Abstract–Triennial bottom trawl survey data from 1984 to 1996 were used to evaluate changes in the summer distribution of walleye pollock in the western and central Gulf of Alaska. Differences between several age groups of pollock were evaluated. Distribution was examined in relation to several physical characteristics, including bottom depth and distance from land. Interspecies associations were also analyzed with the Bray-Curtis clustering technique to better understand community structure. Our results indicated that although the population numbers decreased, high concentrations of pollock remained in the same areas during 1984–96. However, there was an increase in the number of stations where low-density pollock concentrations of all ages were observed, which resulted in a decrease in mean population density of pollock within the GOA region. Patterns emerging from our data suggested an alternative to MacCall's "basin hypothesis" which states that as population numbers decrease, there should be a contraction of the population range to optimal habitats.

During 1984–96 there was a concurrent precipitous decline in Steller sea lions in the Gulf of Alaska. The results of our study suggest that decreases in the mean density of adult pollock, the main food in the Steller sea lion diet, combined with slight changes in the distribution of pollock (age-1 pollock in particular) in the mid-1980s, may have contributed to decreased foraging efficiency in Steller sea lions. Our results support the prevailing conceptual model for pollock ontogeny, although there is evidence that substantial spawning may also occur outside of Shelikof Strait.

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Changes over time in the spatial distribution of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska, 1984–1996

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The incorporation of space into ecological models has increased our knowledge of the competition and co-existence among species (Steinberg and Kareiva, 1997). It has also shown that the distributions of most organisms are not homogeneous throughout their range, but rather occur as patches. Analyses of predator-prey interactions and food-web dynamics are enhanced by considering the habitat association of species. A first step towards this goal is to describe the spatial distributions of the major players in an ecosystem.

The purpose of our study was to examine changes in walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) distribution. Walleye pollock (hereafter called "pollock") are a dominant species in the Gulf of Alaska (GOA). Pollock are the major prey of many species of flatfish and marine mammals and have been the predominant species in Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) diets since at least the mid-1970s (Pitcher, 1981; Merrick and Calkins, 1996). Numbers of Steller sea lions have declined significantly in recent decades in the western and central GOA. Examination of temporal and spatial changes in the abundance and population structure of pollock is important to understanding the decline in sea lion numbers. Existing and proposed management decisions to protect Steller sea lions include temporal and spatial changes to pollock fishing quotas.

The GOA pollock population peaked in the early 1980s as a result of several strong year classes in the late 1970s (Fig. 1A). Since then, the population has had fewer strong year classes. Modeled estimates of total biomass of the population declined in the early 1980s and leveled off in the 1990s (Fig. 1B). Bottom trawl survey biomass estimates (since 1984) have not reflected the decline in the early 1980s (Fig. 1C). Instead, they showed that the demersal fraction of the population changed little. Compared with other gadoid stocks worldwide, the GOA pollock stock has been lightly exploited; average landings have constituted less than 10% of the stock biomass during the last 20 years (Shima et al., 2000).

In this study we document changes in the spatial distribution and population density of juvenile and adult pollock in the western and central GOA (defined as the area between 147°W and 170°W), from 1984 to 1996. Catch per unit of effort (CPUE) (number of fish/km^2) was used as a measure of density throughout our analysis.

We also examine changes in species associations and the distribution of pollock. Analysis is limited to the summer months because the source of our pollock data were summer research surveys.

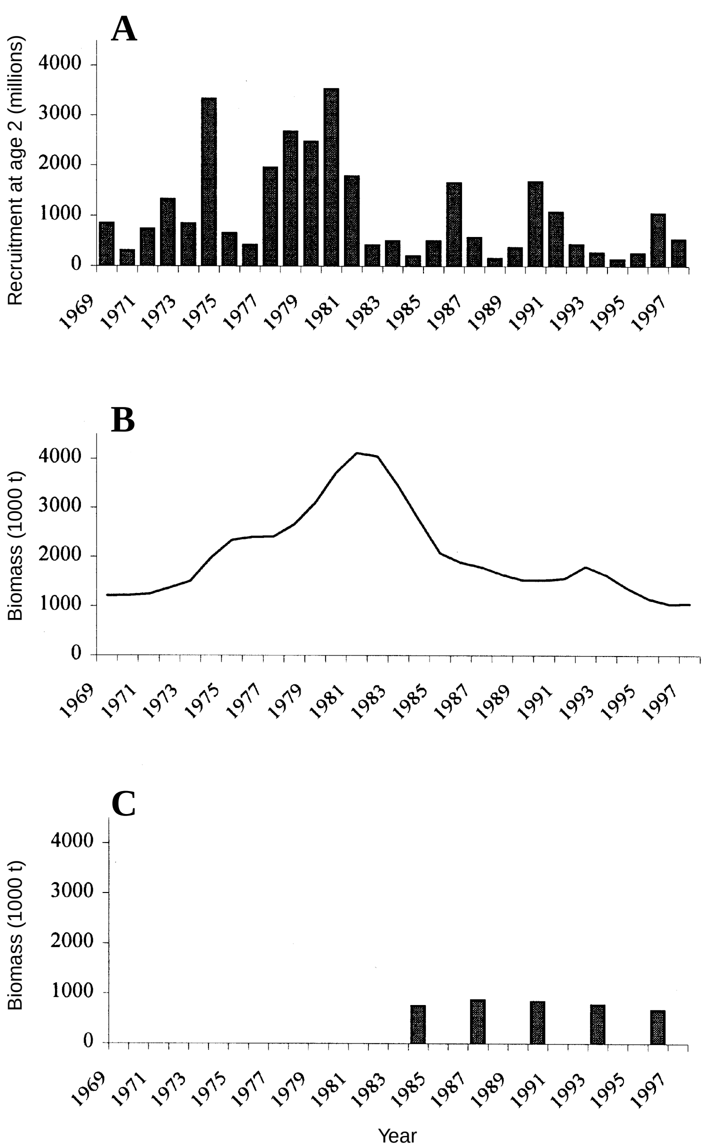

Figure 1

Data for walleye pollock in Gulf of Alaska, 1969–1997: pollock recruitment (**A**), biomass estimates from stock assessment analysis (**B**), and biomass estimates from triennial bottom trawl surveys (**C**). Data are from Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 2000. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 2000 Gulf of Alaska groundfish fishery, 60 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

Methods

Data source

Data were collected from triennial bottom trawl surveys in the GOA conducted by the Alaska Fisheries Science Center of the U.S. National Marine Fisheries Service (RACE division trawl survey relational database, Mundell[1]). The use of bottom trawl data to assess juvenile pollock abundance and distribution has many precedents. In the Bering Sea, bottom trawl survey data have been used to determine estimates of age-1 pollock, which were used as indices of recruitment (Wespestad[2]). Others have used the same data to evaluate the relationship between juvenile pollock and the movement of the ice edge in the Bering Sea (Wyllie-Echeverria and Wooster, 1998). Bottom trawl estimates have also been used to explore the relationships between different age groups of pollock in Shelikof Strait (Schumacher and Kendall, 1991).

Brodeur and Wilson (1996) modeled the depth distribution of pollock in the GOA during their first year and showed that age-1 pollock were found near bottom. Acoustic surveys of spawning pollock in Shelikof Strait have detected age-1 pollock in both nearbottom and pelagic layers. These data suggest that some age-1 pollock may reside off bottom. Therefore, juvenile pollock data from bottom trawl surveys are used as an index rather than an absolute measure of abundance (Bailey and Spring, 1992; Guttormsen and Wilson[3]).

Survey design

Triennial bottom trawl surveys were conducted during the summer months (May–Sep) of 1984, 1987, 1990, 1993, and 1996. These surveys have consistently been conducted in a stratified random sampling pattern (Martin and Clausen, 1995; Munro and Hoff, 1995; Stark and Clausen, 1995; Martin, 1997). The GOA is divided into 49 strata according to water depth

[1] Mundell, G. 1999. Personal commun. Alaska Fisheries Science Center, NMFS/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Wespestad, V. 1995. Walleye pollock. *In* Plan team for groundfish fisheries of the Bering Sea/Aleutian Islands stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1996, 35 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[3] Guttormsen, M. A., and C. D. Wilson. 1999. Echo integration-trawl survey results for walleye pollock in the Gulf of Alaska during 1998. *In* Stock assessment and fishery evaluation report for the 1998 Gulf of Alaska groundfish fishery, 25 p. North Pacific Fishery Management Council, 605 W 4th Avenue, Suite 306, Anchorage, Alaska 99501.

