# Seabird responses to fluctuating prey availability in the eastern Bering Sea*

Alan M. Springer[1], David G. Roseneau[2], Denby S. Lloyd[1,**], C. Peter McRoy[1] & Edward C. Murphy[3]

[1] Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99775-1080, USA
[2] FALCO, 2621 Lingonberry Lane, Fairbanks, Alaska 99709, USA
[3] Institute of Arctic Biology and Department of Biology, Fisheries and Wildlife, University of Alaska, Fairbanks, Alaska 99775-0990, USA

ABSTRACT: Walleye pollock *Theragra chalcogramma* are important prey of piscivorous seabirds at offshore breeding colonies in the southeastern Bering Sea. The reproductive success of kittiwakes *Rissa* spp. is related to the abundance of juvenile pollock. It is proposed that poor pollock recruitment in recent years, as determined by fisheries surveys, led to persistent kittiwake breeding failures in 1981–84. Declines in numbers of kittiwakes and other piscivorous seabirds at 2 colonies also may be related to the decline in pollock abundance. In contrast, planktivorous seabirds, which possibly compete with juvenile pollock for zooplankton, particularly copepods, might benefit from a low abundance of pollock. A conceptual model of food limitation and trophic interactions at several levels in the offshore pelagic food web of the eastern Bering Sea can be developed by relating relations between seabirds and their prey to (1) the high grazing efficiency of the herbivorous zooplankton community, which is dominated by large calanoid copepods, (2) estimates of a high annual loss of copepods, presumably to vertebrates, and (3) regional carbon budgets. The possibility that populations of several species respond to changes in pollock abundance should be considered in management decisions for the commercial pollock fishery.

## INTRODUCTION

The consequences of multispecies interactions in the management of commercial fisheries is a persistent and important problem with the increasing human use of key species in marine food webs (May et al. 1979, Furness 1984, Payne 1984). An important theme of the multispecies concept is that populations of marine organisms are often limited by food availability, and that changes in the numbers of one or more members of a food web can produce cascading effects at the same and other trophic levels (Payne 1984). In the Antarctic, the depletion of stocks of the large baleen whales during the early part of this century is thought to have led to a number of demographic and biological changes in populations of other whales, seals, birds

and fish, by creating a surplus of the shared resource krill *Euphausia superba* (see reviews by Gambell 1985, Laws 1985). Similar examples of interactions in zooplankton-based food webs involving whales, fish and seals in the Arctic (Frost & Lowry 1984) and fishes and squid in the subarctic (Vesin et al. 1981) have been suggested.

Energy availability to vertebrates in the pelagic food web of the eastern Bering Sea is mediated primarily by walleye pollock *Theragra chalcogramma* and calanoid copepods (Iverson et al. 1979, Cooney 1981, Springer & Roseneau 1985, Walsh & McRoy 1986). Pollock comprises about 60 % of the estimated biomass of 13 taxa of commercially important groundfish in the eastern Bering Sea and is presently the target of the largest single-species fishery in the north Pacific Ocean, with a current annual harvest of about 1 million tonnes (Bakkala et al. unpubl.). Juvenile pollock feed on zooplankton, particularly large copepods such as *Neocalanus plumchrus*, *N. cristatus*, and *Calanus marshallae* (Clarke 1978, Lee 1985, Springer et al. unpubl.

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data), as do a variety of other fishes, birds and mammals (Nemoto 1957, 1959, Adams 1979, Lee 1985, Springer & Roseneau 1985). Because of the large number of pollock, and hence their importance as secondary consumers (Walsh & McRoy 1986), it is conceivable that their food share might be sufficiently large to limit the availability of zooplankton to other planktivores. Such an effect might be most apparent during peaks in the abundance of pollock, which occur at intervals of a few years.

Among the consumers of pollock, in addition to man, are piscivorous marine birds including murres *Uria* spp. and kittiwakes *Rissa* spp., which depend on pollock to supply the dominant fraction of their energy requirements during the breeding season (Hunt et al. 1981a, this study). At the next lower level in the food web are planktivorous auklets, principally least auklets *Aethia pusilla*, which, like young pollock, feed predominantly on large calanoid copepods (see Springer & Roseneau 1985). If pollock are important to piscivorous populations as prey and to planktivorous populations as competitors, changes in their numbers should be expressed in opposite ways in the 2 trophic levels. Short and long-term changes in the breeding biology and food habits of murres, kittiwakes and auklets in the eastern Bering Sea, which we describe here, do correspond to interannual changes in the estimates of pollock recruitment and abundance. These relations, and others that have been reported

previously (see below), together suggest that energy transfer through this pelagic food web is highly efficient, and that populations of avian planktivores and piscivores are limited by the availability of prey. The data have implications on management decisions of the pollock fishery, and point to interesting areas for future research.

