

# 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

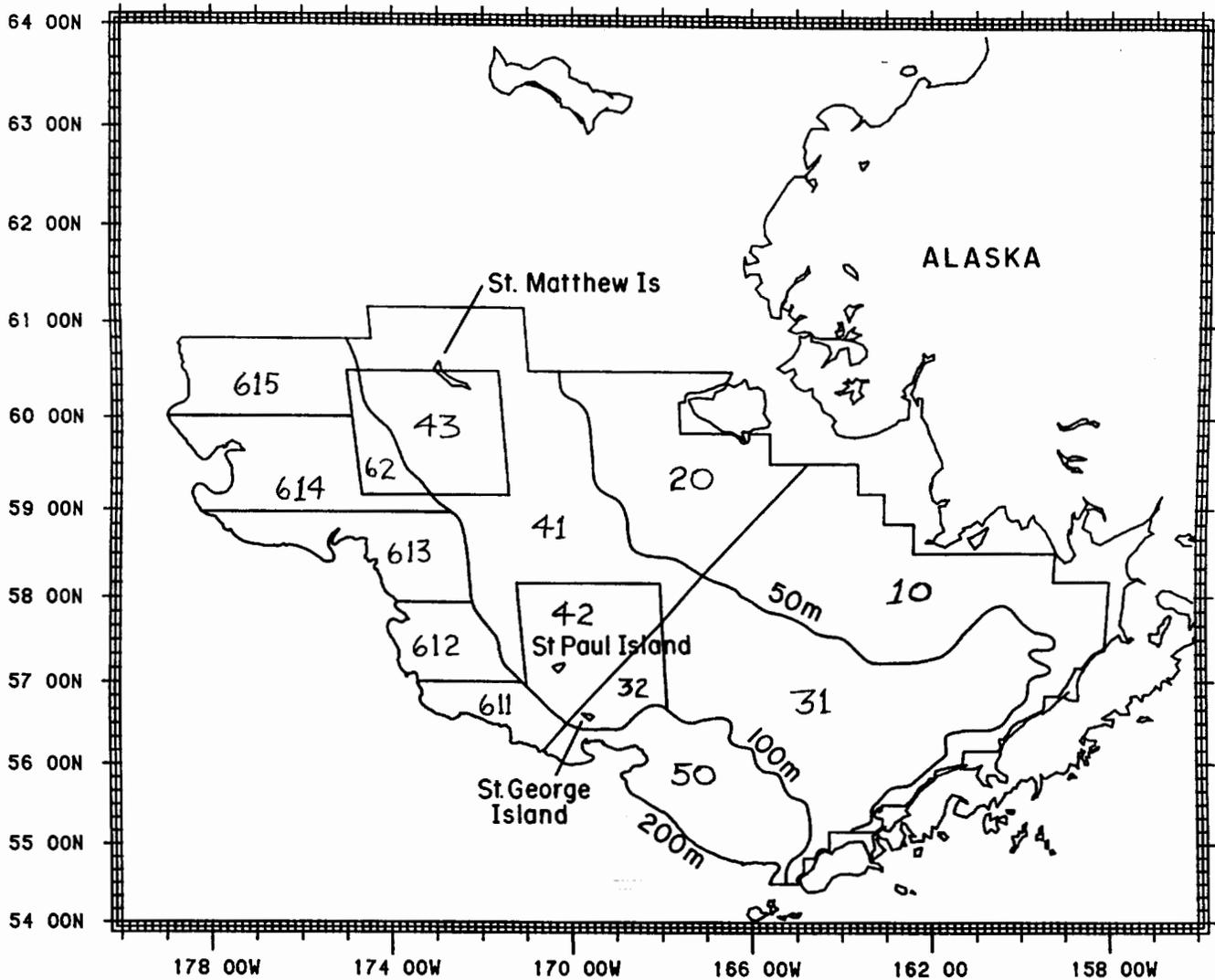


Figure 1

The eastern Bering Sea, showing St. Paul and St. George, the largest of the Pribilof Islands, and the strata (numbered segments) used for assessing 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  $\pm 4.43$  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 pres-