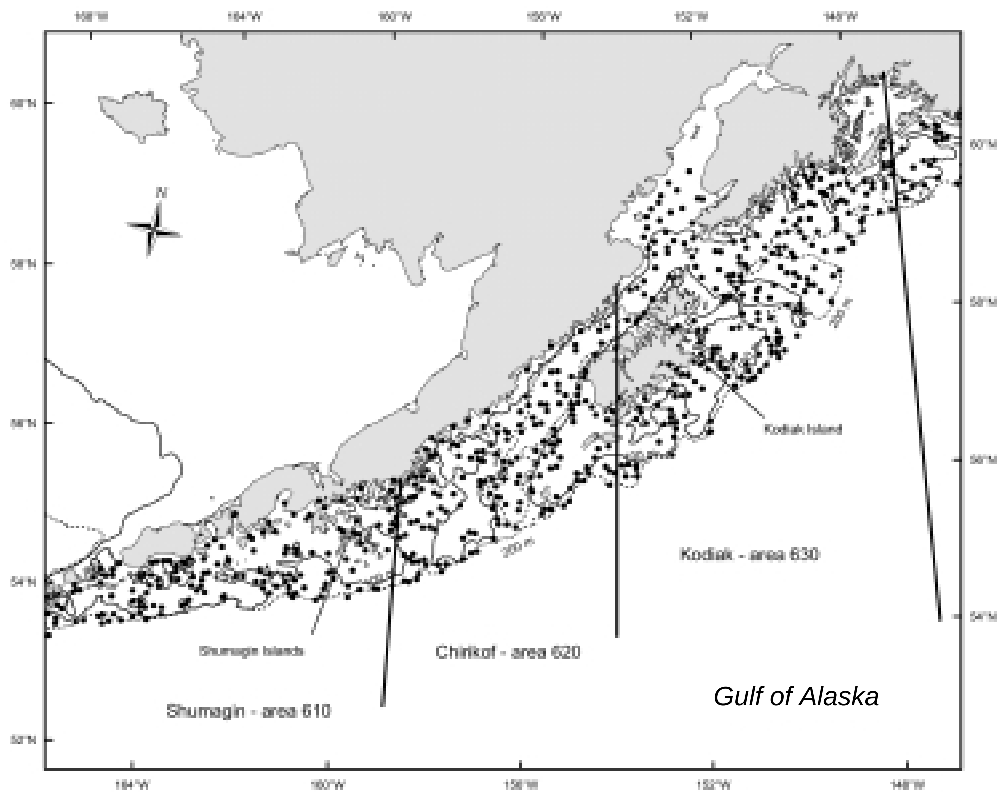

Figure 2

Example of the spatial coverage of the triennial bottom trawl survey for a sample year. Dots indicate station locations.

and area boundaries defined by the North Pacific Fisheries Management Council (http://www.fakr.noaa.gov/rr/figures/fig3.pdf). Allocation of sampling effort within each stratum was based on coefficients of variation, mean CPUE, and sampling densities for all fish species from data collected on previous triennial surveys (see Cochran, 1977). Sampling density within a stratum depended on the anticipated fish density of that particular stratum (Martin and Clausen, 1995; Stark and Clausen, 1995; Martin, 1997). Stations were prioritized within each stratum so that in the event of complications, sampling density would remain controlled. The total survey area was reduced by 7% after 1987 when stations deeper than 500 m were eliminated (Stark and Clausen, 1995). In the interest of consistency, only data from stations less than 500 m in bottom depth were used in our analyses. Station density was spread over a wide range; thus the survey data were most suitable for analyses of geographic distribution and community composition on a large scale (Fig. 2).

For each survey a Nor'eastern trawl (NT) with a 1.25 inch codend liner was used. The liner helped retain juvenile pollock (Brown, 1986). The nylon and polyethylene NTs had net dimensions of 18.3 m wide by 4.7 m high and 18.3 m by 5.5 m, respectively. In 1984 and 1987 a Japanese bottom trawl (JBT) was also used. The horizontal opening of the JBT ranged from 19 to 30 m, the vertical opening from 3.2 to 3.3 m (Brown, 1986). CPUE from the JBT were corrected (using Tables 28 and 31 in Munro and Hoff, 1995) to account for differences between the catchability of the NTs and the JBT.

Data analyses and statistical considerations

Analyses were conducted on total pollock catch as well as on four size groups of pollock: <150 mm (age-0 or young-of-the-year); 150–230 mm (age-1 juveniles); 230–330 mm (age-2 juveniles); and >330 mm (adults). The length-at-age categories were based on a histogram of pollock lengths from a historical database of all NMFS research surveys conducted during the summer. The catchability of age-0 pollock may not have been as high as that for the other juvenile age classes and thus supports the interpretation of all juvenile data as index values (Bailey and Spring, 1992; Guttormsen and Wilson, 1999). Comparable numbers of length measurements were taken every triennial year but measurements were not taken at every station. Thus, analyses of different age groups were based on subsets of the data. The abundance of fish in a specified age category was influenced by year-class strength (Table 1; Megrey et al., 1996; Hollowed et al.[4]). Strong year classes were present in 1984 (age 0), 1990 (age 2), and 1996 (age 2).

[4] Hollowed, A. B., E. Brown, B. Megrey, and C. Wilson. 1996. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 1997 Gulf of Alaska groundfish fishery, 64 p. North Pacific Fishery Management Council, 605 W 4^{th} A.venue, Suite 306, Anchorage, AK 99501.

Table 1
Summary of year-class strength of juvenile walleye pollock in bottom trawl survey years.

	1984	1987	1990	1993	1996
Age 0	Strong	Weak	Weak	Weak	Weak
Age 1	Weak	Weak	Average	Weak	Weak/Average
Age 2	Weak	Strong/Average	Strong	Weak	Strong

Marine surveys typically yield data sets that are highly variable and contain a substantial proportion of zero catches, particularly when the data set is broken down into age groups (Stefansson, 1996). Thus, in some cases the data were analyzed in terms of presence and absence of pollock (hereafter termed "occurrence"). Because nonzero data often follow a lognormal distribution (Pennington, 1996), the lognormal transformations (log(CPUE+1)) of nonzero density data were used during our analyses.

Changes in the depth distribution of pollock were analyzed by 100-m bottom depth intervals, corresponding to the depth stratification used in the triennial surveys. Changes in geographic distribution of CPUE were evaluated by GOA area boundaries, which again corresponded to the stratification design used during the triennial surveys. In our study, three areas were taken into consideration: "Shumagin" (159°–170°W, area 610), "Chirikof" (154°–159°W, area 620), and "Kodiak" (147°–154° W, area 630).

The distribution of pollock in relation to distance from land was evaluated in 20 nautical mile (nmi) increments by using GIS software (ESRI, Inc., 1996). However, the 20-nmi increments crossed the triennial survey strata boundaries, which may have resulted in the disruption of the stratified random sampling scheme. By addressing pollock occurrence or density at each station, instead of biomass, we avoided the need for stratifying the data after collection. Pollock usually reside at depths less than 300 m within the shelf and slope regions of the GOA (NPFMC[5]). Thus, the relatively narrow shelf region would limit the offshore distribution of pollock.

Initial exploratory analyses involved three-dimensional contingency tables to assess the relationship between the occurrence of pollock and year, bottom depth, geographic region, and distance from land. In cases where the three-dimensional analyses rejected the null hypothesis of independence, more detailed partial contingency tables were constructed for the occurrence of pollock against each individual variable. Other studies suggested that bottom depth and geographic location explain most of the variability in fish distribution data (e.g. Overholtz and Tyler, 1985; Jay, 1996).

Single-factor ANOVAs were performed on the nonzero CPUE data to examine the sources of variation in the data. The ln(CPUE+1) of the nonzero data was used as the dependent variable among years. A separate ANOVA was calculated for each category of bottom depth, geographic region, and distance from land.

Examination of the population density data revealed that for most age groups, the number of stations with a low density (<1000 fish/km^2) of pollock increased whereas the number of high-density stations remained relatively stable. This finding suggested that the distribution of suitable habitat for the demersal fraction of the population might have been expanding. Therefore, we examined the distribution of low-density concentrations of pollock separately in relation to the three physical characteristics across the survey years. Although ocean bottom temperature (OBT) was not measured at every survey station, available data were used to help interpret our results. Mean bottom temperature was averaged over bottom depth intervals for each year to provide a general overview (Fig. 3). Additional information on OBT has been summarized by S. Hare (http://www.iphc.washington.edu/staff/hare/html/papers/OBT/obt.html) from a variety of data sources and averaged over five-year periods.

Interspecies associations were examined with Bray-Curtis clustering techniques (Boesch, 1977; Walters and McPhail, 1982). Such classification techniques are useful in generating hypotheses about community structure, which may then be used to aid management actions (Cormack, 1971). Because the surveys used in the cluster analyses were conducted during the summer months, the results could not be extrapolated to other seasons. Triennial survey data were log-transformed and clustered by using the group average fusion strategy. For the species clusters, the top thirty species by weight were chosen in addition to the four age groups of pollock. After careful evaluation of all the cluster dendrograms, a common dissimilarity level (dissimilarity coefficient (h)=27) was chosen for all years as the level at which the most clearly defined clusters occurred throughout the triennial survey years.

Diversity indices were calculated for all five survey years. The top ten species by number of fish were combined for all years to make one list of species for which diversity was analyzed. Simpson's diversity index was calculated both in terms of richness and evenness (Simpson, 1949; Tokeshi, 1993). Richness was interpreted to mean "effective number of species," whereas evenness was un-

[5] NPFMC (North Pacific Fishery Management Council). 1998. Essential fish habitat assessment report for the groundfish resources of the Gulf of Alaska region. NPFMC, 605 West 4th Avenue, Suite 306, Anchorage, AK 99501, 117 p.