## METHODS

Our studies were undertaken on the Pribilof Islands in 1980–81 and on St. Matthew Island and Hall Island in 1982–83 (Fig. 1). The work on the Pribilof Is. extended that from 1975 to 1979 by Hunt et al. (1981b). Subsequent investigators worked there in 1982 (Craighead & Oppenheim 1985) and 1984 (Johnson unpubl.). We have incorporated their data on kittiwake productivity into this report, as well as unpublished 1983 observations on kittiwake productivity by A. Merculieff, a knowledgeable resident of St. George Island on the Pribilof Is. The only year in which seabird studies were made on St. Matthew I. and Hall I. prior to 1982 was 1977 (DeGange & Sowls 1978). A. Sowls and S. Morrell (unpubl. data) obtained information on kittiwake productivity there in 1982 which we have also included.

We determined kittiwake reproductive success in all years by visiting mapped nests at intervals during the breeding season and counting the numbers of active



Fig. 1. The study area in the southeastern Bering Sea

nests, eggs and chicks. We weighed kittiwake and murre chicks on the Pribilof Is. and least auklet chicks on St. Matthew I. at intervals of several days and calculated growth rates during the linear portion of the growth period.

Kittiwakes and murres were collected on St. Matthew I. as they returned to the colonies from feeding. The stomach contents were preserved in 70 % ethanol within 2 h of collection. Fish prey were counted and identified on the basis of otoliths. Invertebrates were identified from whole specimens or from hard parts, such as jaws, rostra and uropods; because invertebrates were usually fragmented and partially digested, it was generally not possible to accurately count the number of individuals. The biomass of fish prey was approximated by using regression equations relating otolith lengths to fish lengths and fish lengths to fish wet weights, or by assigning average weights for different length or age categories (see Springer et al. 1984). The equations we used for estimating the wet weights of fish taxa are:

Pollock:
$$Y = (3.175 \ X) - 9.770 \text{ for otoliths} > 10.0 \text{ mm}$$
$$Y = (2.246 \ X) - 0.510 \text{ for otoliths} \leq 10.0 \text{ mm}$$
where $Y$ = fish length in cm; $X$ = otolith length in mm, from Frost & Lowry (1981);
$$W = 0.0075 \ L^{2.977}$$
where $W$ = fish weight in g; $L$ = fish length in cm, from Pereyra et al. (1976);

Cottidae:
fish length (cm) = $4.009 \times$ otolith length (mm) $-$ 4.364,
from K. Frost & L. Lowry (unpubl. data);
log weight (g) = $-6.016 + 3.46$ log length (mm), from Craig & Haldorson (1981);

Capelin *Mallotus villosus*:
fish length (mm) = $3.42 \times$ otolith length (units) + 29.22; 12.5 units $\text{mm}^{-1}$, from Springer et al. (1984);
fish length < 80 mm: weight estimate = 5 g
80 mm < fish length < 115 mm: weight estimate = 10 g
fish length > 115 mm: weight estimate = 20 g,
from K. Pahlke, University of Alaska, Juneau (unpubl. data).

Pollock with otoliths less than 2.25 mm were assigned a weight of 0.5 g, the approximate mid-point of weights for this size class as determined by T. Nishiyama (University of Alaska, unpubl. data). The otoliths of the Pleuronectidae were all less than 2 mm and the majority were less than 1 mm in length, and the fish were assigned a weight of 0.5 g as suggested by S. Lee (University of Alaska, unpubl. data). Herring *Clupea harengus* were only partially digested and we estimated their weight at 30 g each. Limitations of this

method of analysis, particularly as it applies to the determination of quantitative dietary information, are discussed in Springer et al. (1984). Briefly, the method probably underestimates the consumed biomass of all fish, particularly that of Age 0 fishes, which have very small otoliths that are often difficult to find among prey remains and are lost from the stomachs more rapidly than the larger otoliths.

The methods of data collection and principal results of the food habits studies of least auklets on St. Matthew I. have been described elsewhere (Springer & Roseneau 1985). Here we use these published data and report additional information on interannual differences in numbers of prey recovered from least auklets during the chick-feeding period of the nesting cycle. The prey fed to the chicks are carried by the adults in sublingual pouches where very little digestion takes place, thus providing quantitative as well as qualitative samples.

Because pollock are known to be important prey of piscivorous marine birds in the southeastern Bering Sea (Hunt et al. 1981a, this study), we include recent information on pollock stock size and recruitment reported by the National Marine Fisheries Service (Bakkala et al. unpubl. data). Commercial fishery and research vessel survey data were used in the assessment of the condition of the population.
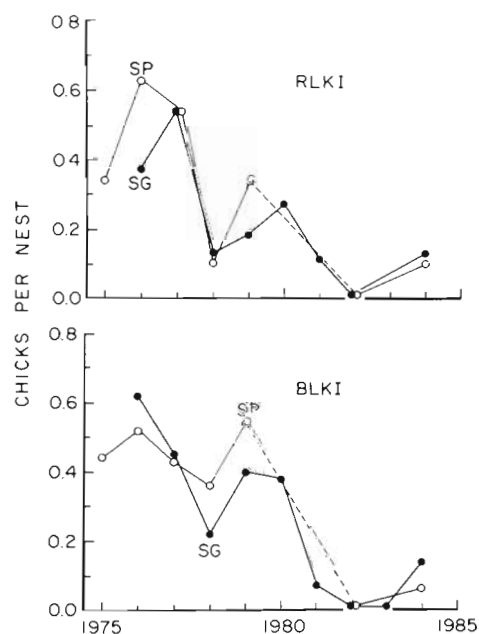


Fig. 2. *Rissa brevirostris* and *R. tridactyla*. Productivity of red-legged kittiwakes (RLKI) and black-legged kittiwakes (BLKI) on St. Paul I. (SP) and St. George I. (SG). Productivity measured as the number of young per nest. Data for 1975–79 are from Hunt et al. (1981b); 1982: Craighead & Oppenheim (1985); 1983: A. Merculieff (pers. comm.); 1984: Johnson (unpubl.)

