+). There has been no such relation on St. George Island.

An inverse relation between productivity of piscivorous kittiwakes and planktivorous least auklets, *Aethia pusilla,* was seen in 3 years of overlapping measurements on St. Paul Island. This, and a similar inverse relation between the abundance of age-1+ pollock and the abundance of copepods around St. Matthew Island, support the hypothesis that pollock is a strongly interacting member of the pelagic food web of the Bering Sea.

Acknowledgments

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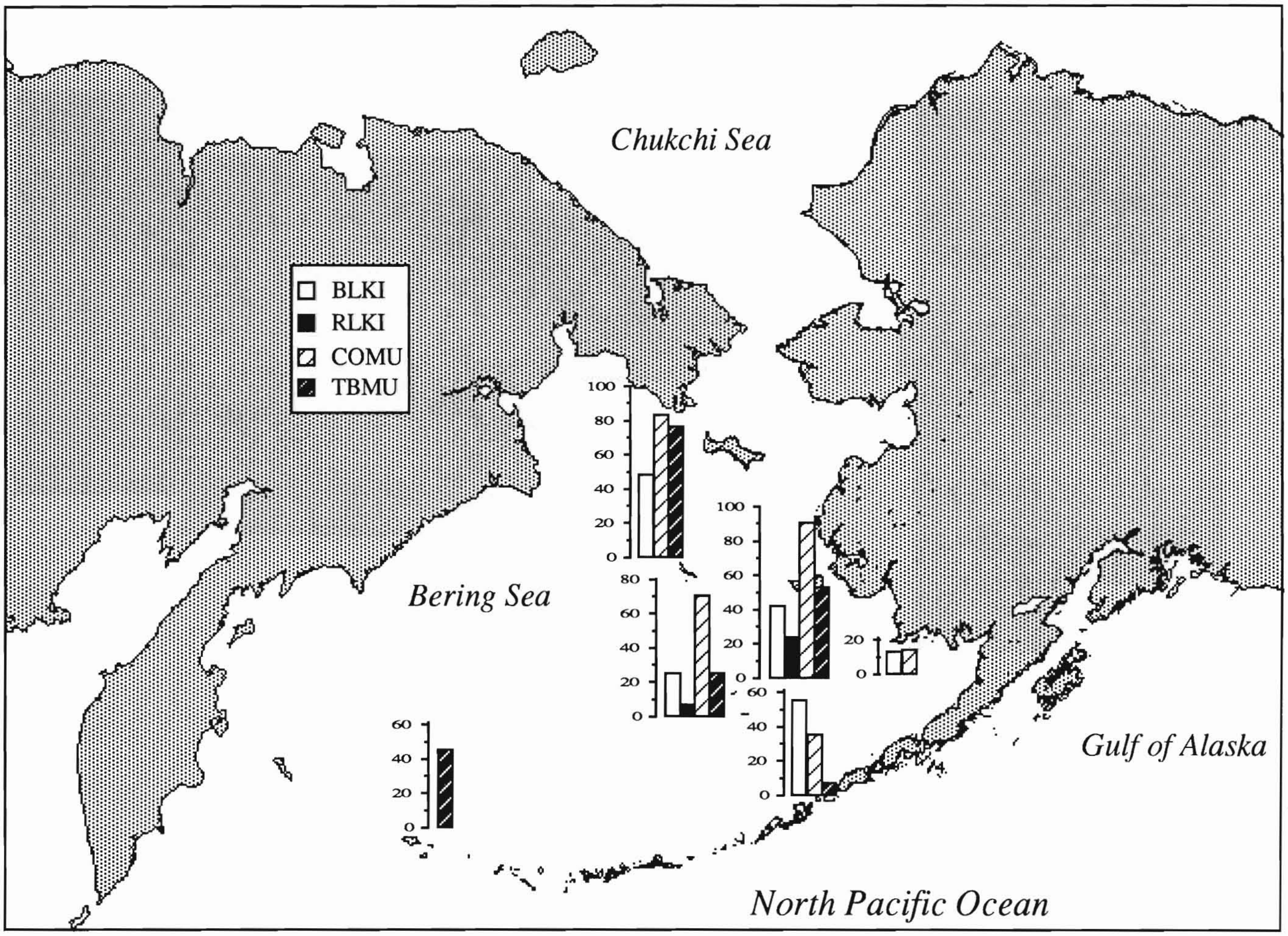

Figure 1

Importance of prerecruit pollock to nesting seabirds in the Bering Sea. Values are percentages of estimated total prey biomass (BLKI = black-legged kittiwakes; RLKI = red-legged kittiwakes; COMU = common murres; TBMU = thick-billed murres).

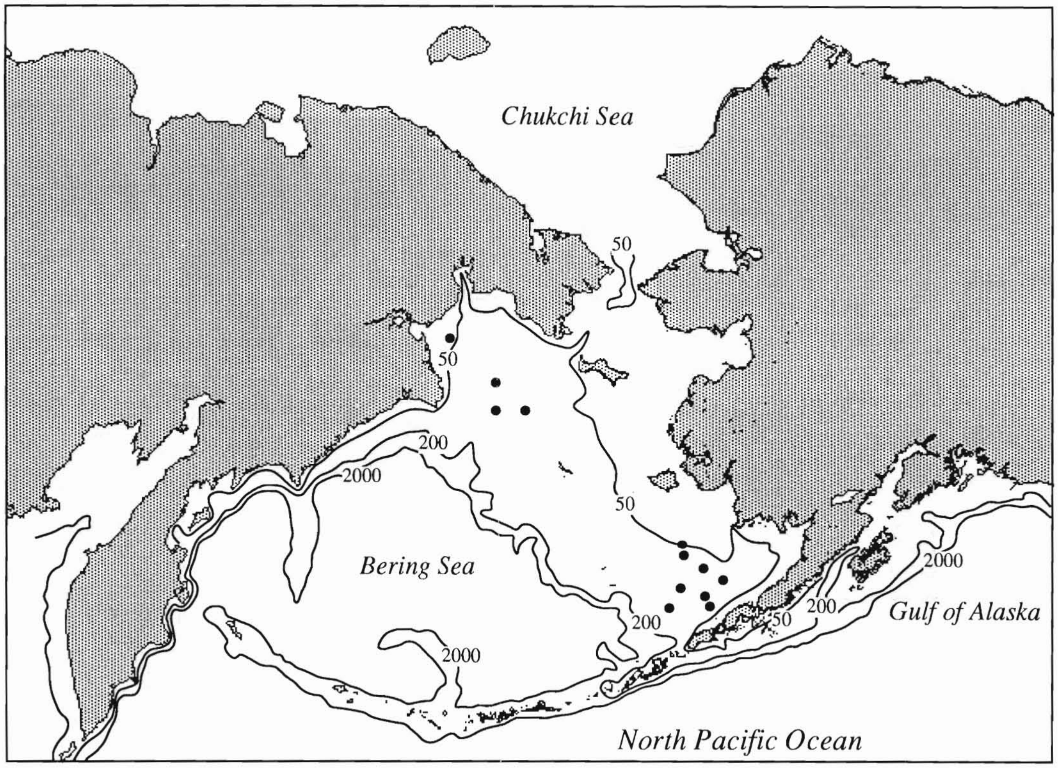

Figure 2
Locations where pollock were recovered from seabirds caught in fishing nets during summer. The pollock were 90–240 mm long. Isobaths in m.

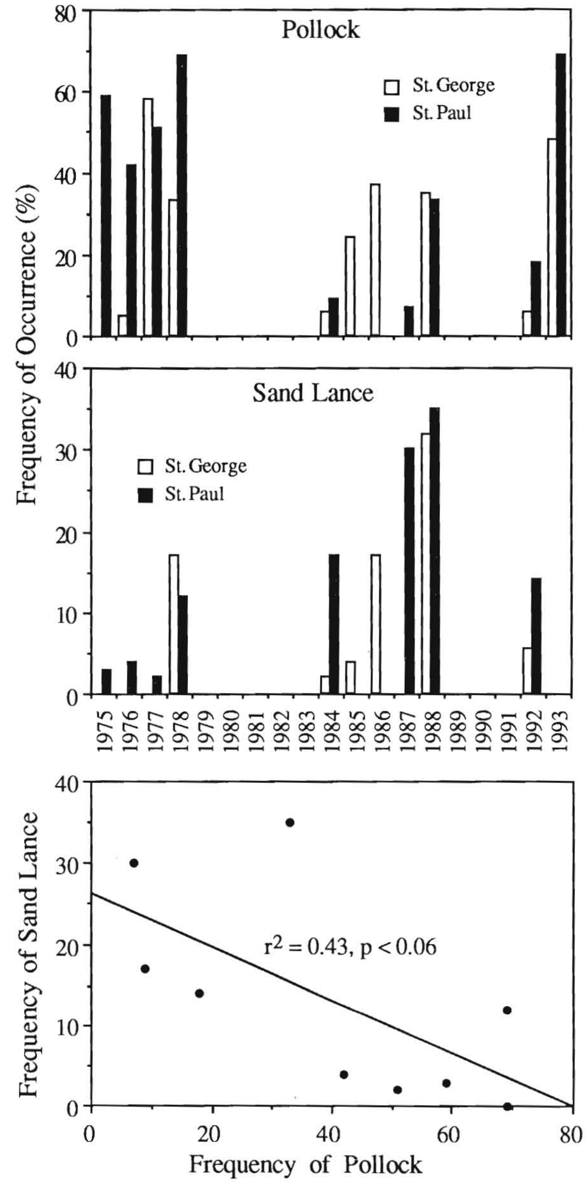

Figure 3
Relation between prerecruit pollock and sand lance in the diets of black-legged kittiwakes on the Pribilof Islands.