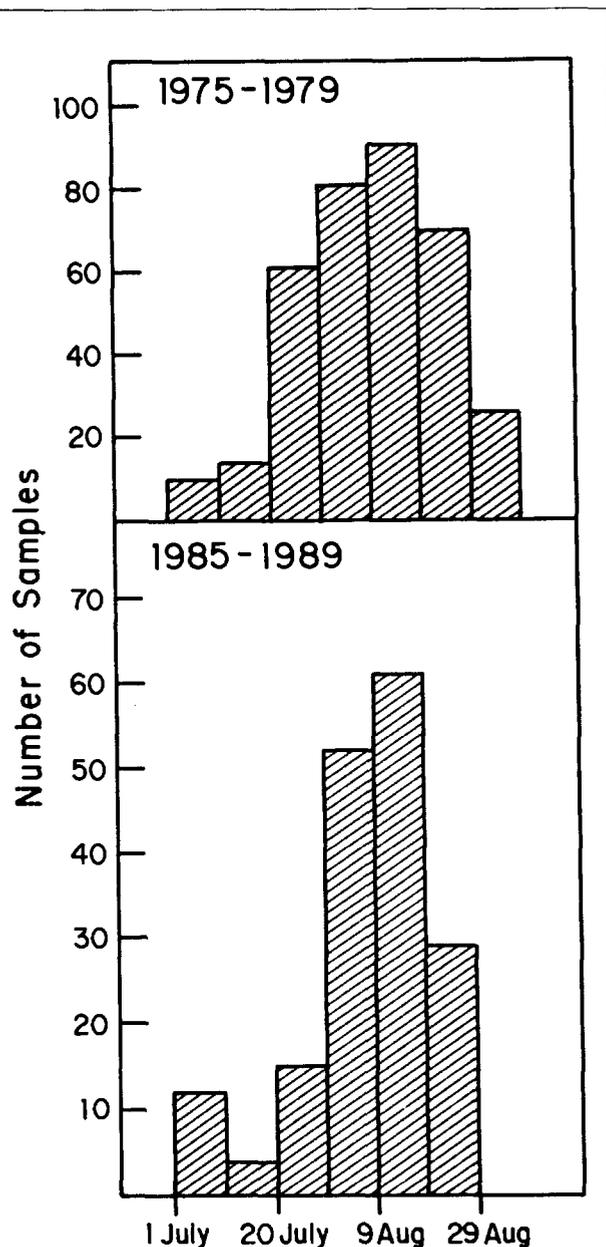


Figure 2

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

ence 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.

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	$\chi^2$	<i>p</i>
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