Table 1. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) on St. Matthew I., 15 Jul to 8 Aug 1982

| | TBMU | | COMU | | BLKI | |
|---|---|---|---|---|---|---|
| | n | %[a] | n | %[a] | n | %[a] |
| Number examined | 34 | (100) | 42 | (100) | 16 | (100) |
| Number empty | 10 | (30) | 9 | (21) | 2 | (13) |
| Frequency of invertebrates | 12 | 35 | 19 | 45 | 12 | 75 |
| Frequency of fishes | 21 | 62 | 31 | 74 | 1 | 6 |
| **A. Frequency of occurrence** | | | | | | |
| *Theragra chalcogramma* | 13 | 54 | 28 | 85 | 0 | 0 |
| *Gadus macrocephalus* | 0 | 0 | 1 | 3 | 0 | 0 |
| Cottidae | 7 | 29 | 7 | 21 | 0 | 0 |
| *Mallotus villosus* | 0 | 0 | 2 | 6 | 0 | 0 |
| Pleuronectidae[b] | 6 | 25 | 20 | 61 | 1 | 7 |
| Unidentified fishes | 3 | 13 | 2 | 6 | 0 | 0 |
| Shrimps | 6 | 25 | 0 | 0 | 1 | 7 |
| Crabs | 1 | 4 | 2 | 6 | 2 | 14 |
| *Parathemisto* spp. | 3 | 13 | 5 | 15 | 1 | 7 |
| Gammaridae | 5 | 21 | 1 | 3 | 1 | 7 |
| *Thysanoessa* spp. | 0 | 0 | 2 | 6 | 2 | 14 |
| Mysidae | 1 | 2 | 1 | 1 | 0 | 0 |
| Snails | 2 | 8 | 0 | 0 | 7 | 50 |
| Squids | 0 | 0 | 0 | 0 | 1 | 7 |
| Polychaetes | 8 | 33 | 4 | 12 | 8 | 57 |
| Unidentified invertebrates | 0 | 0 | 7 | 21 | 1 | 7 |
| **B. Numbers of individuals** | | | | | | |
| *Theragra chalcogramma* | 640[c] | 68 | 464 | 71 | 0 | 0 |
| *Gadus macrocephalus* | 0 | 0 | 1 | < 1 | 0 | 0 |
| Cottidae | 31 | 3 | 8 | 1 | 0 | 0 |
| *Mallotus villosus* | 0 | 0 | 3 | < 1 | 0 | 0 |
| Pleuronectidae[b] | 266 | 28 | 169 | 26 | 1 | 100 |
| Unidentified fishes | 3 | < 1 | 4 | < 1 | 0 | 0 |
| **C. Estimated wet weight (g)** | | | | | | |
| *Theragra chalcogramma* | 536 | 63 | 1247 | 90 | 0 | 0 |
| *Gadus macrocephalus* | 0 | 0 | 5 | < 1 | 0 | 0 |
| Cottidae | 170 | 20 | 0 | 0 | 0 | 0 |
| *Mallotus villosus* | 0 | 0 | 35 | 3 | 0 | 0 |
| Pleuronectidae[b] | 133 | 16 | 85 | 6 | < 1 | 100 |
| Unidentified fishes | 6 | < 1 | 8 | < 1 | 0 | 0 |

[a] Values in parentheses are the frequency among the total number of birds examined. Values not in parentheses are the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains
[b] Tentative identification
[c] One specimen contained 400 young-of-year and a second specimen contained 209 young-of-year

## RESULTS

### Kittiwake reproductive success

The reproductive success of black-legged kittiwakes *Rissa tridactyla* and red-legged kittiwakes *R. brevirostris* on the Pribilof Is. has been very low since 1980 (Fig. 2). On St. Matthew I. and Hall I., black-legged kittiwakes produced few, if any, chicks in either 1982 or 1983; it is unlikely that more than 0.1 chicks fledged per nesting attempt in either year. Red-legged kittiwakes do not nest north of the Pribilof Is.