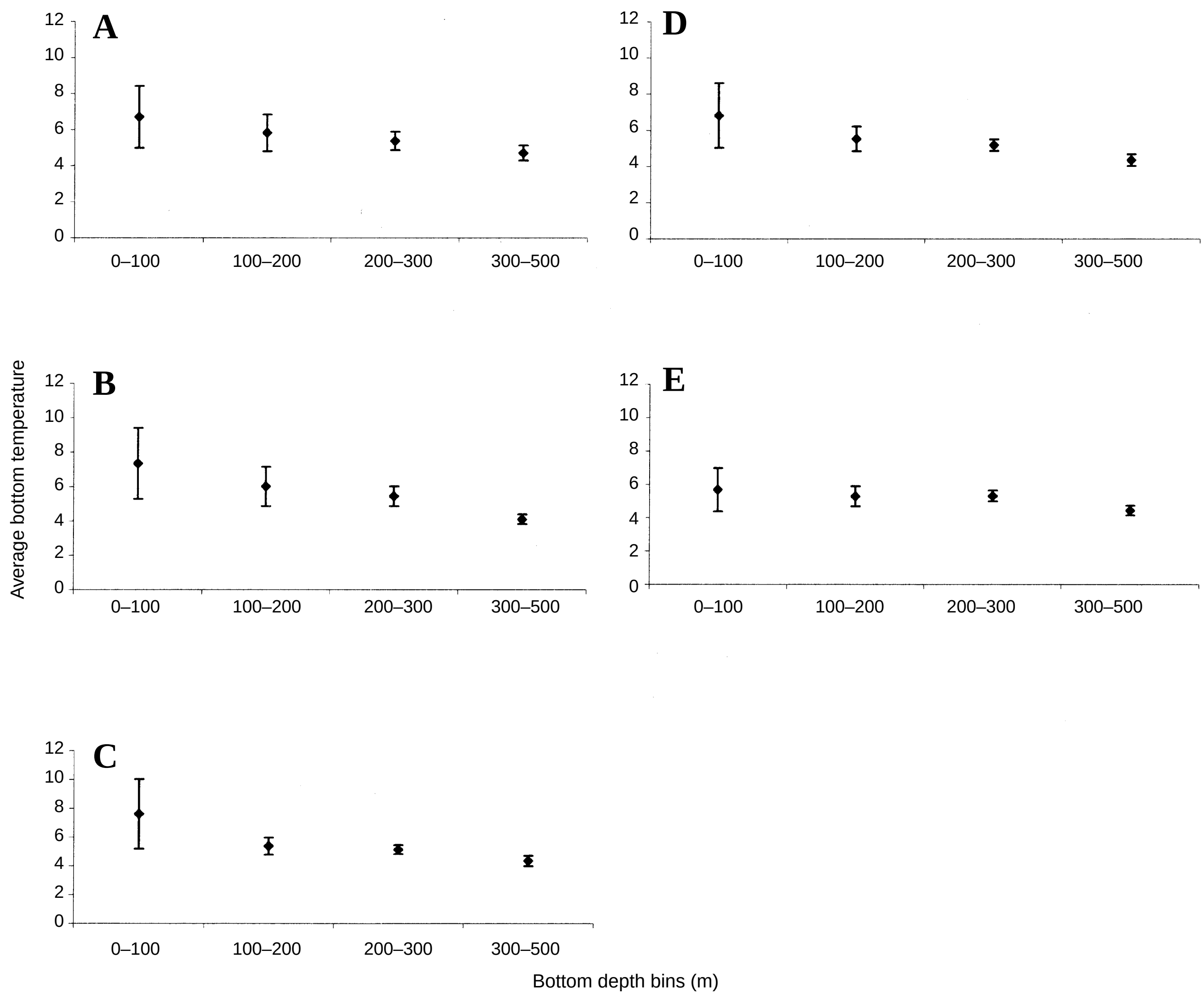

Figure 3

Average bottom temperature by bottom depth category from data collected during the triennial survey; (**A**) 1984, (**B**) 1987, (**C**) 1990, (**D**) 1993, (**E**) 1996. Error bars indicate 1 SD.

derstood to be the "distribution of numbers of fish amongst those species." Confidence intervals were calculated by jack-knifing the diversity index (Magurran, 1988).

Results

All pollock

Three-dimensional contingency tables indicated whether occurrence of pollock was mutually independent of all combinations of bottom depth, geographic region, distance from land, and year. The three-dimensional contingency tables for all three null hypotheses of mutual independence resulted in rejection of the null hypothesis (P<0.001). The null hypotheses considered for the three-dimensional and partial contingency tables are listed in Table 2. A summary of the distribution of stations within categories of the three physical characteristics is given in Table 3. All the hypotheses of partial independence on combinations of two of the physical characteristics could be rejected (P< 0.001). When each physical characteristic was tested separately, the only hypothesis that could not be rejected (α=0.05) was the independence of pollock occurrence against geographic region (P=0.097, Table 2). Graphs of pollock occurrence versus each of the physical characteristics revealed distinctive patterns (Fig. 4). The graphs indicated that pollock are most frequently observed in the 100–200 m bottom depth interval and the 0–20 nmi distance category (Fig. 4, A and B). However, this interpretation may be an artifact of the percentage of stations sampled within each category (Table 3). For all years, the greatest number of stations were sampled in the 100–200 m bottom-depth category and in the 0–20 nmi distance–from-land category.

The results were standardized by taking the proportion of stations within each category that had a positive occurrence of pollock (Fig. 5). These graphs showed that for each bottom depth category, the proportion of positive occurrences had increased over the years. The proportion of stations where pollock were present was consistently high in the 0–20 nmi category (Fig. 5). Farther from land, the proportion of positive stations increased between 1984 and 1996. In all three geographic regions, there was an increase in the proportion of stations where pollock were present.

Table 4 lists the number of hauls with pollock occurrence and summarizes the CPUE values for the nonzero data. Results from the single-factor ANOVAs calculated for the nonzero density data are summarized in Table 5. Significant differences were observed among most years, except for the Chirikof region and the distances from land of 0–20 and 40–60 nmi.

Table 2

Contingency table analysis of walleye pollock occurrence.

Type of table	*P*-value
Three-dimensional tables of mutual independence	
Null hypothesis	
Pollock occurrence, year, and bottom depth are mutually independent	$P < 0.001$
Pollock occurrence, year, and distance from land are mutually independent	$P < 0.001$
Pollock occurrence, bottom depth, and region are mutually independent	$P < 0.001$
Pollock occurrence, region, and distance from land are mutually independent	$P < 0.001$
Three-dimensional tables of partial independence	
Null hypothesis	
Pollock occurrence is independent of year and bottom depth	$P < 0.001$
Pollock occurrence is independent of year and distance from land	$P < 0.001$
Pollock occurrence is independent of bottom depth and region	$P < 0.001$
Pollock occurrence is independent of region and distance from land	$P < 0.001$
Two-dimensional tables of partial independence	
Null hypothesis	
Pollock occurrence is independent of year	$P < 0.001$
Pollock occurrence is independent of bottom depth	$P < 0.001$
Pollock occurrence is independent of region	$P=0.097$
Pollock occurrence is independent of distance from land	$P < 0.001$

Adult pollock

The initial three-dimensional contingency tables of mutual independence between adult pollock occurrence and the three physical characteristics proved significant. Subsequent contingency analyses revealed significant results for all partial independence tests except for the two-dimensional test for independence between occurrence of adult pollock and geographic region ($P=0.58$).

Examination of all the positive data showed that the mean of the log-transformed CPUE decreased and the variance increased over time for bottom depths 100–200 m in each geographic area (Table 6). The mean CPUE also decreased over time for stations <40 nmi from land but there was no trend in the changes in variance (Table 6). The ANOVA confirmed that changes in the distribution of pollock from 1984 to 1996 were significant ($\alpha=0.05$) among years at all depth intervals, all geographic areas , and at a distance from land <60 nmi (Table 7). Thus, although the number of stations where pollock could be encountered increased (e.g. the low-density distribution data), the mean adult pollock density decreased and became more variable between 1984 and 1996 (Fig. 5, Table 6).

Changes in the distribution of adult pollock were further examined by sorting the data into seven CPUE bins and by making histograms of the frequency of stations within each bin (Fig. 6). The histogram revealed that over the years, the occurrence of stations with zero adult pollock CPUE decreased, whereas stations with low-density (CPUE <1000 fish/km^2) concentrations of pollock increased. Higher density stations did not exhibit any particular trend.

To better understand observed changes in the distribution of low-density concentrations of adult pollock, all the stations were characterized by bottom depth, geographic location, and distance from land (Fig. 7). The number of stations that had low-density concentrations of adult pollock increased in all habitat categories over the years. The proportion of stations within each bottom depth bin with low-density concentrations of adult pollock more than doubled from 1990 to 1996. Comparable dramatic increases were observed with regard to distance from land and geographic region.

Juvenile pollock

Contingency table analysis for juvenile pollock occurrence resulted in significant ($P<0.001$) results across all ages for tests of mutual independence among all the physical characteristics. Two-dimensional contingency analyses also resulted in significant results. It was difficult to discern any chronological trends in the mean and variance of all the positive data for juvenile pollock. Minor fluctuations in juvenile pollock density may have been related to interannual differences in year-class strength (Table 1).