Relationship Between Sea-Surface Temperature, Abundance of Juvenile Walleye Pollock, *Theragra chalcogramma*, and the Reproductive Success and Diets of Seabirds at the Pribilof Islands, Southeastern Bering Sea

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Between 1975 and 1990, the reproductive success of seabirds breeding at the Pribilof Islands fluctuated widely, as did sea-surface temperature and juvenile walleye pollock, *Theragra chalcogramma*, populations. We explored how variations in seabird reproductive success and diets may have been influenced by fluctuations in sea-surface temperature and juvenile walleye pollock abundance. We hypothesized that changes in the temperature regime of the southeastern Bering Sea affected the availability of key prey required for successful seabird reproduction. By inspecting annual variations in seabird diets and reproductive success, we sought evidence for interdecadal changes in the marine environment near the Pribilof Islands. Low-frequency fluctuations in ocean temperatures have been found in the northeastern Pacific Ocean and Bering Sea. Sea-surface temperatures were relatively cool in the 1970's, with 1978 being the last cool year in that decade. Sea-surface temperatures were warmer than average from 1979 to 1984, and another cool period began in 1985.

The reproductive success of both surface-foraging black-legged kittiwakes, *Rissa tridactyla*, and red-legged kittiwakes, *R. brevirostris*, showed no significant correlation with sea-surface temperatures. However, both species of kittiwakes had poorer reproductive success after 1978. Kittiwake reproductive success was generally below average during the warm period from 1979 to 1984, and remained below average during the cool period beginning in 1985, except for 1988. Reproductive success of subsurface-foraging thick-billed murres, *Uria lomvia*, was negatively correlated with annual sea-surface temperature when data from populations on both islands were combined. The reproductive success of thick-billed murres breeding on St. Paul Island appeared to decline after 1978, whereas reproductive success on St. George Island was greatest in the cool period starting in 1985.

We examined an alternative hypothesis: that seabird reproductive success was correlated with the abundance of age-1 pollock in the Bering Sea. Correlations of annual reproductive success and the number of age-1 pollock were not statistically significant for any of the three seabirds over the study period.

Each species of seabird showed similar changes in diet over the period of our study. Capelin, *Mallotus villosus*, was eaten during the cool period from 1975 to 1978, but after 1978, capelin was no longer taken by kittiwakes or murres. After 1978, hyperiid amphipods were less important in the diets of black-legged kittiwakes and thick-billed murres. Pacific sand lance, *Ammodytes hexapterus*, increased in the diets of black-legged kittiwakes and thick-billed murres after 1978. Pollock consumption, although important for seabirds, showed no consistent or significant change through the study period. Similarly, the percentage of pollock in seabird diets was not correlated with reproductive success, except for a significant negative correlation for black-legged kittiwakes on St. George Island.

In summary, seabirds nesting on the Pribilof Islands showed decreased reproductive success (black-legged kittiwakes and red-legged kittiwakes) and changes in food habits (black-legged kittiwakes and thick-billed

murres) beginning in about 1978. These changes coincided with the appearance of the unusually large 1978 year class of walleye pollock and the beginning of a period of above-average sea-surface temperatures that lasted until 1984. Seabird reproductive success and diets did not return to pre-1979 values after 1984, which suggests that the changes in the marine ecosystem to which the birds responded lasted longer than the periods of warm and cool surface temperatures observed between 1975 and 1990.

Seabird Predation on Juvenile Walleye Pollock, *Theragra chalcogramma*, and Other Forage Fishes in the Gulf of Alaska

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Juvenile walleye pollock, *Theragra chalcogramma*, is an important component of summer diet for a variety of common seabirds in the northwestern Gulf of Alaska. As indicated by 18,163 prey items collected mostly in the 1980's from tufted (*Fratercula cirrhata*) and horned (*F. corniculata*) puffin chicks at 20 different colonies, the importance of juvenile pollock varies geographically, from little or no use in the north central Gulf of Alaska and Kodiak Island areas, to about 5%–25% of diets in the Semidi and Shumagin Islands, to about 25%–60% of diets at colonies farther west on the continental shelf and in the eastern Aleutian Islands. The proportion of pollock in puffin chick diets varies annually, and is correlated with independent estimates of juvenile pollock cohort strength. Juvenile pollock also constituted about 5%–75% of diets of adult tufted and horned puffins; common murres, *Uria aalge*; marbled murrelets, *Brachyramphus marmoratus*; and black-legged kittiwakes, *Rissa tridactyla*, during the 1980's. This contrasts with diets of these five species during the 1970's when capelin, *Mallotus villosus*, made up 30%–90% of diets, and pollock was relatively unimportant (0%–15%). Concurrent with these changes in diet, breeding success and populations of some seabird species declined through the 1980's. Varying diets and population parameters of seabirds appear to reflect long-term changes in oceanography and fish populations in the Gulf of Alaska.

Predator–Prey Relationships of Juvenile Walleye Pollock, *Theragra chalcogramma*: Summary and Recommendations for Future Research

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The presentations in this session provided reviews and new information about the sizes and quantities of juvenile walleye pollock eaten by various predators, and analyses of the importance of walleye pollock to the well-being of some of those predators. In addition, the predators were viewed as sampling tools which could provide information on the distribution, size, and relative abundance of juvenile walleye pollock.

Summary of Presentations

Because of its high abundance and large biomass, walleye pollock plays an important role in the trophodynamics of the North Pacific (Shuntov and Dulepova). Pollock consume large quantities of zooplankton (especially copepods and euphausiids) and lesser quantities of fish and squid, and are themselves preyed upon by a variety of fish, seabirds, and marine mammals.

Walleye pollock has long been recognized as highly cannibalistic in some geographic areas. Studies in the eastern Bering Sea during May–September of several years in the early 1970's and late 1980's have shown that the level of cannibalism, as measured by percent weight of stomach contents, was higher in the 1970's than in the 1980's (Livingston and Lang). The change over time was found to be related to the abundance of age-0 and age-1 walleye pollock. The shape of the feeding response curve remains uncertain; data are required from additional years, especially years of very high juvenile abundance. Other important prey included copepods (especially for fish <40 cm) and euphausiids. During years when cannibalism was low, the percent contribution of other prey increased. This may be interpreted as evidence that larger walleye pollock can compensate during times when smaller conspecifics are scarce, but such an interpretation requires additional information. One would have to assume as well that the level of consumption of all prey combined did not change. In response to a question, it was noted that there are no independent data on euphausiid abundance. It is therefore not possible to determine if the increased level of predation on euphausiids in the 1980's reflected an increase in euphausiid abundance. Predation by walleye pollock on capelin was low in both the 1970's and the 1980's.

Walleye pollock are preyed upon by many fish in addition to larger conspecifics. A study in the Gulf of Alaska in summer 1990 showed that walleye pollock was very important in the diets of arrowtooth flounder and Pacific halibut, less important for sablefish, and of relatively low importance for Pacific cod and walleye pollock (Yang et al.). Arrowtooth flounder were the major consumers of juvenile walleye pollock, but larger walleye pollock were also important consumers because of their high numbers and their tendency to feed on small, age-0 individuals. Most of the juvenile walleye pollock eaten were age 0.

Juvenile walleye pollock, primarily of ages 0 and 1, are eaten by murres, puffins, kittiwakes, and other piscivorous marine birds. In the Gulf of Alaska, the importance of juvenile walleye pollock in the diet of puffins varies geographically and annually (Piatt and Hatch). There is also longer-term variability. Juvenile walleye pollock was an important prey of five species of birds in the 1980's but was relatively unimportant for those species in the 1970's, when capelin was an important prey. This change in diet was concurrent with changes in breeding success.