The low production of young has resulted from small average clutch sizes and high chick mortality. On St. George I. in 1981, clutch sizes of black-legged kittiwakes averaged 0.79, a value comparable to those during the late 1970's on the Pribilofs (Hunt et al. 1981b), although 7 chicks, at most, fledged from the 102 nesting attempts we monitored. The clutch size of kittiwakes was lower on St. Matthew I., averaging only

Table 2. Occurrence of major taxa in diets of thick-billed murres (TBMU), common murres (COMU), and black-legged kittiwakes (BLKI) on St. Matthew I., 7 Jun to 9 Aug 1983

| | TBMU | | COMU | | BLKI | |
|---|---|---|---|---|---|---|
| | n | %[a] | n | %[a] | n | %[a] |
| Number examined | 57 | (100) | 79 | (100) | 53 | (100) |
| Number empty | 5 | (9) | 4 | (5) | 3 | (6) |
| Frequency of invertebrates | 39 | 75 | 18 | 24 | 35 | 70 |
| Frequency of fishes | 37 | 71 | 71 | 95 | 21 | 42 |
| **A. Frequency of occurrence** | | | | | | |
| *Theragra chalcogramma* | 34 | 65 | 63 | 84 | 17 | 36 |
| Cottidae | 2 | 4 | 2 | 3 | 0 | 0 |
| *Mallotus villosus* | 1 | 2 | 20 | 27 | 3 | 6 |
| *Clupea harengus* | 1 | 2 | 1 | 1 | 0 | 0 |
| Pleuronectidae[b] | 15 | 29 | 24 | 32 | 0 | 0 |
| Shrimps | 1 | 2 | 2 | 3 | 1 | 2 |
| Crabs | 1 | 2 | 0 | 0 | 0 | 0 |
| *Parathemisto* spp. | 6 | 12 | 2 | 3 | 3 | 6 |
| Gammaridae | 10 | 19 | 0 | 0 | 4 | 9 |
| *Thysanoessa* spp. | 2 | 4 | 7 | 9 | 1 | 2 |
| Mysidae | 1 | 2 | 1 | 1 | 0 | 0 |
| Isopoda | 3 | 6 | 0 | 0 | 2 | 4 |
| Squids | 0 | 0 | 0 | 0 | 3 | 6 |
| Polychaetes | 8 | 15 | 1 | 1 | 12 | 26 |
| Pteropoda | 0 | 0 | 0 | 0 | 8 | 17 |
| Unidentified crustaceans | 15 | 29 | 9 | 12 | 5 | 11 |
| Mollusca | 0 | 0 | 0 | 0 | 3 | 6 |
| **B. Numbers of individuals** | | | | | | |
| *Theragra chalcogramma* | 317 | 84 | 786 | 64 | 41 | 91 |
| Cottidae | 15 | 4 | 4 | < 1 | 0 | 0 |
| *Mallotus villosus* | 2 | < 1 | 52 | 4 | 4 | 9 |
| *Clupea harengus* | 1 | < 1 | 2 | < 1 | 0 | 0 |
| Pleuronectidae[b] | 43 | 11 | 378[c] | 31 | 0 | 0 |
| **C. Estimated wet weight (g)** | | | | | | |
| *Theragra chalcogramma* | 1533 | 90 | 5773 | 83 | 388 | 80 |
| Cottidae | 75 | 4 | 7 | < 1 | 0 | 0 |
| *Mallotus villosus* | 40 | 2 | 955 | 14 | 100 | 20 |
| *Clupea harengus* | 30 | 2 | 60 | < 1 | 0 | 0 |
| Pleuronectidae[b] | 22 | 1 | 189[d] | 3 | 0 | 0 |

[a] Values in parentheses are the frequency among the total number of birds examined. Values not in parentheses are the percent frequency, numbers, or weight, respectively, among birds containing identifiable prey remains
[b] Tentative identification
[c] One specimen contained 310 young-of-year
[d] One specimen contained 155 g

0.35 in 1982 (A. Sowls & S. Morrell unpubl. data) and 0.51 in 1983. Of only 4 chicks known to have hatched prior to our departure in 1982, 3 died within a few days of hatching. By the time we departed the island in 1983, only 3 chicks remained from 117 eggs that were laid in 230 nests. As in the year before, most chicks died, generally within a week of hatching.

Red-legged kittiwakes on St. George I. fledged about 0.3 chicks per nesting attempt in 1980; in 1981 they laid about 0.4 eggs and fledged at most 0.1 chick per attempt. Reproductive success since 1981 has been low in at least 2, and probably all 3, yr. The average production during the late 1970's was about 0.38 chicks per nest (Hunt et al. 1981b).

### Murre and kittiwake prey

The prey of thick-billed murres *Uria lomvia*, common murres *U. aalge* and kittiwakes on St. Matthew I. included a variety of fishes and invertebrates (Tables 1 & 2). Invertebrates were apparently important in the
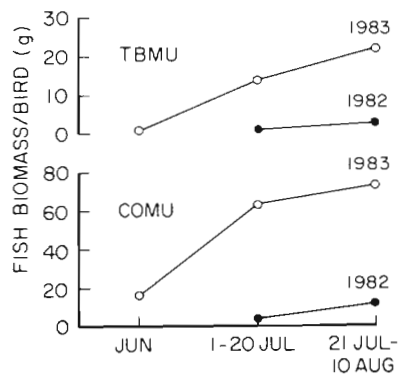
Fig. 3. *Uria lomvia* and *U. aalge.* Estimated biomass (geometric mean wet weight) of fishes in diets of thick-billed murres (TBMU) and common murres (COMU) at St. Matthew I.