Histograms similar to those for adult pollock were made for all three juvenile age groups of pollock, where juvenile

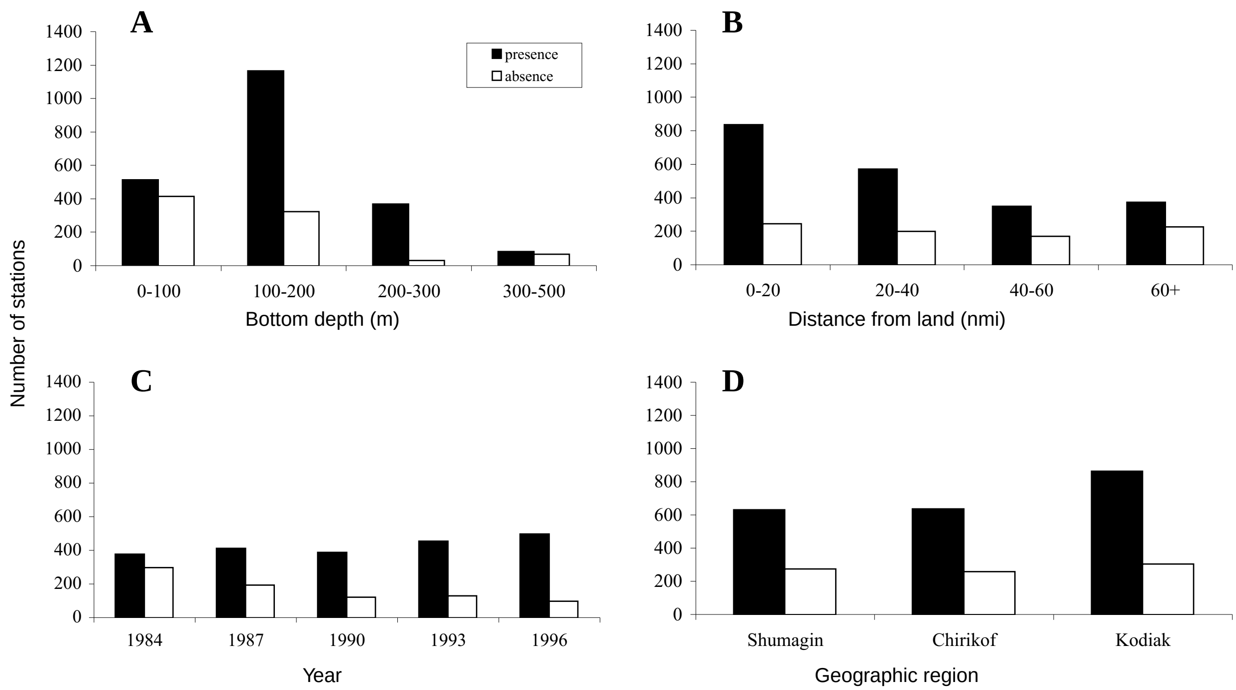

Figure 4

The number of stations at which walleye pollock occurred by physical characteristic: (**A**) bottom depth (m); (**B**) distance from land (nmi); (**C**) year; and (**D**) geographic region.

Table 3

Summary of the percentage of stations within each bin for the three types of physical parameters discussed in the text. The number in parentheses indicates the total number of stations.

	Percentage of stations in category by year				
Physical category	1984 (749)	1987 (648)	1990 (534)	1993 (616)	1996 (613)
Bottom depth (m)					
0–100	29.9	33.7	23.7	32.8	35.4
100–200	46.1	53.7	59.1	50.9	43.2
200–300	16.5	9.6	13.8	12.0	14.7
300–500	7.4	3.0	3.4	4.3	6.7
Geographic location					
Shumagin	33.2	28.5	26.7	29.3	33.7
Chirikof	27.5	32.5	30.8	29.5	30.9
Kodiak	39.3	40.0	42.5	41.2	35.4
Distance from land category (nmi)					
0–20	28.9	39.3	36.2	38.1	40.6
20–40	27.2	25.7	25.5	27.4	23.9
40–60	19.2	16.9	20.4	16.6	14.3
60+	24.7	18.1	17.9	17.8	21.1

pollock density was parsed into bins and plotted (Fig. 8). The same trend seen in the adults was also seen with the juvenile pollock. As the years progressed, there was an increase in the proportion of stations that had low-density (<1000 fish/km^2) concentrations of all juvenile age groups of pollock. For age-0 and age-1 pollock, there was about a tenfold difference in the proportion of stations with low-density concentrations after 1987 (Fig. 8). Age-2 pollock

Table 4

Summary information of walleye pollock occurrence and CPUE by triennial survey year. CPUE values are given in number of fish/km^2 and summarize only the nonzero positive tows.

	Number of hauls		CPUE			
Year	Total	Pollock present	Minimum	Maximum	Mean	SD
1984	672	375	11.48	397079.10	9759.45	31564.10
1987	603	412	13.85	602901.72	9640.16	43282.89
1990	506	386	16.77	130009.85	6866.74	15946.86
1993	583	454	19.03	218130.41	4994.91	15947.79
1996	593	497	32.22	239402.07	5434.23	18829.21

Table 5

Single-factor ANOVAs of ln(CPUE+1) of positive walleye pollock catches among years by bottom depth category, geographic region, and distance from land. SS = sum of squares; MS = mean square.

	SS	df	MS	*F*	*P*
Bottom depth (m)					
0–100	73.60	4	18.40	3.37	0.01
100–200	91.04	4	22.76	4.24	<0.001
200–300	77.22	4	19.31	6.47	<0.001
300–500	19.00	4	4.75	3.19	0.02
Geographic area					
Shumagin	84.68	4	21.17	3.94	<0.001
Chirikof	24.29	4	6.07	1.16	0.33
Kodiak	185.06	4	46.27	10.47	<0.001
Distance offshore (nmi)					
0–20	23.80	4	5.95	1.21	0.30
20–40	71.94	4	17.99	3.51	0.01
40–60	29.94	4	7.49	1.66	0.16
60+	56.66	4	14.17	3.99	<0.001

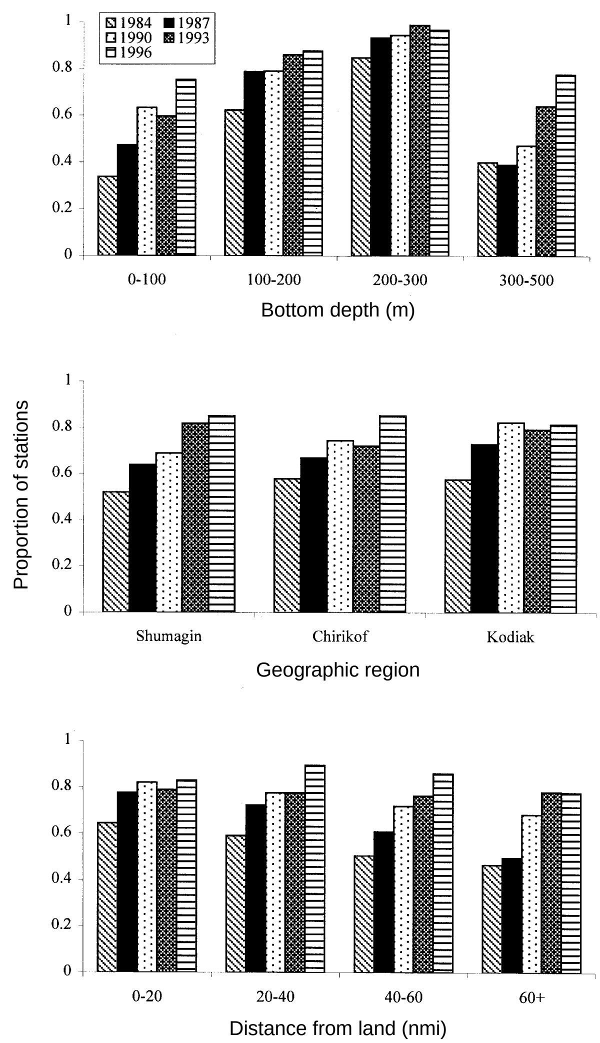

Figure 5

The proportion of stations within each category of physical characteristic where walleye pollock were found .

also exhibited this trend but not to the same degree as age-0 and age-1 pollock.

Stations with low-density concentrations of juvenile pollock were examined with respect to bottom depth, geographic area, and distance from land (Fig. 9). For all ages of juvenile pollock there was a marked difference between 1984–87 and the 1990s. A greater proportion of stations with age-0 pollock was observed at bottom depths <200 m than at deeper depths, especially in 1996. Age-0 pollock occurrence increased in the Chirikof and Shumagin regions before also increasing in the Kodiak region in 1996. Age-0 pollock also occurred more frequently at distances <60 nmi from land.

In 1990, the proportion of stations with low-density concentrations of age-1 pollock increased the most at bottom depths >200 m, before the same increasing trend was also observed at shallower bottom depths in 1993 and 1996 (Fig. 9). The increase was observed across all geographic regions and at all distances from land.