In the Bering Sea, juvenile walleye pollock are known to be important prey of seabirds during the nesting season at certain well-studied sites such as St. Matthew Island and the Pribilof Islands (Springer). Their importance to birds at many colonies is not well known because of a low level of study. Walleye pollock may also be important prey for birds away from the colonies, in both summer and winter, but feeding data are sparse. There is evidence that juvenile walleye pollock may compete for prey with planktivorous birds.

Studies of seabirds on the Pribilof Islands revealed that, beginning in about 1978, some species showed both a reduction in the quantity of capelin and hyperiid amphipods in the diet and a decline in reproductive success (Decker et al.). Two seabird species also ate fewer juvenile walleye pollock, but there was no positive correlation between the consumption of pollock and seabird reproductive success. These changes coincided with the appearance of the unusually large 1978 year class of walleye pollock, prompting the hypothesis that cannibalism and other predation by adult walleye pollock might reduce prey availability to birds. The decline in reproductive success also coincided with the beginning of a period of above-average sea-surface temperatures, prompting the hypothesis that temperature-mediated changes in distribution had reduced prey availability. Reproductive success and feeding on walleye pollock did not increase when sea temperature cooled, prompting the suggestion of a "regime" change.

Analyses of juvenile walleye pollock's importance to predators such as seabirds is complicated by variability in reproductive success among species and among colonies within a species. Additional insight might be gained by narrowing the focus of the studies. For example, one can determine the importance of specific age classes of juvenile walleye pollock in the diets of the seabirds, and examine seasonal and annual variation in the geographic distributions of specific age classes of juvenile walleye pollock. The proportion of age-1 walleye pollock in the diet of seabirds on the Pribilof Islands declined between the 1970's and 1980's (Hunt et al.). During the same period the catches of age-1 walleye pollock declined in bottom-trawl surveys near the islands. These changes in age-1 walleye pollock were not correlated with the extent of sea ice or with potential cannibalism, as measured by the abundance of adult walleye pollock near the Pribilof Islands. In addition, changes in the ratio of age-1 to age-0 walleye pollock in the seabird diets did not explain a significant portion of the variability in seabird reproductive success.

Walleye pollock is also important prey for certain marine mammals. Age-0 and age-1 juveniles dominated the prey of northern fur seals in the vicinity of the Pribilof Islands in the 1980's (Sinclair et al.). The age distributions reconstructed from otoliths found in gastrointestinal tracts of northern fur seals caught at sea in 1981–85 reflected the relative strength of the 1978–85 year classes of walleye pollock. In contrast, otoliths found in scats in 1987–90 revealed a dominance of age-0 juveniles in all years. Northern fur seals collected in the 1960's and early 1970's had been feeding to a great extent on capelin and herring, both of which were uncommon in collections in the 1980's. This change in diet from the 1960's to the 1980's reflects ecosystem changes recognized in many other studies.

Long-term (decadal) changes in diet have also been documented for Steller sea lions in the Gulf of Alaska (Merrick and Calkins). In the Kodiak Island area, the proportion of animals that consumed walleye pollock increased from the 1970's to the 1980's. The proportion that consumed alternate small fish prey declined dramatically. It is hypothesized that a decline in abundance of small schooling fish, coupled with a reduction in year-class strength of walleye pollock, may have been responsible for the observed reduction in juvenile sea lion survival and decrease in individual weight, and may have contributed to the population decline of Steller sea lions in the Kodiak Island area.

A review of the literature on diets of phocid seals throughout the northwestern Pacific Ocean and Bering Sea revealed that walleye pollock is an important prey of harbor, spotted, and ribbon seals, but a minor prey of bearded and ringed seals (Lowry et al.). Most of the walleye pollock eaten are small (<20 cm), but larger individuals may be consumed, especially by harbor seals.

Additional information on the distribution and relative abundance of juvenile walleye pollock comes from bycatches in various commercial fisheries, especially the walleye pollock fishery (Fritz). Few walleye pollock <20 cm are caught in these fisheries, so the information provided is for fish that are larger and older than most of those taken by natural predators. Catch rates of juvenile fish vary seasonally and with geographic area. Annual changes in catch rates generally reflected changes in the abundance of young fish, but were also influenced by changes in fleet behavior.

Recommendations

Recommendations were compiled from the formal presentations and general discussions. Many of these recommendations are of a general nature and similar to those put forward following other symposia or workshops on multispecies interactions (e.g., Mercer, 1982; Sissenwine and Daan, 1991) and the biology of juvenile fishes (e.g., de Lafontaine et al., 1992).

Measuring the Intensity of Predation on Walleye Pollock

Who Are the Predators?—The workshop included studies of predation on walleye pollock by several species of fish, seabirds, and marine mammals. There was no attempt to review the feeding habits of all abundant or large predators in the North Pacific, so it is not clear if any important predators may have been neglected. If such a review has not been conducted elsewhere, it may be informative to summarize the feeding habits of groups such as cetaceans, squids, and seabirds away from colonies, including those seabirds that breed in the Southern Hemisphere but feed in the North Pacific during the summer.

Temporal and Spatial Heterogeneity—It is clear that there can be considerable spatial and temporal heterogeneity in the distribution of predators and prey, and in the quantity and type of prey consumed by predators. Data should be collected on time and space scales that are as fine as practical. Data can be aggregated during analysis if such aggregation is more appropriate to the specific study. Distribution of walleye pollock and the occurrence of walleye pollock in predator stomachs should be reported by age (or size group).

Importance of Predator Size and Sex—Numerous studies have emphasized that foraging strategy and diet composition may vary with predator size (or age) and sex, partly because animals of different sizes or sexes may have different capabilities, and partly because they may have different geographic distributions. Data collection and analysis should include consideration of predator size and sex.

Functional Feeding Response—In large natural ecosystems, the relation between predators' feeding rates and the abundance of prey can be determined only by monitoring these variables over time. A time series may have to continue for many years to capture information during periods of low and high abundance of both predator and prey. Existing time series of predator feeding, such as the study of cannibalism in walleye pollock, should be continued. There may be opportunities for creating new time series.

Many studies of functional feeding response use a proxy for feeding rate. In some studies, feeding is expressed as percentage contribution (by weight) of the specific prey to the total stomach contents of the predator. This percentage depends not only on the quantity of the prey of interest but also on the quantity of all other prey. A more appropriate measure would be independent of the level of predation on other prey. For predatory fish, one could use, for example, the average weight of the prey of interest in stomachs of the predator, taking into account variability associated with predator size.

Importance of Walleye Pollock to Predators

Compensation in Diet—Several populations of predators have been found to be in decline. In some instances these declines can be traced to low performance at specific points in the life cycle (e.g., reduced juvenile survival in Steller sea lions, and low fledging success in some birds), and in some instances the declines are associated with reductions in individual fitness (e.g., weight at age in Steller sea lions). Tests of hypotheses regarding the influence of changes in abundance or availability of juvenile walleye pollock as prey must take into account the availability and suitability of other prey. Can the predator compensate for low availability of juvenile walleye pollock by preying more intensively on alternate species? When examining such hypotheses, one perhaps should not express diet as percentage of stomach content weight, because this measure reveals changes in diet composition, not changes in consumption of specific prey.

Compensation in diet may occur because the predator can increase its rate of feeding on a prey that has not changed in abundance or availability. There is also the possibility that some prey or competitor of walleye pollock has become more abundant because of the decline in walleye pollock. To understand the biological mechanisms behind compensation, more independent information is required on the abundance of other prey such as macrozooplankton (particularly euphausiids); squid; and small schooling fishes such as capelin and Pacific sand lance.

An associated question is whether changes that have been observed in the diet of some predator populations in the past two decades result from broad-scale ecosystem changes or regime shifts. If the large-scale phenomena reported elsewhere have strong local effects, it will be important to understand the causes of these phenomena and the geographic area over which they operate. Since much of the evidence in support of long-term ecosystem changes comes from analyses of predator diets, it may be helpful to thoroughly document the spatial and temporal variability in the diet sampling that has been conducted for each predator. This may help resolve apparent inconsistencies, such as the contrast between a decline in the level of feeding on capelin by seabirds and northern fur seals near the Pribilof Islands, and the consistent low level of feeding on capelin by walleye pollock in the eastern Bering Sea.