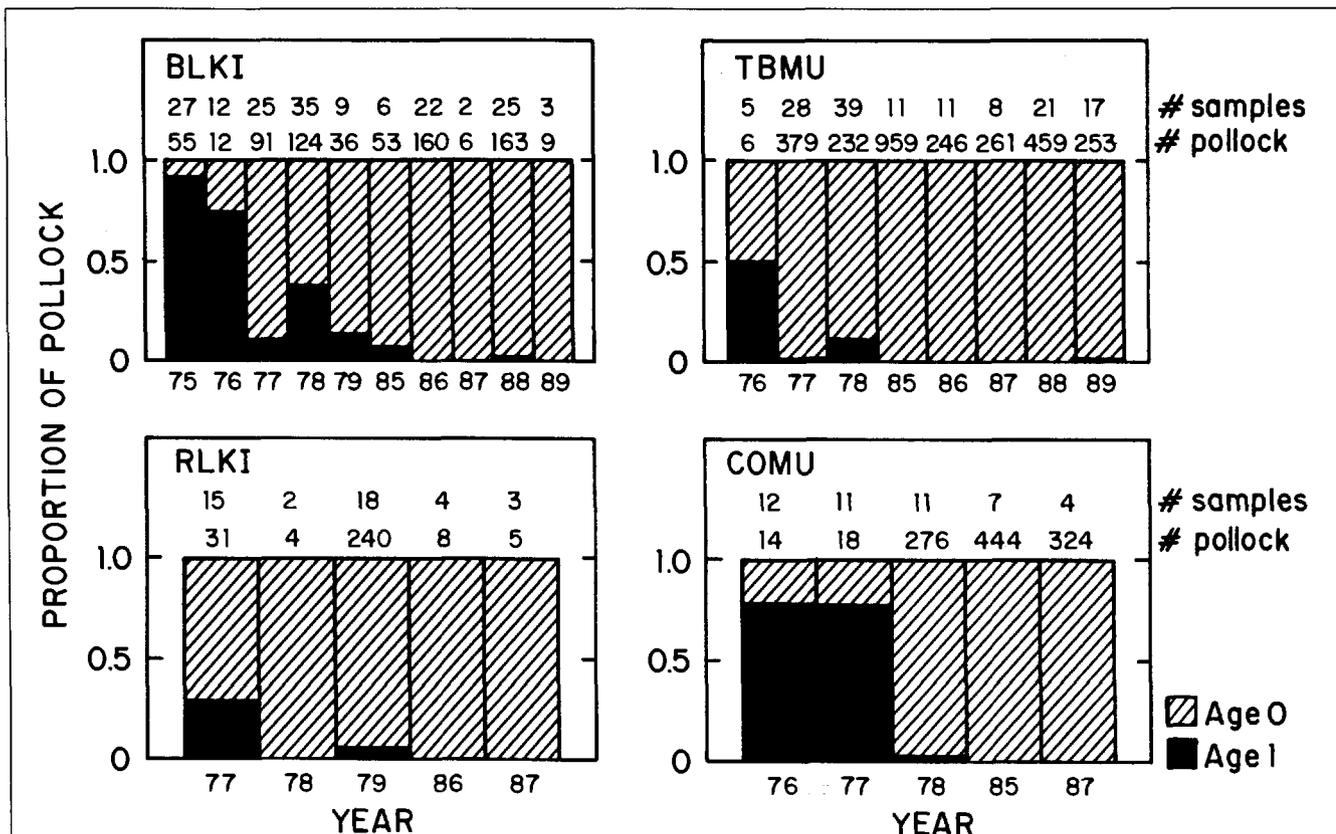


Figure 3

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

**Table 3**

Interannual variation in the size of age-0 walleye pollock as estimated from otoliths obtained from kittiwakes and murrens 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  $U=1111$ ,  $N=72$ ,  $p<0.001$ ).