Table 3. Importance of Age 0 pollock (as a proportion of all pollock) to murres and kittiwakes on St. Matthew I

| | TBMU 1982 | TBMU 1983 | COMU 1982 | COMU 1983 | BLKI 1982 | BLKI 1983 |
|---|---|---|---|---|---|---|
| Frequency | 69 | 37 | 82 | 45 | 0 | 0 |
| Number | 99 | 68 | 88 | 21 | 0 | 0 |
| Biomass | 59 | 8 | 16 | 1 | 0 | 0 |

diets, judging from their frequency of occurrence in the samples, particularly so for kittiwakes in 1982 when only 1 fish was found in 16 samples. Among the fish, pollock contributed the most biomass to murres and kittiwakes in both summers. The diets of murres and black-legged kittiwakes on the Pribilof Is. (Hunt et al. 1981a) are similar to those on St. Matthew I., in that pollock is the single most important prey species. Red-legged kittiwakes on the Pribilof Is. feed on a significant amount of fishes in the family Myctophidae in addition to pollock (Hunt et al. 1981a).

The biomass of fish, primarily pollock, in murre diets

on St. Matthew I. increased by about an order of magnitude between 1982 and 1983 (Fig. 3). Age 0 pollock were much less important in 1983 than in 1982 (Table 3), and the only other age class that contributed to the diets was the Age 1 cohort. The increase in pollock biomass in murre diets probably reflected an increase in the availability of Age 1 pollock in 1983, a conclusion supported by data on pollock recruitment discussed below.

## Murre and kittiwake growth

The growth rates of red-legged kittiwake chicks in 1980 and of black-legged kittiwake chicks and murre chicks on St. George I. in 1981 were all lower than growth rates during earlier years (Table 4) when the reproductive success of kittiwakes was higher. Positive correlations have been found between growth rates of kittiwake and murre chicks and their survival to the time they leave the nests (Hunt et al. 1981a, Springer et al. 1985a).

## Auklets

The diet of least auklets on St. Matthew I. during the chick period, mid-July to mid-August, consisted of 80 to 90 % *Calanus marshallae* (Springer & Roseneau 1985). *C. marshallae* is the dominant large copepod of the middle shelf domain of the southeastern Bering Sea (Cooney 1981, Smith & Vidal 1984).

Adult auklets carry prey from feeding areas to chicks in sublingual pouches. The average number of copepods per adult pouch load declined between 1982 and 1983 (Mann-Whitney $P < 0.001$), a change that is correlated with a similar decline (Mann-Whitney $P < 0.025$) in chick growth rates (Fig. 4). Both changes indicate that copepod abundance declined between the 2 yr.

Table 4. Growth rates of kittiwake and murre chicks on St. George I. Arithmetic mean, g $d^{-1}$ ± standard deviation (sample size). Data for 1976–1978 are from Hunt et al. (1981b)

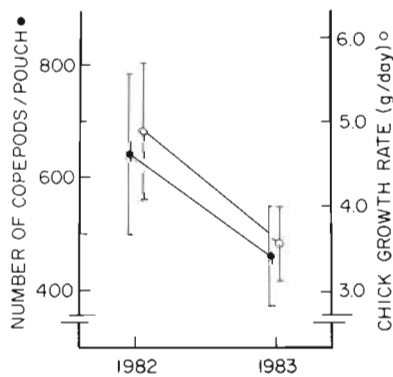| Bird species | 1976 | 1977 | 1978 | 1980 | 1981 |
|---|---|---|---|---|---|
| Black-legged kittiwake | 11.5 ± 2.6 (24) | 13.8 ± 1.8 (21) | 13.0 ± 2.2 (16) | nd | 10.3 ± 4.6 (2) |
| Red-legged kittiwake | 10.5 ± 2.1 (12) | 13.1 ± 2.3 (42) | 13.1 ± 2.2 (13) | 8.0 ± 3.5 (12) | nd |
| Common murre | 7.0 ± 2.9 (4) | 6.9 ± 1.2 (3) | 7.1 ± 3.6 (12) | nd | 4.9 ± 2.1 (5) |
| Thick-billed murre | 6.0 ± 3.0 (23) | 7.9 ± 3.2 (34) | 9.3 ± 2.2 (25) | nd | 4.5 ± 2.6 (8) |
| nd: no data | | | | | |

Fig. 4. *Aethia pusilla*. Number of *Calanus marshallae* carried by adult least auklets to chicks, and chick growth rates at St. Matthew I.

## Pollock abundance

Estimates of the numbers of Age 1 pollock in the eastern Bering Sea (Fig. 5) reveal a trend since the mid-1970's that corresponds closely with the pattern of breeding success and failure in the kittiwake populations. A sustained, moderate level of pollock abundance in the mid-1970's was associated with relatively high but declining kittiwake reproductive success; a peak in abundance in 1979 apparently resulted in somewhat improved reproductive success; and generally low levels of abundance during the 1980's have apparently been responsible for the recent reproductive failures. The smaller peak in pollock abundance in 1983 matches the increase in kittiwake clutch size and increase in pollock biomass in seabird diets on St. Matthew I. in 1983 compared to 1982.