Importance of Spatial Scale—To expand upon an earlier point, some predators, particularly seabirds foraging around colonies, have limited ranges. In order to assess how prey availability influences predator well-being (e.g., breeding success), it may be insufficient to determine prey abundance on large spatial scales, such as the eastern Bering Sea. It may be necesssary to determine the abundance of specific age classes of walleye pollock and other prey on local scales (such as the foraging areas around seabird breeding islands), and to ascertain the factors that influence prey abundance in these specific geographic areas. Factors that may be influential include 1) changes in other stages of the walleye pollock life cycle (e.g., spawning location, abundance of larger conspecifics); 2) changes in abundance or distribution of other organisms (e.g., prey such as copepods and euphausiids); and 3) changes in the physical environment (e.g., ice cover, temperature). The area around the Pribilof Islands may be a good choice for additional, well-integrated, multidisciplinary studies.

Effect of Predators on Dynamics of Walleye Pollock

The quantities of walleye pollock consumed by various species of fish, seabirds, and marine mammals have been estimated (Springer, 1992; Livingston, 1993; and abstract by Shuntov and Dulepova), but for various reasons the reliability of these estimates is unknown. The number or biomass of walleye pollock estimated to be removed by specific predators is often large, but how this removal contributes to total mortality of walleye pollock is difficult to determine, partly because of uncertainty about the magnitude of the removals and partly because of uncertainty about the abundance of walleye pollock at ages 0–2.

The information on consumption of walleye pollock comes from a variety of predators sampled at different times and places (see, for example, Livingston [1993] and various papers in these proceedings). If practical, it may be very useful to select a single year for extensive and intensive study of feeding by all (major) predators on walleye pollock, and to accompany these studies with broad-scale trawl and acoustic surveys to determine the distribution and abundance of walleye pollock of ages 0–3. Such a study would make it easier to quantify the removal of walleye pollock by age, and to reconstruct cohorts to the beginning of the year by combining the information on abundance (from surveys), removals by predators, and discards from commercial fisheries. This exercise would help reveal the most important contributors to mortality of juvenile walleye pollock.

Predators as Sampling Tools

There is much to be learned about the distribution and relative abundance of juvenile walleye pollock of specific ages or sizes by examining the diets of predators (see, for example, Hatch and Sanger [1992] and the paper by Hunt et al.). It may be useful to create maps illustrating the locations where predators have found walleye pollock. There could be a map for each 3- or 4-month period of the walleye pollock's life up to age 3 or 4. Such maps could be compared with the information coming from surveys, and may prove useful in modeling exercises and the planning of further studies.

Of course, one would like to know the extent to which information on prey abundance and distribution derived from predator feeding studies may be biased by the feeding behavior of the predator. Such information could come from studies comparing the prey taken by the predator with the prey available in the environment (see, for example, Sinclair et al. [1994]). Studies of prey selectivity are not common for predators feeding in the open ocean because of difficulties in simultaneously measuring the distribution and abundance of a variety of potential prey, particularly when such prey might include plankton, nekton, and various types of benthos.

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An Individual-based Model of the Juvenile Stage of Walleye Pollock, *Theragra chalcogramma*, in the Western Gulf of Alaska

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As part of an effort within NOAA's Fisheries-Oceanography Coordinated Investigations Program, we have been developing a biophysical model of the early life history of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. Combining an individual-based biological life-stage model with a three-dimensional hydrodynamic model, the model is process-oriented, mechanistic, and spatially explicit. Its purpose is to investigate how recruitment variability relates to the interaction of mechanisms affecting growth and survival of the different life stages of pollock.

The individual-based model tracks fish separately throughout the study period and the region. It follows each fish from spawning through the egg, yolk-sac larval, feeding larval, and 0-age juvenile life stages, and through the processes (such as mortality, feeding, and growth) of each stage. An individual-based approach was chosen for several reasons. First, it was thought that modeling the "average" fish (as do most traditional deterministic models) may be misleading; that it was important, instead, to understand the history of unique individuals, particularly those that survive to recruitment. Second, the environment of these fish was not homogeneous (an important assumption of aggregate models). Each fish traces a unique trajectory through space, which is strongly affected by mesoscale circulation features and results in differing exposure to environmental variables (i.e., temperature, salinity, predators, and prey). These different trajectories result in unique growth histories and probabilities of survival among individuals. Third, mechanisms and behaviors thought to be important to recruitment variability can be included with much more detail in individual-based models than is possible in aggregated models.

The initial effort to model the juvenile stage had several objectives. First was to use the model to validate the horizontal distribution of juveniles seen in the field data. In the model we treat juveniles as passively advected particles. In examining the divergence between modeled and real horizontal distributions, we hope to examine the question of how much of the horizontal distribution that we need to explain by directed horizontal swimming behavior. The second major objective in the preliminary version of the model was to identify gaps in our knowledge about the juvenile life stage.

The juvenile-stage model has several components. It predicts daily consumption as a probabilistic function of body size—i.e., a developmental response. No functional response (consumption as a function of prey density) information was available for this life stage of pollock. Metabolic rates of juveniles had to be obtained by interpolation between the larval stage and older juvenile stages. Daily growth is based on the difference between daily consumption and daily metabolic costs. Mortality of juveniles is neglected in this preliminary version of the model to reduce the number of individuals that need to be followed. Mortality is not critical in the process that we are examining here (advection).

Depth of individuals in the water column affects the direction of horizontal advection due to vertical shear and the effects of bottom topography. It is therefore important to include a prediction of depth of each individual at each time step for correct advection. Determination of the depth of individuals varies by life stage in the model. Eggs are spawned and hatch deep in the water column, and yolk-sac larvae rise quickly to the upper 60 meters. When feeding larvae reach 6 mm, they begin diel migration, which increases in amplitude as they increase in length. The depth distribution and vertical migration of juvenile pollock are not well understood. We therefore used two simple schemes to predict individual juvenile depths. We then used each scheme to examine the resulting horizontal distribution of the juvenile stage. In the first scheme, average depth increased with increasing juvenile size; in the second scheme, the average depth of juveniles was constant. In both schemes, normally distributed random noise was added to the depth of an individual at each time step.

Modeled length-at-age curves agree well with empirical length-at-age curves derived from otolith data. An increased variability in length with increasing age is seen in the model output, which agrees with what is observed in the data. Length frequencies from field data from September 1990 are normally distributed with a mean of 71 mm (range 55–110 mm). Modeled length frequencies are also normally distributed with a mean of 76 mm (range 45–100 mm).

The actual distribution of juvenile pollock in September 1990 was concentrated just east of the Shumagin Islands. The distribution was patchy, and the highest concentrations were inshore. The modeled distribution of juveniles using the first scheme of depth determination showed good agreement in degree of patchiness and the location of the highest concentration (east of the Shumagins), but the center of the distribution was somewhat farther offshore. Advection along bottom contours significantly affected the distribution, because near-bottom oceanic flows tend to follow bathymetric contours. When the second scheme was used, the distribution of juveniles was farther inshore. In this scheme, juveniles were generally shallower in the water column, and the flow and thus their advection were less influenced by bottom topography.

In conclusion, many of the features of actual juvenile pollock distributions (in September) were reproduced by the model. It is interesting that treating juveniles as passively advected particles did not result in large discrepancies between modeled and real distributions, at least for September 1990. This suggests that active, directed horizontal swimming behaviors during the juvenile (or earlier) stages may be less important than advective processes over all of the early life stages in determining September distributions. The directed swimming behaviors that do exist appear to transport juveniles toward inshore areas.

On the Relationship of Juvenile Walleye Pollock, *Theragra chalcogramma*, Abundance to Adult Recruitment and Linkages with the Environment

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I examined the relationship of trends in juvenile pollock abundance to recruitment time series of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska. I also explored the relative importance of various biological and physical factors to abundance of juvenile pollock. Two recent findings are that there is a relation between survival of first-feeding larval pollock and local wind mixing, and that year-class strength is usually set by September following the spring spawning. Based on these findings, the analysis focused on the period from January through August. The primary biological data for the analysis consisted of an age-2 recruitment time series covering the period 1962–89, and egg, larval, and juvenile abundance time series dating from 1981 to 1989. A suite of physical data, which overlapped the biological data, consisted of various time series describing atmospheric and oceanic features of the region. These included estimates of turbulent wind mixing of the oceanic mixed layer, volume transport, simulated subsurface drifter trajectories, and sea-surface temperature. Univariate and multivariate statistical techniques were used to qualitatively and quantitatively determine how the biological and physical variables relate to juvenile abundance.