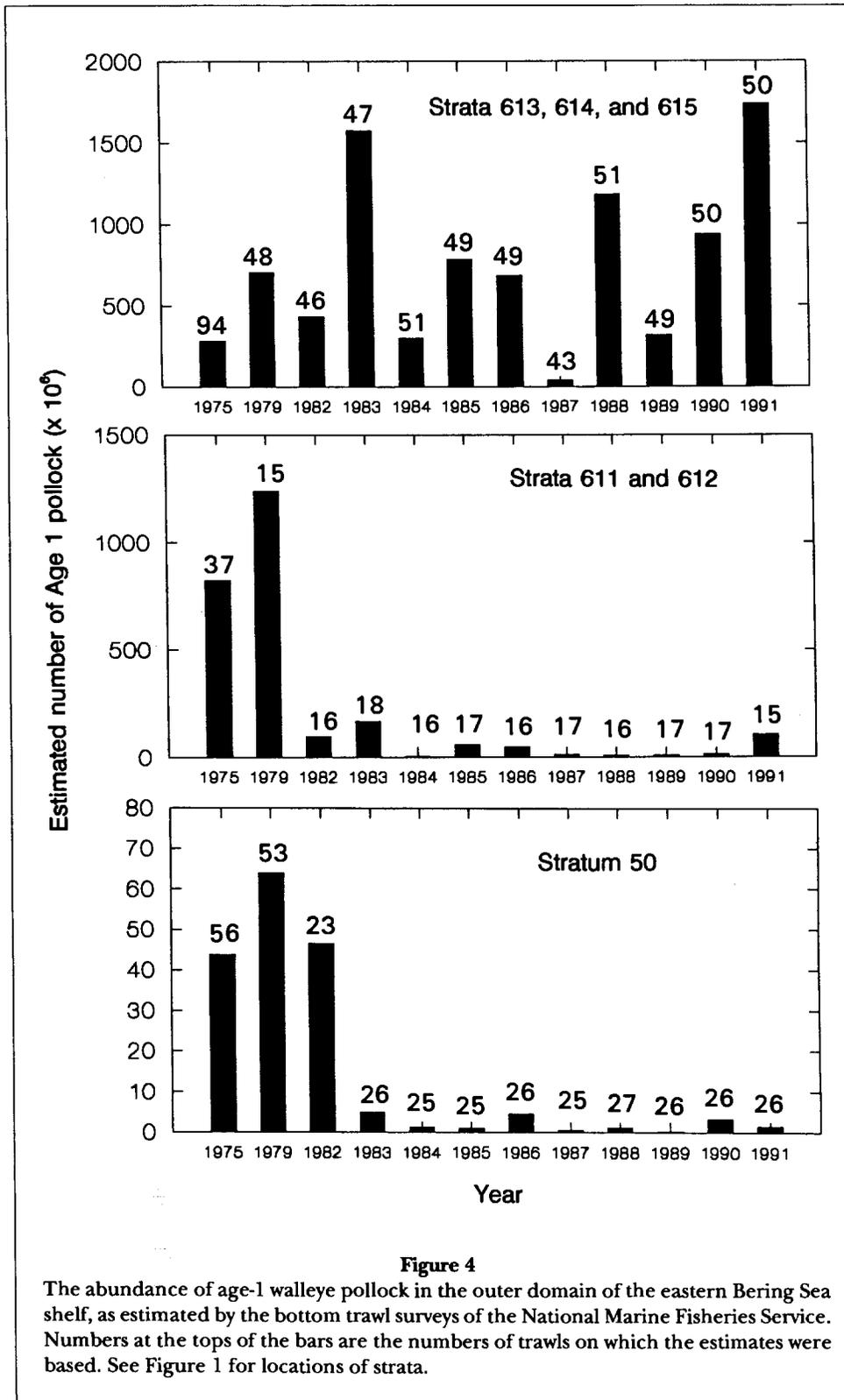
Year	# samples for which mean fish length was estimated	Mean length (mm)	± standard deviation
1976	1	35.9	
1977	13	70.2	2.15
1978	12	71.3	2.04
Total 1970's	26	69.4	7.14
1986	9	45.3	2.14
1987	2	59.7	
1988	17	66.50	3.31
1989	18	57.3	3.35
Total 1980's	46	58.4	8.26

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 ( $r=0.558$ ,  $n=7$ ,  $p=0.193$ ).

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 rela-

tion 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 num-

ber 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.