Table 6

Mean and variance estimates of ln(CPUE+1) for 1984–96 for nonzero adult pollock data by physical characteristic. The number of observations is given in parentheses.

	Mean					Variance				
Physical characteristic	1984	1987	1990	1993	1996	1984	1987	1990	1993	1996
Bottom depth (m)										
0–100	8.05 (24)	8.59 (37)	7.05 (23)	6.73 (74)	6.41 (108)	3.45	2.80	3.87	7.71	5.38
100–200	8.84 (121)	8.66 (110)	8.17 (158)	6.74 (204)	6.20 (192)	2.77	2.43	2.56	3.81	4.23
200–300	7.82 (52)	8.14 (24)	7.68 (60)	6.58 (64)	5.88 (82)	2.40	0.70	1.59	1.68	1.69
300–500	7.02 (1)	0 (1)	7.43 (1)	5.28 (12)	4.70 (30)	0	0	0	0.30	0.88
Geographic area										
Shumagin	8.80 (63)	8.45 (37)	7.40 (33)	6.63 (101)	6.32 (121)	2.65	2.35	2.30	5.54	3.72
Chirikof	8.09 (57)	8.62 (49)	7.91 (52)	6.65 (83)	5.74 (125)	3.64	2.47	2.65	3.23	3.71
Kodiak	8.47 (78)	8.62 (82)	8.22 (134)	6.91 (138)	6.42 (138)	2.53	2.23	2.50	3.94	4.21
Distance from land (nmi)										
0–20	8.49 (141)	8.67 (140)	8.04 (161)	7.02 (236)	6.40 (269)	2.90	2.15	2.76	4.42	4.28
20–40	8.50 (42)	7.76 (19)	7.59 (57)	5.79 (96)	6.12 (86)	3.57	2.33	1.93	2.75	1.36
40–60	8.16 (13)	8.66 (10)	5.31 (16)	6.23 (20)	8.00 (40)	1.88	3.46	2.20	2.52	2.24
60+	5.38 (2)	5.95 (2)	8.26 (8)	6.66 (10)	5.66 (7)	4.54	4.55	2.53	4.42	2.55

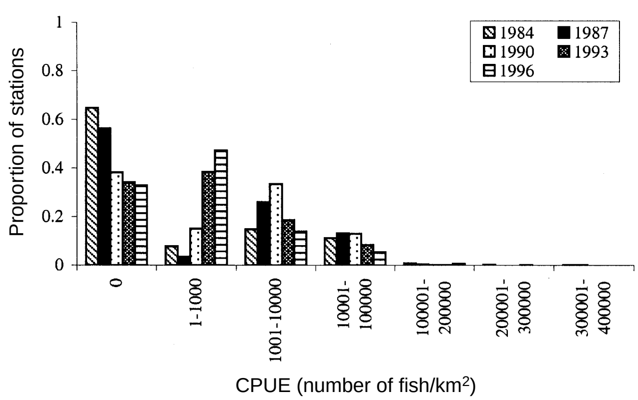

Figure 6

Porportion of stations for different density levels of adult walleye pollock.

There was a general increase over time of low-density concentrations of age-2 pollock with respect to bottom depth and geographic region (Fig. 9). The increase in the proportion of low-density concentrations of age-2 pollock was the greatest 20–60 nmi from land until 1996, when the proportion of stations with low-density concentrations increased the most >60 nmi from land.

Community composition

Results of clustering by species by using the triennial bottom trawl data are presented in Table 8. The top 30 species or species types (e.g. adult and juvenile pollock) by weight over all survey years were chosen. Adult pollock were consistently associated over the years most closely with flathead sole (Table 8). The cluster containing adult pollock usually included 3–6 other species of importance, either commercially or in terms of abundance. These included arrowtooth flounder (*Atheresthes stomias* (Jordan

Table 7

Single-factor ANOVAs of ln(CPUE+1) of positive adult walleye pollock catches among years by bottom depth category, geographic region, and distance from land. SS = sum of squares; MS = mean square.

	SS	df	MS	*F*	*P*
Bottom depth (m)					
0–100	162.23	4	40.56	7.55	<0.001
100–200	872.70	4	218.17	65.99	<0.001
200–300	196.38	4	49.09	30.76	<0.001
300–500	37.80	4	9.45	13.04	<0.001
Geographic area					
Shumagin	345.66	4	86.42	22.87	<0.001
Chirikof	448.03	4	112.01	34.19	<0.001
Kodiak	453.24	4	113.31	35.09	<0.001
Distance (nmi)					
0–20	758.52	4	189.63	53.61	<0.001
20–40	417.66	4	104.41	40.42	<0.001
40–60	174.97	4	43.74	18.59	<0.001
60+	30.82	4	7.70	2.48	0.071

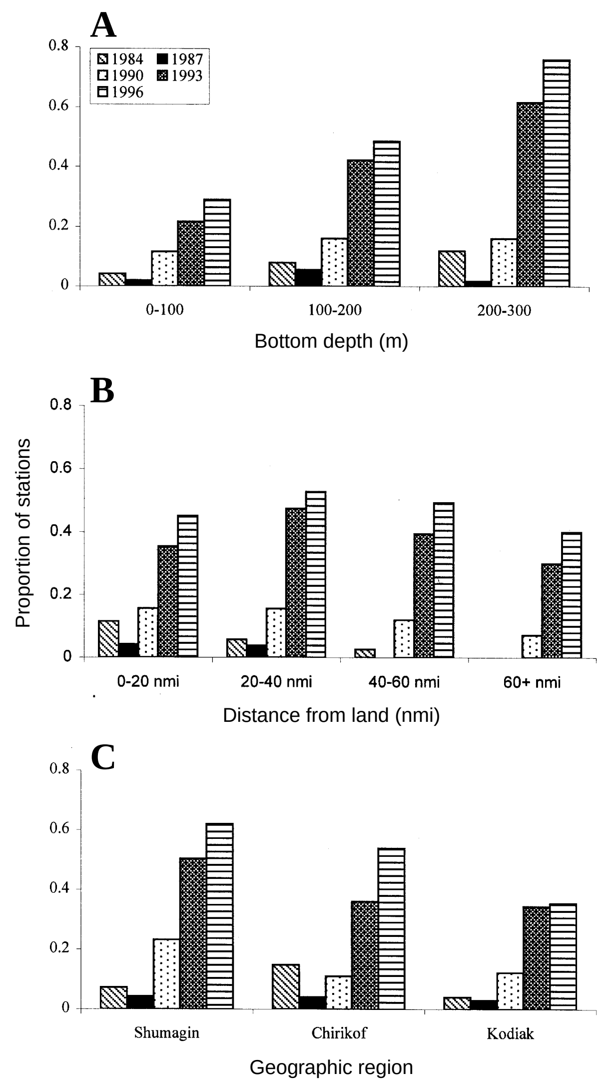

Figure 7

Proportion of stations where low-density concentrations (<1000 fish/km^2) of adult walleye pollock were observed, binned by bottom depth (**A**), distance from land (**B**), and geographic region (**C**).

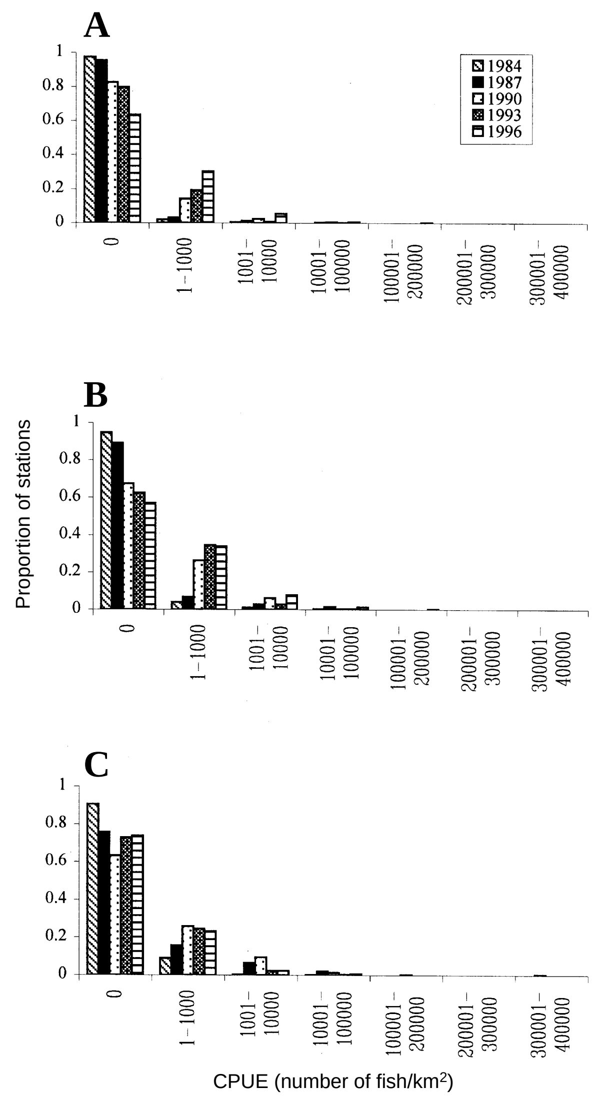

Figure 8

Proportion of stations with different levels of juvenile walleye pollock CPUE; age 0 (**A**), age 1 (**B**), and age 2 (**C**).

and Gilbert, 1880)), Pacific halibut (*Hippoglossus stenolepis* Schmidt, 1904), Pacific cod (*Gadus macrocephalus* Tilesius, 1810), sablefish (*Anoplopoma fimbria* (Pallas, 1814)), Dover sole (*Microstomus pacificus* (Lockington, 1879)), and rex sole (*Glyptocephalus zachirus* Lockington, 1879). This small cluster was usually isolated from the larger main cluster (i.e. high dissimilarity between the two clusters). Adult pollock were also clustered separately from the juvenile pollock age groups. In all years except 1987, age-1 and age-2 pollock were clustered with each other, whereas age-0 pollock were clustered separately. In 1987, age-0 and age-1 pollock clustered together, although not as closely associated as ages 1 and 2 in the other years. Until 1996, age-0 pollock clustered with Pacific sleeper shark (*Somniosus pacificus* Bigelow and Schroeder, 1944), Aleutian skate (*Bathyraja aleutica* (Gilbert, 1896)), or silvergray rockfish (*Sebastes brevispinis* (Bean, 1884)). In the larger cluster that contained all the juvenile pollock age groups, it was common to find Pacific herring (*Clupea pallasii* (Cuvier and Valenciennes, 1847)) in all years.