Results suggested that age-0 and age-1 abundance estimates are related to freshwater input and an index of storminess; linear regression models accounted for 95% and 96% of the variation in those dependent variables, respectively. The influence of these factors was consistently demonstrated over the larval, juvenile, and adult life stages. From these results several hypotheses were proposed: spring wind mixing in Shelikof Strait affects larval survival, large-scale atmospheric circulation directly affects the Shelikof region; baroclinicity may generate features conducive to larval survival; and effects of the physical environment on predation and behavior may affect juvenile survival. Another important finding is that significant processes (yet unknown) may be occurring during the summer months.

Importance of Cannibalism in the Population Dynamics of Walleye Pollock, *Theragra chalcogramma*

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A spawner-recruit time series of nearly 30 years suggests a strong density dependence in eastern Bering Sea pollock recruitment (Fig. 1). The underlying cause of this density dependence is believed to be cannibalism of juvenile pollock by adults. To test the effect of cannibalism on population size and yield we used the historic age-structured population data to simulate population trends with varying fishery removals of adult pollock. We relate cannibalism to Ricker parameter β. Abundance at time t during the early life history is denoted $N(t)$. The dynamics of the population during the early life stage are related to spawning and mortality. It is assumed that

1) T, the age of recruitment, is constant;
2) the number of eggs, N_0, is proportional to spawning stock S, and $N_0 = fS$, where f is average net fecundity;
3) the total mortality, Z_t, at life stage t between times 0 and T contains both density-independent (q) and density-dependent effects, represented by $Z_t = a + bS$.

Assumption 3 implies that the spawning stock inhibits the population of young fish in some way before recruitment. One mechanism is cannibalism, which is known to occur in eastern Bering Sea pollock. The Ricker spawner-recruit relationship,

$$R = \alpha N_0 e^{-\beta N_0},$$

was used to model pollock, where recruits at age 2 (R) are expressed in terms of egg production (N_0) instead of spawning stock (S). Productivity parameter α is related only to density-independent mortality parameter a. Parameter β is proportional to density-dependent parameter b and inversely proportional to fecundity parameter f. For our purposes, we call β the "cannibalism" parameter since we have no evidence to suggest major changes in average net fecundity.

Population parameters for the simulations include estimates of abundance and fishing mortality from cohort analysis for 1964–92 for ages 2 to 12+, where the last age is a plus group. We set $T=2$ for the starting age of recruitment since this was the starting age in the data. Full-recruitment fishing mortality, F_{hist}, was estimated for each year t as the average fishing mortality for ages 4 and 5. Selectivity was estimated by age and year. Natural mortality, M_a, was set to 0.45 at age 2 and 0.30 for ages 3 to 12+. Annual estimates of egg production, N_0, were calculated with maturity m_a and fecundity f_a values at age. The Ricker spawner-recruit relationship was fitted to the egg production and recruitment estimates from the cohort analysis. We used egg production rather than spawning stock in developing the spawner-recruit relationship because the ratio of recruitment to egg production is an estimate of early life survival. Estimates of parameters are

$$\ln\hat{\alpha} = 9.84 \pm 0.25 (\pm 1\text{ S.E.}),$$
$$\hat{\beta} = 1.53 \times 10^{-15} \pm 0.18 \times 10^{-15}, \text{ and}$$
$$\hat{\sigma} = 0.55.$$

The latter is an estimate of the standard deviation about the spawner-recruit line on a log scale. Thus, on the original scale, a coefficient of variation of about 0.55

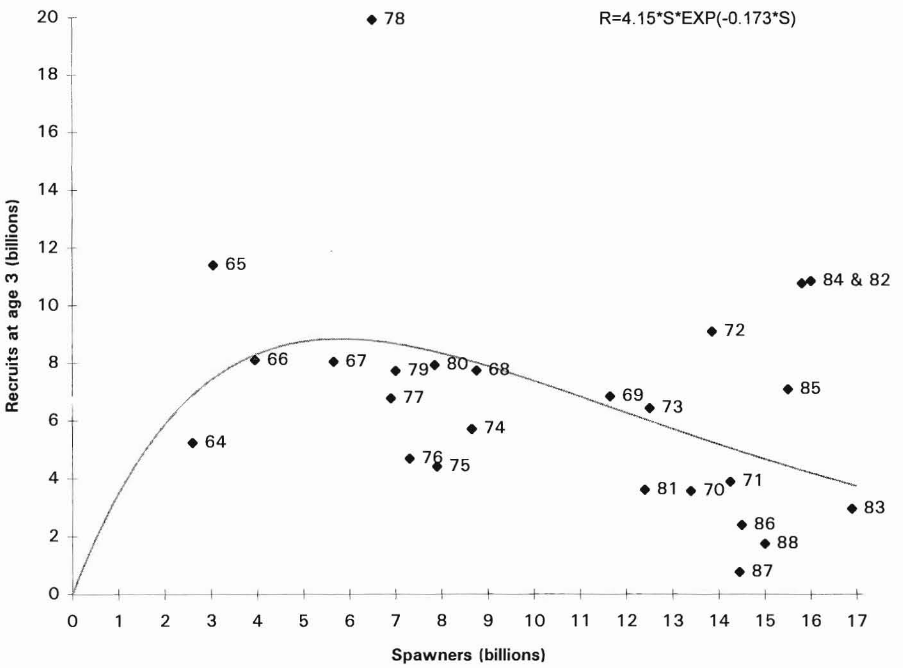

Figure 1
Eastern Bering Sea pollock spawner-recruit relationship, 1964–88. Numbers are years.

about the spawner-recruit line is estimated. In the regression, the value of r^2 was 73%, the amount of variability in the data explained by the spawner-recruit relationship. The cannibalism coefficient β was significantly different from zero ($P<0.001$), suggesting empirically that cannibalism is an important component of pollock dynamics.

We constructed a simulation to explore the interaction of cannibalism and fishing mortality on the population from 1979 to 1992, the most recent years of management under the Magnuson Act and the years that are supported by trawl-survey estimates of abundance. We used starting estimates of abundance for ages 2 to 12+ in 1979 from cohort analysis, as well as egg production in 1977 and 1978. We calculated recruitment at age 2 in year t+2 from egg production in year t as

$$R_{t+2} \equiv N_{2,t+2} = \alpha N_{0,t} \exp(-\beta N_{0,t} + \varepsilon_t),$$

for the years 1979 to 1992. If α and β are replaced with their estimates $\hat{\alpha}$ and $\hat{\beta}$, then the recruitments obtained are identical to those obtained from cohort analysis. Mortality and abundance at later ages and years were projected from the typical age-structured model equations.

We constructed a base simulation to reproduce the cohort analysis results. We used the historical fishing mortalities F_{hist} for F_t, the cannibalism coefficient from the spawner-recruit analysis, age- and year-specific selectivities, and the starting abundance values described above. We analyzed twelve scenarios, including the base case: three sets of cannibalism coefficients (β's) crossed with four fishing mortality scenarios. The three sets of β's represented weak, medium, and strong levels of cannibalism (density dependence) and corresponded to 0.5, 1.0, and 1.5 times the historic $\hat{\beta}$. As we were not interested in the effect of density-independent mortality on the population, we estimated a value of ln α that gave the best fit to the spawner-recruit model by using the recruitment–egg production estimates. For a given β, this estimate is

$$\ln\hat{\alpha} = \overline{\ln(R/N_0)} + \beta\overline{N_0},$$

where the overline denotes the average of the variable beneath it, over the range of years used in the spawner-recruit analysis. The four fishing mortality scenarios were no fishing (F_t=0), fishing at half the historical rate (F_t=0.5 F_{hist}), fishing at the historical rate (F_t=F_{hist}), and fishing at 1.5 times the historical rate (F_t=1.5 F_{hist}). For each scenario, we summarized the results in terms of total biomass across age, total yield across age, egg production, and recruitment trends over time.

Results suggest that fishing has little effect on pollock recruitment if density dependence is either strong or weak, but can exert some influence when density dependence is moderate (Fig. 2). Variation in recruitment pattern through density dependence affects biomass trends (Fig. 3). At observed, moderate levels of density dependence, increasing or decreasing fishing from observed levels would not have altered the population trend, and the level of fishing would have no effect in the most recent years. If strong density dependence operated in the eastern Bering Sea pollock population, the rate of removals would have less effect, and the population would rise to a higher level and fall more rapidly and to a lower level than under moderate density dependence. With weak density dependence, recruitment is greater in the midyears of the period examined than that observed, and the resulting biomass trend indicates greater stability (Fig. 2, 3). In general, recruitment is increased by fishing under the observed moderate density dependence, but it is only slightly increased under strong and weak density dependence. Yield is enhanced at intermediate population levels. It appears from this analysis that maintaining high population levels is detrimental and causes population oscillations, especially if density dependence is strong.