## DISCUSSION

### Carbon budget

Thick-billed murres on St. George I. account for an estimated 84 % of the daily pollock consumption by the principal piscivorous birds species, while common murres account for another 11 % (Table 5). Approximately 77 % of the total food requirement of the murres is obtained from an area within a radius of 40 km around the island (Wiens 1984). Thus, the areal pollock requirement for the murres from this feeding area is about $250 \times 10^6$ g wet weight $d^{-1}$, or $25 \times 10^6$ g C $d^{-1}$ $\div 5 \times 10^3$ $m^2 = 5$ mg C $m^{-2}$ $d^{-1}$. Over a 120 d period, when the birds are usually consolidated at breeding colonies, they require about 0.6 g C $m^{-2}$ of pollock. This value is an order of magnitude greater than the estimated total carbon requirement of seabirds for a similar period over the outer shelf domain away from the breeding colonies (Schneider & Hunt 1982).

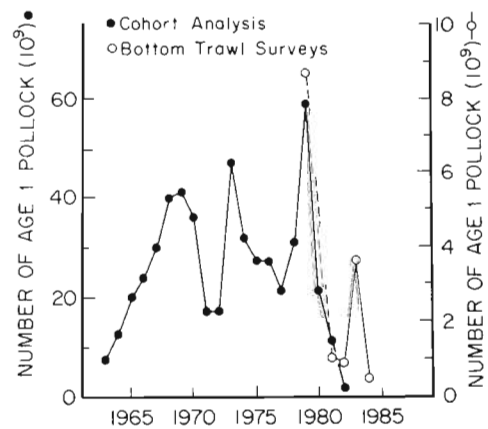Vidal & Smith (1986) estimated that the annual



Fig. 5. *Theragra chalcogramma*. Estimates of numbers of Age 1 pollock in the eastern Bering Sea. Data from Bakkala et al. (unpubl. data)

pelagic secondary production is about 30 g C $m^{-2}$ $yr^{-1}$ in the middle shelf domain and 40 g C $m^{-2}$ $yr^{-1}$ in the outer shelf domain; Cooney (1981) reported values as high as 64 g C $m^{-2}$ $yr^{-1}$ from the area of the shelf break. Approximately 15 % of the secondary production is consumed by fishes over the outer shelf (Walsh & McRoy 1986). By using a transfer efficiency of 15 % between zooplankton and fish and a growth efficiency of 30 % for juvenile pollock (Harris 1985), and by assuming that the pollock account for half of the consumption of zooplankton, they could provide about 0.7 to 1.5 g C $m^{-2}$ $yr^{-1}$ to higher trophic levels in the middle and outer domains, respectively.

From these calculations, 40 to 80 % of the pollock production would be necessary to meet the estimated pollock requirement of seabirds around St. George I. At St. Paul I., where many fewer birds nest, the energy requirement from pollock for both the murres and kittiwakes is about an order of magnitude less (Table 5), or 0.06 g C $m^{-2}$ $yr^{-1}$. At St. Matthew I. the pollock requirement is 0.26 g C $m^{-2}$ $yr^{-1}$, and because the island lies well within the middle shelf domain where secondary production is relatively low, this requirement is 37 % of the calculated pollock production. Wiens & Scott (1975) estimated that murres along the coast of Oregon consume about 11 % of the annual production of pelagic fishes in the neritic zone, while the consumption by all seabirds may be as high as 22 %. Furness (1978) estimated that seabirds consumed 29 % of the annual fish production within a radius of 45 km around Foula, Shetland Islands.

Pollock are important prey of seabirds as well as several marine mammals, particularly northern sea lions *Eumetopias jubatus* and northern fur seals *Callorhinus ursinus*. These 2 species consume an estimated $4.4 \times 10^5$ tonnes of pollock annually from the Bering Sea (McAlister unpubl.). Combined with the

Table 5. Estimates of pollock consumption by murres and kittiwakes breeding on the Pribilof Is. and St. Matthew I

| Bird species | Weight (g)[a] | St. George I. Number[b] | St. George I. % Pollock[c] | St. George I. Con-sump.[d] | St. Paul I. Number[b] | St. Paul I. % Pollock[c] | St. Paul I. Con-sump.[d] | St. Matthew & Hall Is. Number[e] | St. Matthew & Hall Is. % Pollock[c] | St. Matthew & Hall Is. Con-sump.[f] |
|---|---|---|---|---|---|---|---|---|---|---|
| Black-legged kittiwake | 450 | 72 000 | 58 | 6 | 31 000 | 58 | 2 | 70 000 | 80 | 8 |
| Red-legged kittiwake | 375 | 220 000 | 28 | 7 | 2 200 | 28 | < 1 | | | |
| Common murre | 980 | 190 000 | 71 | 40 | 39 000 | 71 | 8 | 300 000 | 87 | 76 |
| Thick-billed murre | 1 080 | 1 500 000 | 60 | 290 | 110 000 | 60 | 21 | 300 000 | 77 | 75 |
| | | | | 343 | | | 31 | | | 159 |

[a] From Hunt et al. 1981b
[b] From Hickey & Craighead 1977
[c] Percent pollock volume of diet total volume; from Hunt et al. 1981b
[d] Grams wet weight ($\times 10^{-6}$) $d^{-1}$, calculated as weight of bird $\times$ number $\times$ % pollock $\times$ food requirement (% body wt. $d^{-1}$). The food requirement of all species was set at 0.3, a conservative estimate (see Wiens & Scott 1975, Schneider & Hunt 1982)
[e] From Sowls et al. 1978
[f] This study