Cluster analysis by station of the triennial data resulted in clusters that fell into clean zoogeographic groups that followed depth contours. Maps of clusters identified seven groups of species that could be tracked in the GOA throughout most years (Table 9). Groups 1, 2, and 5 were present only in 4 out of the 5 triennial survey years. In 1984, groups 2 and 5 were absent whereas in 1990, group 1 was absent. The species within each cluster were listed in order of dominance. Although many of the clusters had

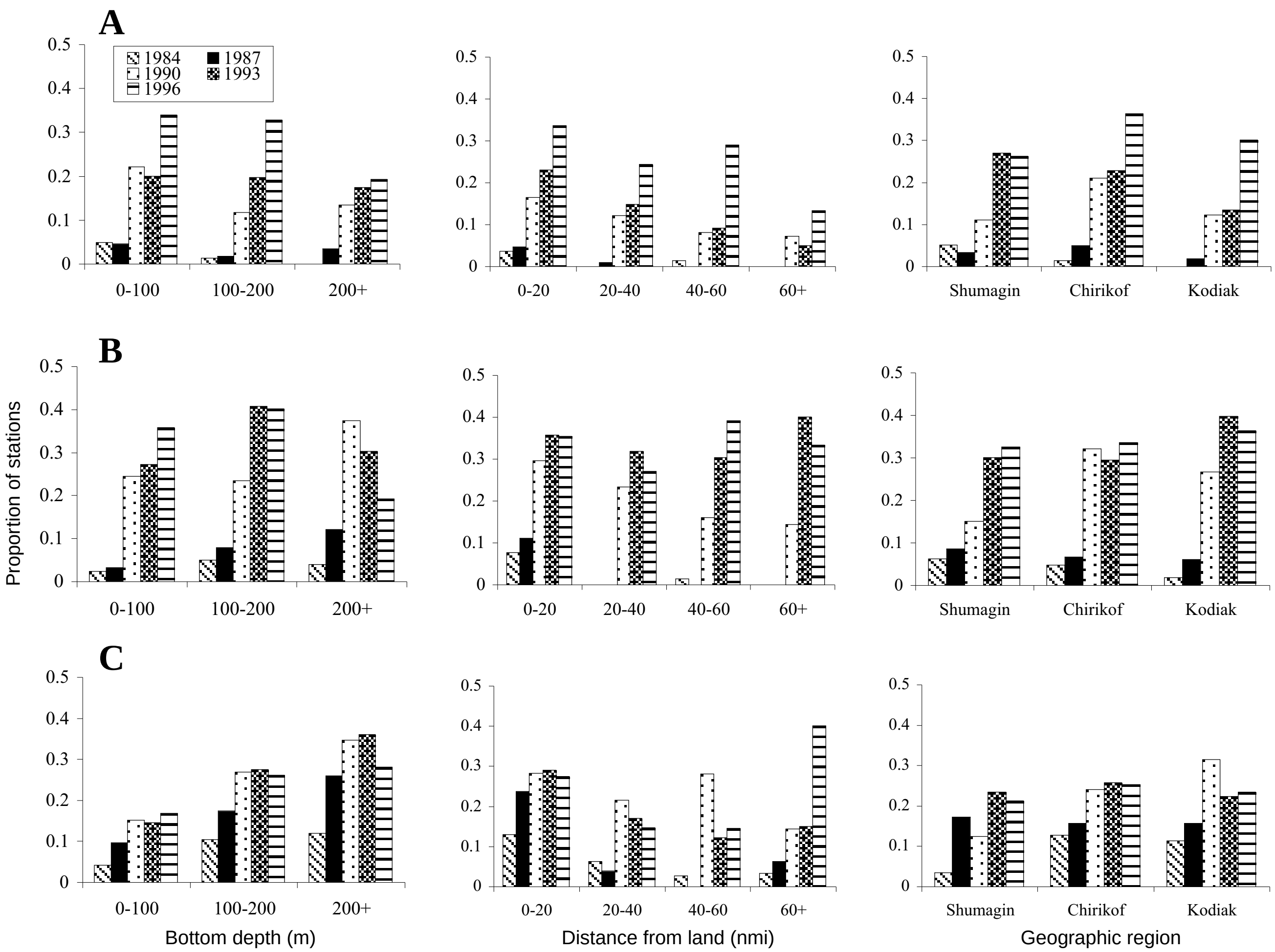

Figure 9

Proportion of stations with low-density concentrations (<1000 fish/km^2) of juvenile pollock by bottom depth (first column), distance from land (second column), and geographic region (third column) for age 0 (**A**), age 1 (**B**), and age 2 (**C**) juveniles.

the same main species in common, as listed in Table 9, differences in dominance distinguished the various clusters. Adult pollock were most dominant in groups 1, 3, and 6, which were either made up of nearshore or deep shelf stations (Table 9). Mean values of several environmental variables in these station groups in which pollock were found indicate that bottom depth and temperature varied (Table 9). Shallow water stations (groups 1 and 2) were grouped into warm (6.4°C) and average (5.7°C) bottom temperature clusters (Table 9). As expected, deeper water stations tended to be characterized by cooler temperatures. Juvenile (ages 0–2) pollock were found mostly in the nearshore stations.

Diversity

Separate diversity indices were calculated for habitat between 0–100 m bottom depth and 100–200 m bottom depth. In the 0–100 m habitat, there was a slight decrease in richness from 9–10 in the 1980s to 7–9 effective number of species in the 1990s (Fig. 10A). Calculations of evenness for the same data indicated that there had been little change in the evenness component of species diversity in the 0–100 m habitat (Fig. 10C). Histograms of the proportion (in terms of number of fish) contributed by each of the top species indicated that the decrease in richness might partially be explained by an increase in the predominance of pollock and a decrease in the presence of rockfish species (Fig. 11, A–E).

Richness in the 100–200 m category increased from 5 to 10 effective numbers of species (Fig. 10B). The predominance of pollock and arrowtooth flounder in the 1980s had shifted to include eulachon (*Thaleichthys pacificus* (Girard, 1858)) and Pacific ocean perch (*Sebastes alutus* (Gilbert, 1890); Fig. 11, F–J). Evenness was relatively consistent throughout the survey years (Fig. 10D).

Discussion

A major result of our study was that for all age groups of pollock, the number of stations where pollock occurred at low densities (<1000 fish/km^2) increased during 1984–96 while the mean density decreased. This pattern suggests that the pollock population was increasing its range, a characteristic often seen in growing populations that is consistent with the "basin hypothesis" (MacCall, 1990). MacCall hypothesized that at low-densities, marine fish will occupy habitats that are optimal for survival. As populations grow, however, some portions of the populations will expand into locations of less suitable habitat quality.

Our analyses of the data indicated that the demersal portion of the pollock population was stable but that the overall (pelagic and demersal) pollock population declined during the study (1984–96, Fig. 1, B and C). Year-class strength was only sporadically strong and therefore would not account for the sustained increased positive occurrence by station during the early- to mid-1990s. Under MacCall's hypothesis, the range of the population should have been stable or contracting. Thus, patterns emerging from our data are not entirely consistent with MacCall's model.

Analysis of CPUE of all positive tows revealed that there was a decrease in mean CPUE over the years from 1984 to 1996. The data showed an increase in low-density concentrations of adult pollock stations across all categories but in particular at bottom depths 200–300 m and in the Chirikof and Shumagin regions. We conclude that adult pollock had expanded into deeper water in the 1990s but that the expansion had resulted in a decrease of adult pollock in high-density stations, combined with decreased mean density of adult pollock throughout the region. We hypothesize that the expansion of pollock was due to an increase in the suitability of habitats for adult pollock, possibly caused by a spread in the distribution of pollock forage, during a period of stable or decreasing pollock population trends. If predators of pollock rely on high-density patches, the decreased mean density of pollock may have negative ramifications for the successful foraging of top predators. We refer to this as the "forage density hypothesis"; i.e. habitat suitability has changed, perhaps on a local scale, such that there has been an expansion of the overall population distribution. However, the expansion, combined with decreasing population numbers, had caused the density of pollock patches to decrease below a threshold at which top predators can successfully forage. The underlying assumption here is that the predators need patches of high prey density rather than a uniform distribution of average or low prey density.