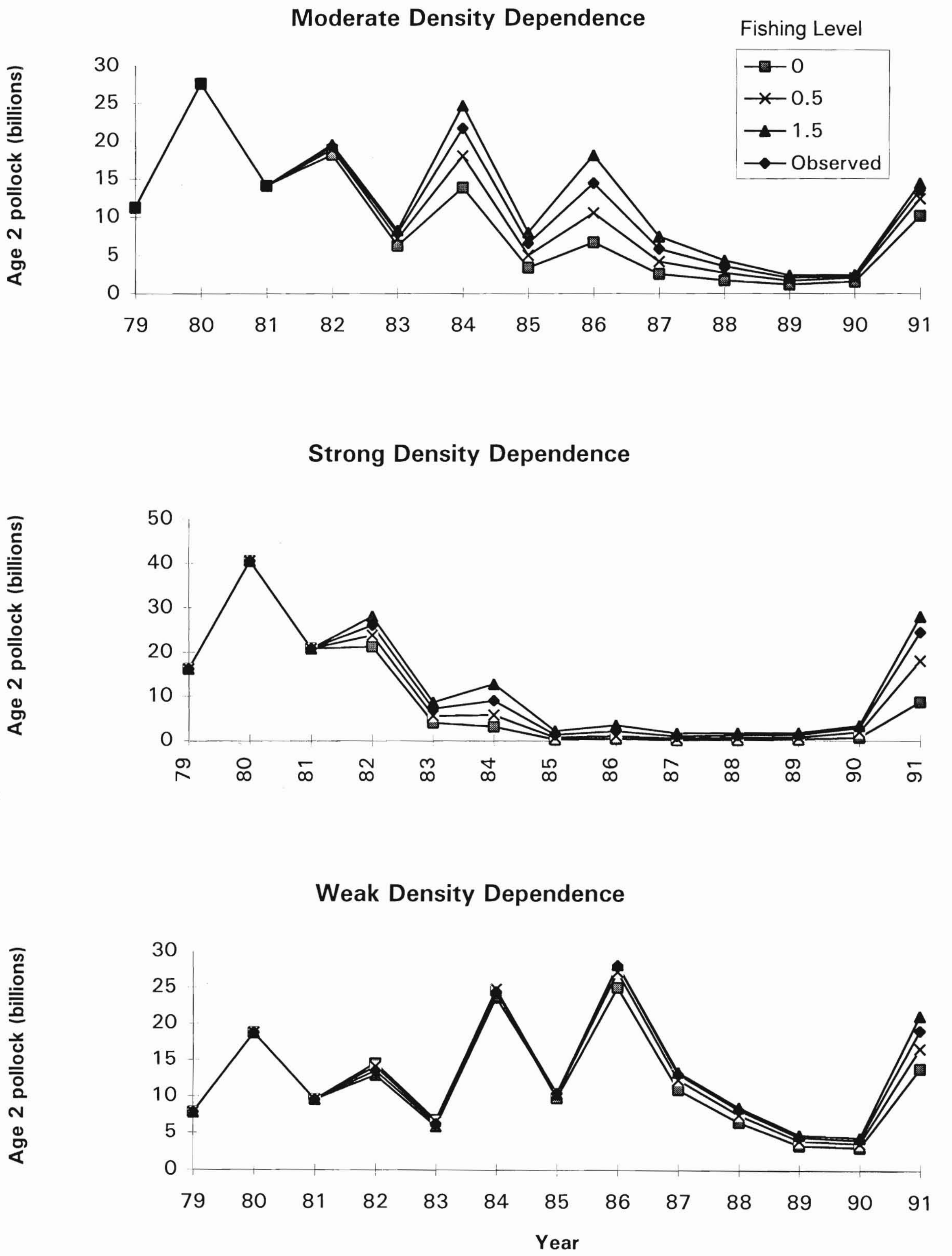

Figure 2

Estimated recruitment trend of eastern Bering Sea pollock, 1979–91, under three levels of density dependence and four levels of fishing: 0, 0.5 observed, observed (1.0), and 1.5 observed.

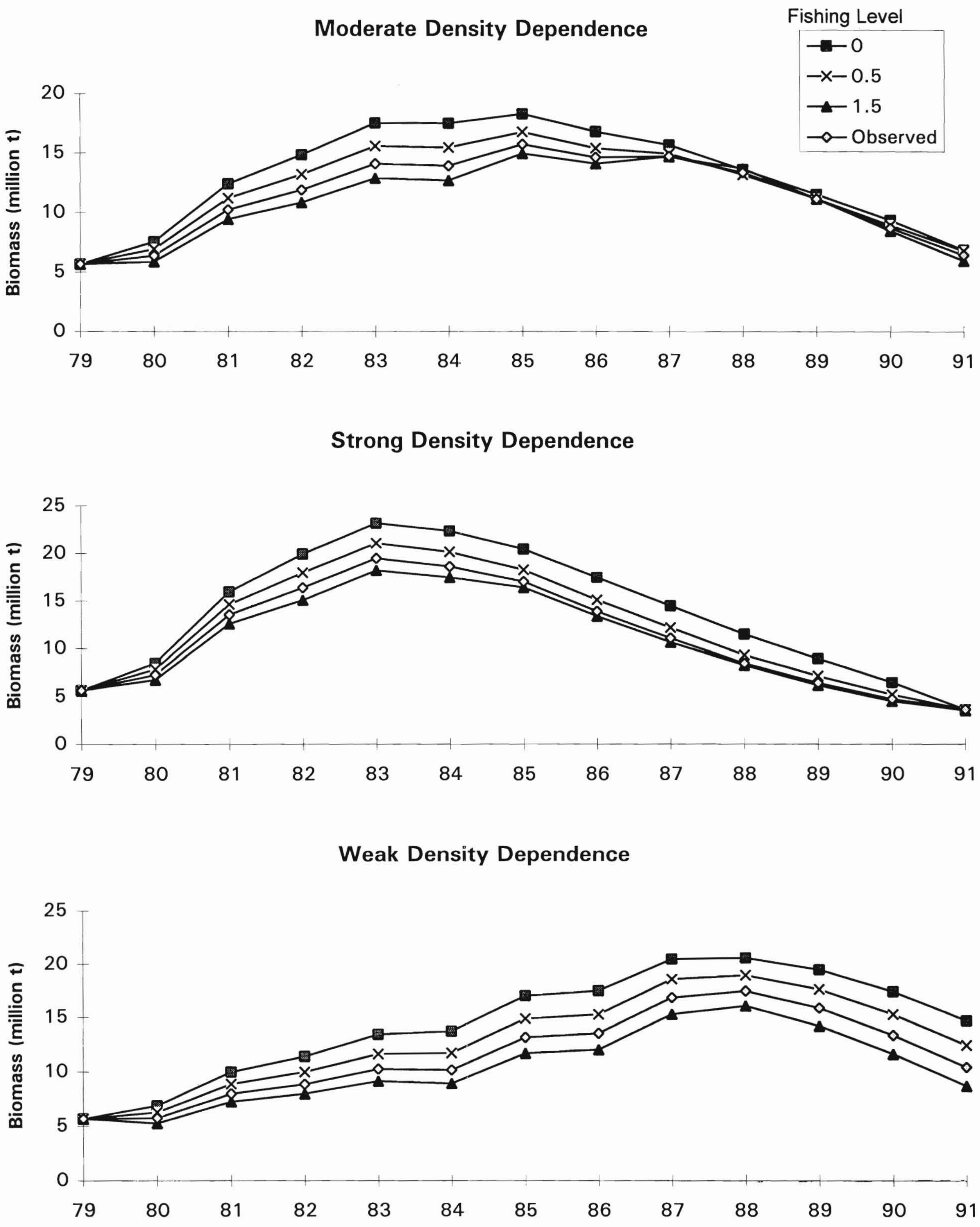

Figure 3

Estimated biomass trend of eastern Bering Sea pollock, 1979–91, under three levels of density dependence and four levels of fishing: 0, 0.5 observed, observed (1.0), and 1.5 observed.