Table 6. Estimates of the size of the pollock population in the eastern Bering Sea. From Smith (1981) and Bakkala et al. (unpubl.)

| Region and time period | Method | Estimated population ($\times 10^{-6}$ tonnes) |
|---|---|---|
| **A. Based upon research survey data** | | |
| Eastern Bering Sea shelf, Unimak Pass to 61° N (Aug to Oct 1975) | 1 | 2.426 |
| Eastern Bering Sea shelf, Unimak Pass to 59° N (Apr to Jun 1976) | 1 | 0.679 |
| **B. Based upon commercial fisheries data** | | |
| Eastern Bering Sea shelf, INPFC Areas 1 and 2 (1969–1970) | 1 | 2.3 –2.6 |
| Eastern Bering Sea shelf, INPFC Areas 1 and 2 (1970) | 2 | 2.3 –2.4 |
| Eastern Bering Sea, primarily (INPFC Areas 1 and 2 (1964–1971) | 1 | 3.45–5.83 |
| **C. Based upon model estimates** | | |
| Eastern Bering Sea shelf (1983) | 2 | 8.8 |
| Eastern Bering Sea shelf (1983) | 3 | 9.0 |
| Eastern Bering Sea shelf (1983) | 4 | 7.9 |

Estimation methods; 1, area swept; 2, cohort analysis; 3, fishable biomass virtual population analysis; 4, catch-age analysis International North Pacific Fisheries Commission

estimated annual consumption of pollock by all sea-birds on the eastern Bering Sea shelf, about $1.4 \times 10^5$ tonnes (Hunt et al. 1981a), the total is about 50 % of the present commercial catch. The harvest of pollock by marine birds and mammals and by the commercial fishery, therefore, comes to about $1.5 \times 10^6$ tonnes annually.

Estimates of the population size of pollock in the eastern Bering Sea during the 1970's and 1980's are variable (Table 6). The annual removal by the 3 groups of consumers equals only about 20 % of the highest biomass estimate of the population based on models (Table 6C), but is a much higher percentage of the estimates made from survey and fisheries data (Table 6A,B). Based on a carbon budget for the southeast Bering Sea, Walsh & McRoy (1986) concluded that a harvest level of $1.7 \times 10^6$ tonnes removed all of the annual pollock production. Their model used a production to biomass ratio of 1 for pollock, which implies a smaller standing stock than most of the estimates based on survey and fisheries data, and considerably smaller than that based on model estimates.

The value of Walsh & McRoy (1986) was calculated on the basis of production over the outer shelf domain. However, because juvenile pollock, particularly Age 1 fish, tend during summer to migrate higher onto the shelf, into the middle domain (Smith 1981), the pollock production calculated by Walsh & McRoy probably

underestimates the actual value. Still, the combined harvest of pollock by all consumers appears to be a significant fraction of the annual production, and could lead to food limitation in this food web.

## Trophic interactions

The herbivorous zooplankton community, chiefly calanoid copepods, of the outer shelf domain consumes an estimated 42 % of the annual phytoplankton production (Walsh & McRoy 1986). This value is misleading, however, because about half of the fixed carbon each season derives from the production of *Phaeocystis pouchetti*, a non-silicous haptophyte not generally grazed by the zooplankton: the zooplankton community controls the population of diatoms such as *Thalassiosira* spp. and *Chaetoceros* spp. by consuming nearly the entire production (Kocur 1982). Because of this, annual differences in diatom production, which can vary at least 30 % between years, might account for observed variations in zooplankton production over the southeastern shelf (Sambrotto & Goering 1983).

Close coupling between diatoms and zooplankton can serve as the basis for a conceptual model of highly efficient energy transfer throughout the pelagic food web. Thus, the suggestion by Smith & Vidal (1984, 1986) that numbers of *Neocalanus plumchrus* and *N. cristatus* decline rapidly in early summer because of predation by fishes and other vertebrates can be placed in the context of such a model. Although losses from the upper water column occur seasonally as the Stage 5 copepodites begin their ontogenetic migrations to deep water off the continental shelf, the sampling by Smith & Vidal extended essentially to the bottom, which, in their opinion, provided evidence of predatory rather than migratory losses. The authors supported their conclusion by citing evidence of substantial mortality of late copepodite stages of other large-bodied copepods, which has been attributed to fish predation (see Mullin & Brooks 1970, Steele 1974).

The relations between the biology of seabirds and the abundance of pollock also fit with this model by indicating that food limits populations of avian planktivores and piscivores, and by suggesting the following trophic interactions among these taxa, the copepods and the pollock.

(1) Over the longer term, i.e. decade, the pattern of reproductive success of both kittiwake species on the Pribilof Is. matches very closely the pattern of recruitment of Age 1 pollock. Uniformly lower growth rates of kittiwake and murre chicks in the early 1980's compared to those in 1976–78 reinforces the impression that a lack of sufficient food has been responsible for the kittiwake breeding failures.