Analysis of trends in the distribution and abundance of juvenile age groups is more difficult because data for

Table 8

Species associated with walleye pollock according to Bray-Curtis cluster analyses of triennial survey data. The species are listed in order of association.

Adults	Age 0	Ages 1 and 2
Flathead sole	Pacific sleeper shark	Atka mackerel
Sablefish	silvergray rockfish	eulachon
Dover sole	lingcod	Pacific herring
Rex sole	longnose skate	bigmouth sculpin
Arrowtooth flounder	sharpchin rockfish	lingcod
Pacific halibut	Pacific herring	chinook salmon
Pacific cod		

Table 9

Description of consistent station groups found as a result of cluster analyses of the triennial bottom trawl survey data. The group designation "flatfish" includes all flatfish except arrowtooth flounder. Mean values are given for the environmental variables. Standard deviations are given in parentheses.

Group no.	Location	Bottom depth (m)	SST (°C)	Temperature at depth (°C)	Main species
1	Nearshore 1	85.9 (32.1)	9.7 (2.4)	5.7 (4.9)	Age 2 and Adult pollock, Flatfish
2	Nearshore 2	83.7 (38.4)	9.4 (2.4)	6.4 (1.7)	Adult pollock, Flatfish, Pacific cod
3	Shallow shelf	119.9 (47.7)	9.0 (2.5)	5.8 (1.9)	Arrowtooth flounder, Adult pollock, Pacific halibut, Pacific cod
4	Deep shelf	120.6 (31.9)	9.5 (2.2)	5.5 (0.7)	Arrowtooth flounder, Flatfish, Pacific cod, Adult pollock
5	Inner slope	167.0 (50.3)	10.9 (2.2)	5.6 (0.8)	Northern rockfish, Pacific ocean perch, Arrowtooth flounder
6	Middle slope	197.1 (80.4)	10.1 (2.9)	5.3 (0.7)	Adult pollock, Pacific ocean perch, Arrowtooth flounder, Sablefish
7	Outer slope	412.9 (153.5)	10.7 (3.1)	4.9 (0.9)	Giant grenadier, Sablefish, Rockfish

these age groups are strongly influenced by interannual variations in year-class strength. However, spatial trends in distribution were consistent with those seen for adult pollock. For all age groups of juvenile pollock there was an increase in the proportion of stations where low densities occurred, and a decrease in the mean CPUE during the time period examined.

The spatial expansion by a species should be reconciled with more detailed analyses of the characteristics of the area it occupied to determine whether changes in habitat suitability have occurred. Adult pollock are not expanding into areas with physical characteristics previously not associated with pollock. Cluster analysis revealed that adult pollock are associated with average bottom temperatures between 5.2°C and 6.4°C. The bottom temperature data from field surveys revealed a consistent range over time of 5–6°C (Dorn et al.[6]). It was difficult to discern a trend from either our bottom temperature or the OBT data. Temperatures may have been slightly warmer in the 1980s than in the 1990s. Temperature changes, together with the shoaling of the mixed layer depth (Polovina et al., 1995; Shima, 1996), may have caused a redistribution of prey, possibly contributing to changes in pollock distribution.

Evidence of the importance of external forcing on the spatial range of fish species has been noted in other ecosystems. Movement of fish in response to environmental change was recorded in the Barents Sea when Atlantic cod (*Gadus morhua* Linnaeus, 1758) shifted westward as a consequence of cooler waters (entering from the east) across the region from 1977–81 (Loeng, 1989). Primary shifts in distribution, in response to temperature changes, were seen in younger age classes of fish. Because there were some species (e.g. haddock, *Melanogrammus aeglefinus* (Linnaeus, 1758)) that did not respond to changes in temperature, it may be that the movement of the fish may be dependent on the sensitivity of fish prey to the temperature shifts (Shevelev et al., 1987). Cod (like pollock) feed mostly on planktonic organisms that may respond rapidly to temperature changes whereas haddock feed mostly on benthic species (Shevelev et al., 1987).

External forcing may also include anthropogenic factors. Domestication (U.S.) of the pollock fishery occurred during the period investigated (Megrey, 1989) with the result that fishing operations shifted from at-sea processors

[6] Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 1999. Walleye pollock. *In* Stock assessment and fishery evaluation report for the 2000 Gulf of Alaska groundfish fishery, 65 p. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

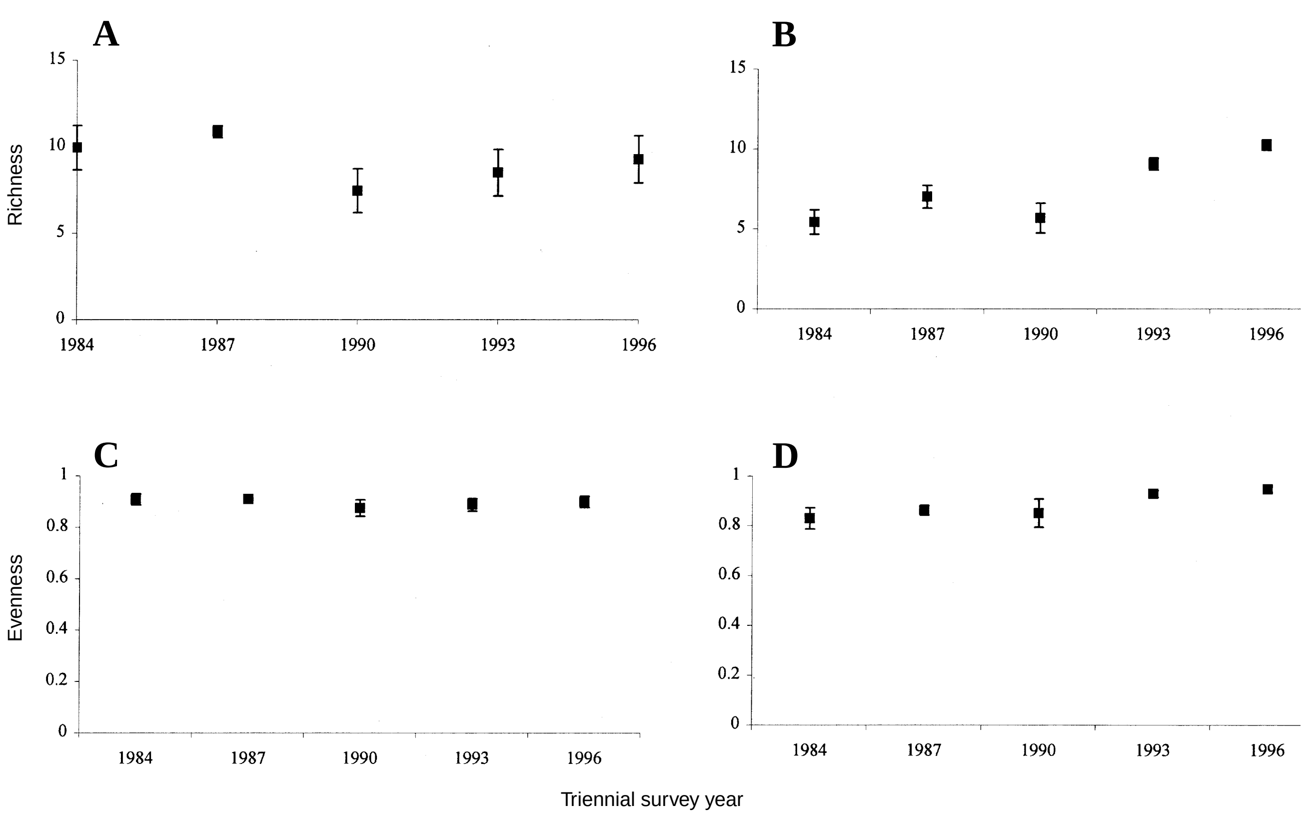

Figure 10

Simpson's diversity indices: richness for the 0–100 m bottom depth (**A**) and for the 100–200 m bottom depth (**B**); evenness for the 0–100 bottom depth (**C**) and for the 100–200 m bottom depth (**D**). Error bars indicate 1SD.