Stock Synthesis Model of Walleye Pollock, *Theragra chalcogramma*, Including Predation

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Predation is often thought to be an important influence on the population dynamics of some groundfish populations. Because most traditional stock assessment models do not have a way to incorporate predation into the assessment process, predation is often entered as a constant rate across time. The stock synthesis model offers a framework for incorporating predators as "fisheries" in a single-species catch-at-age analysis. We investigated the effect of including predation by adult walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; and northern fur seals, *Callorhinus ursinus*, into a stock assessment of walleye pollock in the eastern Bering Sea. These predators were thought to be the main sources of predation mortality for age-1+ walleye pollock. Predators were entered into the model by defining 1) a time series of predator abundance (i.e., effort) over the whole modeled period, 2) a series of consumption data (i.e., catch per unit of effort) for each predator for each year where data on food habits were available, and 3) the age composition of pollock consumed for each year where data on food habits were available. Instantaneous annual predation mortality rates estimated from cod and fur seal were small, ranging from about 0.02 to 0.04. However, mortality rates of age-1 pollock due to cannibalism were high. Adding predation and particularly cannibalism to the model improved the fit of the stock–recruitment relation at age 1 by increasing the amount of variation accounted for by the relation by a factor of 2. The largest outliers from the relation were years when the physical environment favored larval survival. Environment and predation both appear to play an important role in pollock year-class recruitment.

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Natural Mortality Estimates of Juvenile Walleye Pollock, *Theragra chalcogramma*, in the Gulf of Alaska

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Juvenile walleye pollock, *Theragra chalcogramma*, is an important component of the marine ecosystem in the Gulf of Alaska, serving as primary prey for many marine fishes, mammals, and birds. Although the amount of juvenile pollock consumed by various predators has been estimated, and survey indices of juvenile pollock abundance are available, estimates of the total abundance of age-0 walleye pollock have not been advanced. This paper presents an exploratory method for converting indices of abundance to total abundance, provides a life-history table, and gives a brief analysis of ontogenetic change in abundance.

Indices of abundance can be converted to total abundance estimates if natural mortality, availability, and net selectivity are known. The Fisheries Oceanography Coordinated Investigations (FOCI) program has endeavored to produce estimates of natural mortality for larval and early juvenile pollock, and net selectivity of plankton gear for these early stages. We used the FOCI estimates of natural mortality, in conjunction with larval and juvenile abundance indices, to estimate a life table for Gulf of Alaska pollock during their first 3 years of life. We assumed that natural mortality was known for egg and larval stages and that survey selectivity and availability were unknown. Egg mortality was set equal to the mean egg mortality (0.208) measured for 1981 and 1985–91. Mortality during the early larval period was estimated from mortality estimates for three size categories (yolk-sac–6 mm, 6 mm–7 mm, 7 mm–15 mm) estimated from a logistic fit to observed mortality rates provided by K. Bailey (unpubl. data). The *y* intercept of the logistic equation was set at the maximum daily instantaneous mortality (0.38) for the youngest age group observed, yielding the equation

$$M = 0.38 - \gamma / \left[1 + \mathrm{EXP}\left(-\lambda * (\xi - x)\right)\right], \qquad (1)$$

where M = mortality, $\gamma = 0.362$, $\xi = -7.172$, $\lambda = -0.208$, and x was the midpoint of the age range for the size interval in days. Natural mortality for 15–60-mm pollock was set equal to 0.02. Age in days for a given size range was determined from a length–age relationship derived from otolith microstructure analysis:

$$\mathrm{SL} = \left[Y1^{\beta} + (Y2^{\beta} - Y1^{\beta}) * \left(1 - \mathrm{EXP}(-\alpha * \mathrm{age})\right) / \; 1 - \mathrm{EXP}(-\alpha * 150)\right]^{\frac{1}{\beta}}, \qquad (2)$$

where SL is the standard length, $Y1 = 4.52$, $Y2 = 90.2$, $\alpha = -0.81$, $\beta = 0.026$, and age is in days. Model estimates of total abundance were adjusted to fit the survey indices of abundance by estimating a "catchability" coefficient (Q) for each survey with the following simple form:

$$N_t = Q * \left[N_{t-d} * \mathrm{EXP}(-M * d)\right], \qquad (3)$$

where N is the estimated number at age t (days) and d is the duration of the life stage. The central assumption here is that research survey estimates of population abundance are directly proportional to the true abundance. Estimates of total pollock abundance were made for three age groups: 53 d (late larvae, 15 mm), 167 d (age 0), and 639 d (age 2). Embryonic stage durations were taken from previous studies, and larval stage durations were estimated from Equation 2.

Model parameters in Equation 3 were adjusted to minimize the mean square error between observed and estimated pollock abundance at the three life stages. Three parameters were adjusted to tune the expected survey indices to the observed survey indices: Q for the larval and age-0 surveys and M for juvenile pollock. All other model parameters were fixed at the values shown in Table 1.

Estimates of Q were 1.90 for larval surveys and 0.24 for age-0 surveys. The value of 1.90 would indicate that the initial abundance of eggs used to initiate the model was underestimated, the natural mortality schedule was

Table 1

Life table for Gulf of Alaska walleye pollock for ten life stages. Initial abundance, estimates of natural mortality, and stage duration based on FOCI research. Italicized mortality value indicates a free parameter in the modeling exercise.

Stage	M daily	Duration (d)	Initial abundance	d since hatch	Tons consumed
Egg	0.208	12.5	132,536,728,571,429	0.001	
Yolk-sac	0.239	8.8	9,843,977,075,822	12.5	
6 mm	0.119	5.9	1,201,606,971,406	21.3	
7 mm	0.057	5.2	595,448,606,975	27.2	
7–15 mm	0.020	25.5	442,710,068,451	32.4	13,820
15–60 mm	0.020	110	265,845,438,801	57.9	
Age 0	*0.014*	207	29,456,514,255	167.9	254,977
Age 1	0.005	265	1,624,037,094	374.9	253,276
Age 2	0.00082	365	431,673,865	639.9	83,346
Age 3			320,015,797	1004.9	

too high, or spawning occurred outside of Shelikof Strait. The value of 0.24 for the age-0 survey suggests that the natural mortality schedule used was too low, that the age-0 surveys missed a large fraction of juveniles, or both. Juvenile mortality was estimated to be 0.014, a value higher than previously reported.

The life table for juvenile pollock provided a reasonable life-history trajectory (Table 1) in which the expected number of age-2 pollock at the beginning of the year corresponded to the average observed year classes of pollock. The proposed mortality schedule indicated that the biomass of pollock at age 0 would exceed the biomass at age 1 or 2. If one assumed that the mortality of juvenile pollock >15 mm was all due to predation, the biomass of juvenile pollock consumed would be 592,000 t.

Time series of observed pollock recruitment show that the 1985 and 1988 year classes were average to above average, and that the 1981, 1986, 1987, and 1989–91 year classes were all below average. The observed and predicted abundance of late larvae showed a good fit to the 1981, 1985, and 1988 year classes, whereas predictions of the 1986, 1987, and 1992 year classes were higher than the observed survey index (Fig. 1). This suggests that natural mortality was higher than expected in 1986, 1987, and 1991.

The model overestimated the survey index of age-0 and age-2 pollock in 1981, and underestimated the survey index of age-0 and age-2 pollock in 1985 and 1988 (Fig. 1). This pattern suggests that in 1981 natural mortality was higher than expected during the first summer. Likewise, the results suggest that in 1985 and 1988, natural mortality was lower than expected during the first summer. These results indicate that significant adjustment (positive or negative) to year-class strength can occur during the summer of the first year of life, well beyond the larval stage.