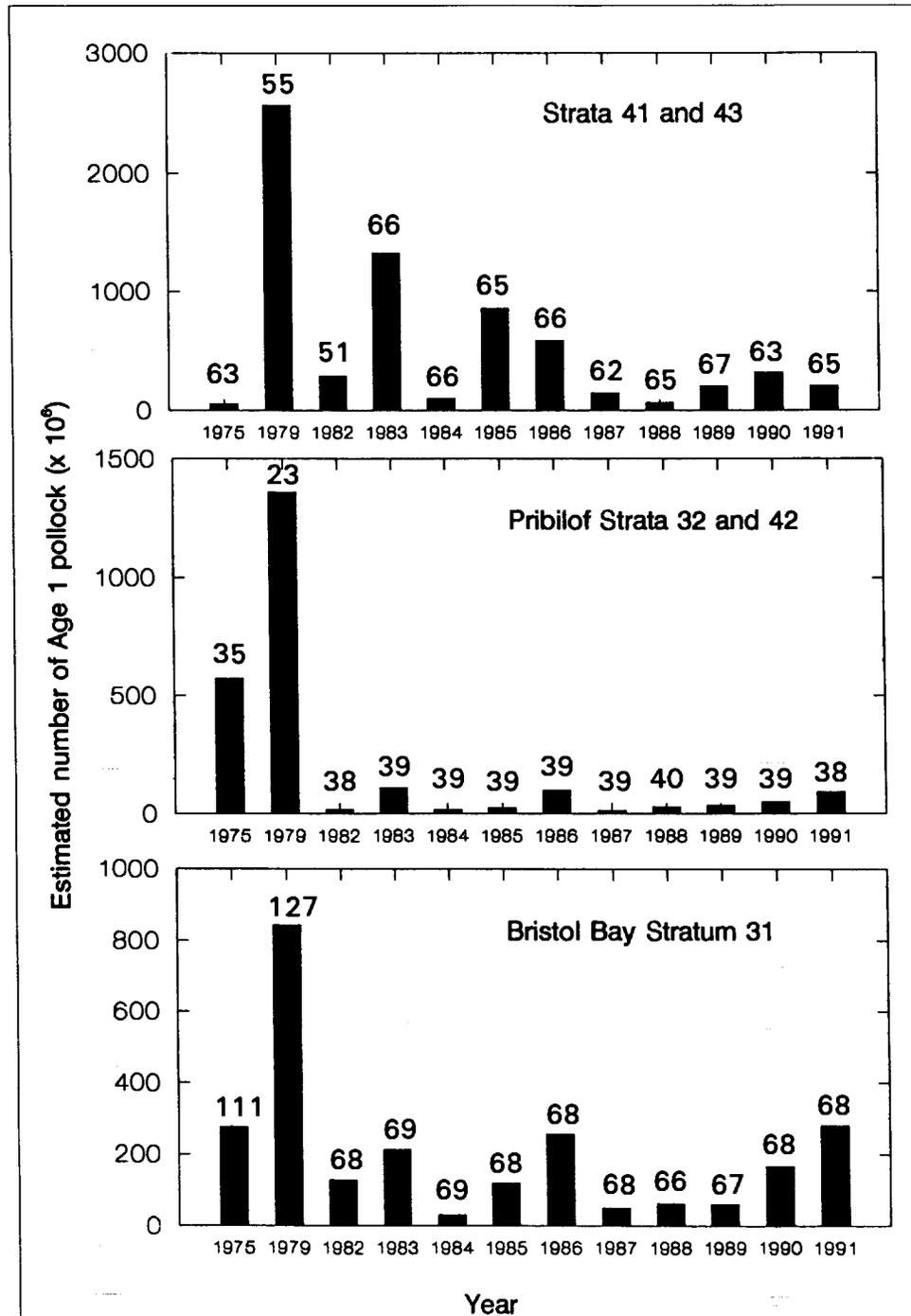


Figure 5

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.



diets of kittiwakes and murrens 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 murrens 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						
<i>Calanus marshallae</i>	85.3	73.4	21.2	0.0	4.1	0.6
<i>Neocalanus cristatus</i>	0.0	0.0	2.9	32.5	76.3	92.6
<i>Neocalanus plumchrus</i>	0.0	0.0	5.9	59.1	2.8	1.5
<i>Parathemisto libellula</i>	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 Pribilof Islands 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 medi-

ated 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<sup>1</sup>).

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<sup>2</sup>) 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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