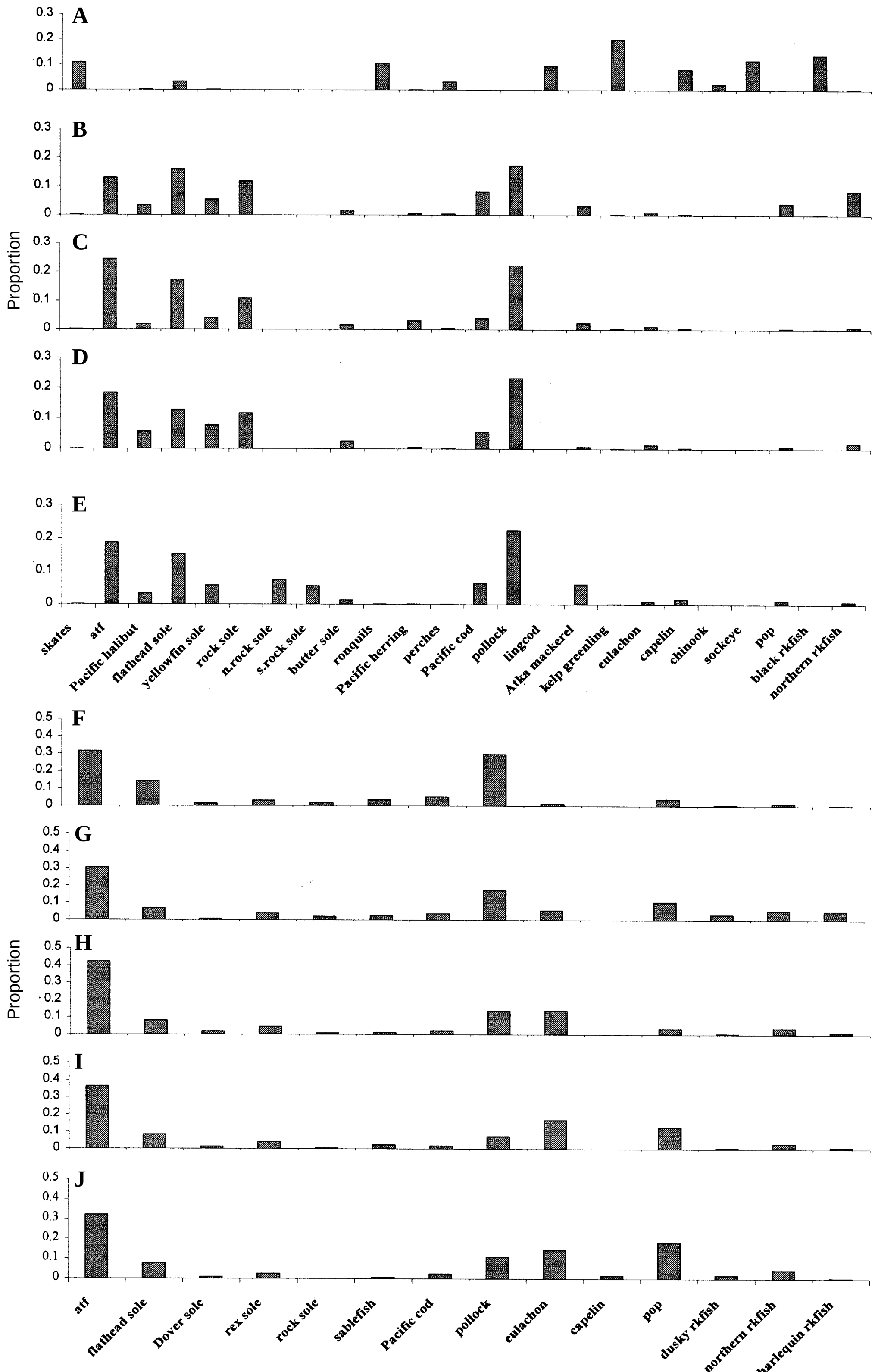

Figure 11

Proportion of the top species included in the diversity index calculations for 1984–96 in the 0–100 m bottom depth interval (**A–E**) and the 100–200 m bottom depth interval (**F–J**). Some fish species names have been abbreviated: atf = arrowtooth flounder, n. rock sole = northern rock sole, s. rock sole = southern rock sole, pop = Pacific ocean perch, rkfish = rockfish.

to a reliance on shoreside processing. The shift moved fishing operations closer to shore after the mid-1980s (Fritz[7]). Studies in other regions have found that groundfish species (Pacific whiting and haddock) disperse as a result of trawling. However, within minutes of a vessel's passage, the fish usually revert back to their original distribution (Ona and Godøø, 1990; Nunnallee[8]). It should be noted that this behavior is the result of disturbance by a single vessel. It is possible that the activity of multiple vessels that make up commercial fisheries could cause long-term redistribution of pollock. Studies are currently underway to examine the potential effect of commercial fisheries on the distribution of pollock (Hollowed et al.[9]).

Predator-prey interactions also influence the distribution of marine fish. Adult pollock are capable of exhibiting a strong top-down influence on juvenile abundance through cannibalism (Livingston, 1991). However, in the GOA the incidence of cannibalism is minimal (Yang, 1993), perhaps because, as shown in our study, the ranges of adult and juvenile pollock do not overlap. Spatial distributions showed that the bulk of both adult and juvenile pollock occurred in the Kodiak and Chirikof regions in the GOA. Mean density for both juveniles and adults was high within 20 nmi from land. However, age-0 (and often age-1) pollock were in greatest density in shallow waters <20 nmi from land, whereas adult pollock tended to occupy deeper waters. Age-2 pollock, which are beyond the size range that adult pollock target as food in the Bering Sea, tend to have a distribution similar to that of adults. The separation between juveniles and adults could be a seasonal effect due to the summer sampling season of the surveys because juvenile pollock are known to migrate ontogenetically (Brodeur and Wilson, 1996). However, the pattern of spatial separation between age-0 and age-1 pollock and adult pollock may indicate avoidance of adults by juvenile pollock.

An examination of changes in density of juvenile pollock in relation to geographic location allowed evaluation of the prevailing conceptual model for pollock ontogeny in the Gulf of Alaska (Kendall et al., 1996). The majority of spawning for the GOA stock occurs in the Shelikof Strait region (Kendall and Picquelle, 1989; Hinckley et al., 1991; Kendall et al., 1996). Survey and ocean modeling studies show that larvae and early juveniles are advected by the Alaska Current towards the Shumagin Islands (Hinckley et al., 1991; Hermann et al., 1996; Hinckley, 1999). Our results are partially consistent with the conceptual model for pollock ontogeny: the area encompassing Shelikof Strait and west to the Shumagin Islands (i.e. the Kodiak and Chirikof regions) was important for all juvenile age groups. However, the disproportionate increase of pollock in the Kodiak region in the 1990s, with two strong year classes (1988 and 1994), supports the suggestion that substantial spawning may also occur outside of Shelikof Strait (Smith et al., 1984; Brodeur and Wilson, 1996).

The species composition of the cluster in which pollock was included changed little over the course of the survey years. Adult pollock were usually located together with commercially important flatfish, arrowtooth flounder, and Pacific cod. This finding is consistent with other findings from the eastern Bering Sea where pollock often were associated with snow and Tanner crabs (*Chionoecetes* spp.), Pacific cod, flathead sole, Greenland turbot (*Reinhardtius hippoglossoides* (Gill, 1861)), and yellowfin sole (*Limanda aspera* (Pallas, 1814)) from 1978 to 1981 (Walters and McPhail, 1982).

Depth contours served as demarcations of station clusters in our study as well as in others conducted in the eastern Bering Sea and the eastern Pacific Ocean along the western coast of the United States (Gabriel and Tyler, 1980; Walters and McPhail, 1982; Jay, 1996). The consistency in how the stations were grouped together is common throughout all these studies. Walleye pollock in the eastern Bering Sea also dominated clusters of stations in the central shelf or the outer shelf. Other species commonly found together with pollock in these groups were yellowfin sole and Pacific cod.

A hypothesis relating pollock distribution to sea lion foraging behavior

Because pollock predominate the Steller sea lion diet (Merrick and Calkins, 1996), the temporal and spatial changes in pollock abundance and distribution could affect Steller sea lions. The Steller sea lion population underwent precipitous declines in the 1980s and declines continued in the 1990s but not as steep (Sease et al., 1999; NMFS[10]). The rate of decline continues to be high towards the center of the Gulf of Alaska (150–158°W), whereas the western Gulf region (158–162°W) has stabilized (i.e. the rate of decline has decreased).

Survey results suggest that the "forage density hypothesis" may apply to Steller sea lions in the GOA. There is evidence indicating that Steller sea lions target dense aggregations of prey (Sinclair and Zeppelin, in press), so that the lower mean density of pollock may reduce the number of successful Steller sea lion foraging trips in the central GOA. This effect may have prevented the sea lion population from recovering from the precipitous decline that oc-

[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. U.S. Dep. Commer., AFSC Processed Report 93-08, 162 p.

[8] Nunnallee, E. P. 1991. An investigation of the avoidance reactions of Pacific whiting (*Merluccius productus*) to demersal and midwater trawl gear. ICES C.M. 1991/B:5, 16 p. [Available from Alaska Fisheries Science Center, NMFS/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.]

[9] Hollowed, A. B., C. Wilson, M. Shima, and P. Walline. 2001. Study to determine the effect of commercial fishing on walleye pollock distribution and abundance. *In* Steller sea lion investigations, 2000 (B. S. Fadely, ed.), p. 89–104. U.S. Dep. of Commer., NOAA, NMFS, AFSC Processed Report 2001-05.

[10] NMFS (National Marine Fisheries Service). 1995. Status review of the United States Steller sea lion, *Eumetopias jubatus*, population. National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, 61 p.

curred in the 1980s. However, it is important to keep in mind that pollock are only one component of the Steller sea lion diet and that all pollock survey data are collected during the summer.

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