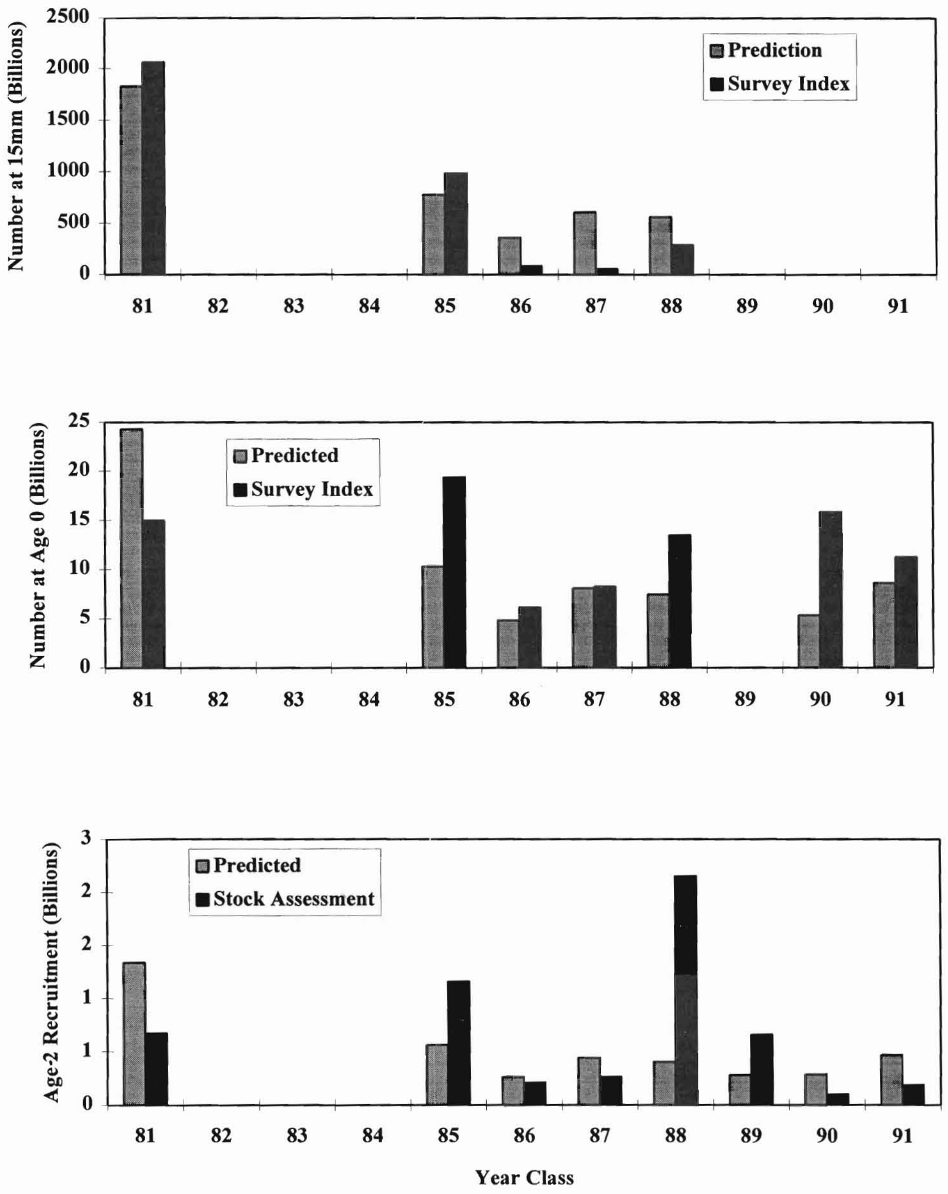

Figure 1
Comparison of observed and predicted indices of juvenile pollock abundance in the Gulf of Alaska for 15-mm fish (upper), age-0 fish (middle), and age-2 fish (lower).

Using Mechanistic Models to Test Hypothesized Causes for Steller Sea Lion, *Eumetopias jubatus*, Declines

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The most contentious issue in the decline of the Steller sea lion, *Eumetopias jubatus*, in the Bering Sea and the Gulf of Alaska is the possibility that the walleye pollock, *Theragra chalcogramma*, fishery contributes to the decline. Some have suggested that the commercial fleet is reducing the forage available to the sea lions, and that the resultant energetic stress has reduced survival and reproductive success. Others have argued that pollock abundance was greater during the period of the decline than previously. We initially attempted to link the historical data on the food available to Steller sea lions to their trends in abundance using a mechanistic model with three components: 1) a prey-capture model linking the abundance and spatial distribution of food species to the amount of fish consumed by individuals in specific sea lion colonies, 2) a bioenergetics model relating the amount of fish consumed to the survival and reproductive success of an individual sea lion, and 3) a population dynamics model relating individual survival and reproductive rates to changes in sea lion abundance.

We abandoned this approach because abundance data for many of the fish species and species size classes eaten by sea lions were sparse. Instead, we restricted ourselves to the population dynamics component of the model and compared how the various hypotheses about the causes of Steller sea lion declines explain the observed declines. Using this methodology, we were able to eliminate a delayed effect of 1970's sea lion harvests, short-term environmental fluctuations, and transient effects of perturbations in population age structure as potential causes. The only remaining hypothesis capable of explaining sea lion declines was a significant long-term degradation in environmental conditions. Unfortunately, this hypothesis is so broad as to include many divergent scenarios, only one of which is a reduction in food intake.

We attempt to narrow this ambiguity by using the bioenergetics component of our original model. We determine how large a reduction in caloric intake would be necessary to reduce survival and reproduction to the levels necessary to produce the observed population declines.

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Population Dynamics and Modeling of Juvenile Walleye Pollock, *Theragra chalcogramma*: Summary and Recommendations for Future Research

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The session on population dynamics and modeling reviewed a variety of research perspectives taken by modelers working on the dynamics of juvenile pollock, *Theragra chalcogramma*, in the North Pacific and Bering Sea ecosystems. The general theme of the session focused on biological and environmental mechanisms that are important in the overall scheme of population change in these marine systems. Topics included environmental effects on pollock recruitment, the magnitude of natural mortality, and compensation and its relation to the natural mortality rates of juvenile pollock. Other analyses focused on the survival and growth of juvenile pollock from the perspective of the individual organism, and on how additional sources on predation mortality might change our perspective on overall pollock abundance. Several researchers also concentrated on cannibalism as an important mechanism in juvenile pollock population dynamics. Another study attempted to relate declines in Steller sea lions, *Eumetopias jubatus*, to changes in juvenile pollock abundance by studying alternative hypotheses with simulation.

Hinckley et al. gave an overview of their bottom-up modeling approach to juvenile pollock dynamics. The model was individual-based, concentrating on the effects of predation, prey availability, fish growth, physical factors, and other important mechanisms controlling juvenile abundance. Participants felt the approach was useful because details and important mechanisms could be easily incorporated into this model structure. The senior author discussed ways of incorporating additional complexity into the method. Some discussion centered on whether accumulation of individual responses is the best method for obtaining aggregate population results.

Megrey's presentation focused on the importance of various biological and environmental factors as regulators of juvenile pollock abundance in Shelikof Strait. Results suggested that spring weather conditions may affect larval survival, predation rates, and behavioral traits. The models accounted for a large percentage of the variation in larval and juvenile abundance and may lead to a better understanding of the mechanisms controlling recruitment in this species. Discussion centered on future areas of investigation, methods, and the next generation of models that will be developed.

Wespestad and Quinn reviewed a study on the underlying causes of density dependence in Bering Sea walleye pollock. One current hypothesis is that cannibalism is a strong regulatory mechanism influencing this stock. Simulations under varying fishing mortality regimes were used to ascertain the level of population response. Results suggested that yields are highest at middle levels of stock size and would be much more variable at high pollock abundances, presumably because of heavy cannibalism.

For their study of the sources of natural mortality of juvenile pollock in the Gulf of Alaska, Hollowed et al. chose a life-stage approach addressing the period from prerecruit surveys to the time of recruitment. By estimating an average catchability factor for a set of survey years (1981 and 1985–92), the researchers calculated annual fluctuations from this constant Q and used them to examine different recruitment and predation hypotheses. This approach appeared promising, although perhaps data hungry, to participants because it allowed for a direct focus on causes of variation in year-class strength of walleye pollock.

A study by Livingston and Methot incorporated predation rates into a stock synthesis model of Bering Sea pollock. The model included the impact of predation by adult pollock, Pacific cod, and northern fur seals. Age-specific estimates of predation mortality were produced, and model results suggested that predation rates by northern fur seals and Pacific cod were low, whereas cannibalism may produce a fairly high mortality rate in juvenile pollock.

A study of the mechanisms controlling abundance of juvenile pollock off Japan was reported by Wada and Yabuki (not published here). They analyzed the mortality rate of juveniles relative to food type and availability, and whether adult pollock abundance might significantly influence juvenile survival. Results suggested that when food was in high abundance, especially euphausiids, mortality rates were low. Correlation analyses indicated that cannibalism was not an important regulatory mechanism of year-class strength.

The presentation by Adkison and Pascual centered on the causes of decline in the Steller sea lion population of the Bering Sea. They used a simulation model to study various hypotheses. They initiated various model scenarios and examined results for causal links. Results suggested that general demographic responses, previous harvests, and short-term environmental processes were not important. Longer-term environmental conditions did appear to be a possible cause of the decline, but mechanisms were not readily apparent. Future work will center on the energetics of the species and how survival and reproduction might be affected.

The session successfully integrated important information and studies of the pivotal species in these two large North Pacific ecosystems. The breadth and quality of modeling approaches to study how walleye pollock interact with important biological mechanisms and environmental forcing was impressive. Results should lead to a better understanding of the relevant networks and linkages in these systems. The directions of future research on this timely subject appear to be centered on the right set of questions and hypotheses, and a better level of understanding seems assured.

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