(2) Over the shorter term, i.e. between years, kit-

tiwakes and murres on St. Matthew I. consumed a much greater biomass of Age 1 pollock in 1983 than in 1982. According to the available data on pollock stocks, the recruitment of Age 1 pollock was about 3-fold greater in 1983 than in 1982. The concomitant decrease in the importance of Age 0 pollock in murre diets between the 2 yr could have been related to the relative survival of the 1981–1983 year classes. Greater food availability for the piscivorous species in 1983 could account for the increase in clutch sizes of kittiwakes that year, even though the overall reproductive success of kittiwakes remained very low. It could also account for laying dates of murres that were about 2 wk earlier in 1983 than in 1982 (Springer et al. 1985b); earlier laying by murres is also often associated with higher levels of reproductive success (Birkhead & Nettleship 1981, Murphy et al. 1986). At other colonies in northern Alaska, we have seen similarly close relations between murre and kittiwake food habits, breeding phenology and reproductive success during continuous studies over the past decade (Springer et al. 1984, 1985a,b, unpubl. data, Murphy et al. 1986).

(3) In contrast to the improvement for the piscivorous species on St. Matthew I. between 1982–1983, conditions declined for the planktivores, apparently because of a change in the availability of copepods. The number of copepods brought to least auklet chicks, which we use as a measure of copepod abundance, and the subsequent chick growth rates were both significantly lower in 1983 than in 1982. Opposite trends in populations of planktivores and piscivores would be expected if pollock are sufficiently numerous to affect copepod biomass. With all other factors remaining equal, the estimated 3-fold increase in numbers of Age 1 pollock between 1982–1983, and the consequent increase in their total food share, might account for the decline in copepod abundance; pollock brought by adult murres to chicks on St. Matthew I. had been feeding on *Calanus marshallae*, as well as on other zooplankton, fishes and amphipods.

(4) Earlier studies of the diets of seabirds on the Pribilof Is. indicated that myctophid fishes were perhaps the most important prey of red-legged kittiwakes, although they fed on pollock also (Hunt et al. 1981a). This proposed dependence on myctophids has been cited as evidence of a trophic distinction between red-legged kittiwakes and black-legged kittiwakes, which take a much greater proportion of pollock (Iverson et al. 1979, Hunt et al. 1981a). The parallel decline in the reproductive success of the 2 kittiwake species suggests either that pollock are much more important in the diet of red-legged kittiwakes than was previously thought, or that stocks of myctophids have undergone changes in abundance similar to those of pollock.

## CONCLUSIONS

Notwithstanding the higher productivity of both kittiwake species on the Pribilof Is. in 1979–80, there has been a prolonged, downward trend in productivity since 1975–76. Also, in spite of peaks in 1979 and 1983, apparently there has been a decline in pollock recruitment during the same time. Evidence of declining numbers of breeding piscivorous seabirds on the Pribilof Is. since 1976 (Craighead & Oppenheim 1985, Johnson unpubl.) could be related to this trend. The strong relation between seabird biology, on a local scale, and estimates of pollock recruitment, on a regional scale, suggests that such comparisons are valid.

The carbon budget calculations indicate that breeding seabirds on the Pribilof Is. and St. Matthew I. consume a large fraction of the pollock production. The demand on St. George I., i.e. at least 40 to 80 %, seems excessive, yet it is consistent with the suggestion that food limitation depresses reproductive performance of seabirds on St. George I. compared to St. Paul I. (Hunt et al. 1981b). Factors that would change the estimate of the potential pollock production operate in 2 directions. For example, the seasonal declines in zooplankton abundance reported by Smith & Vidal (1984, 1986) might indicate that more than 15 % of the annual secondary production is eaten, which could lead to a greater production of pollock. On the other hand, pollock might not consume as much as half of the zooplankton, which would lower the estimate of pollock production.

There is no accepted explanation of the conditions that determine year class strength in pollock (Wooster 1983, Ito 1984). Pollock broadcast large numbers of pelagic eggs (Smith 1981), and occasional years of exceptional recruitment can be important in maintaining the population. Peaks in the abundance of Age 1 fish, as occurred in 1979 and 1983, might in turn be important in maintaining seabird populations. This possibility is suggested by the substantial improvement in kittiwake reproductive success on the Pribilof Is. in 1979, and by the sharp rise in pollock biomass in murre and kittiwake diets between 1982–83 on St. Matthew I. with the associated earlier laying by murres and increase in kittiwake clutch sizes in 1983. The concomitant decrease in the number of copepods brought to auklet chicks by adults and in the chick growth rates on St. Matthew I. from 1982 to 1983 suggests trophic interactions among the members of this pelagic food web.

The commercial pollock fishery began in the mid-1960's, reached a peak in total catch in 1972, and then declined through 1976 due in part to the enactment of catch quotas and the establishment of the 200 mile Fishery Conservation Zone (Bakkala et al. unpubl.). By

1974, 2 indices of relative stock abundance, catch per unit effort (CPUE), United States method, and CPUE, International North Pacific Fisheries Commission method, had fallen 70 and 40 %, respectively, a trend that might have started as early as 1969. These declines in the CPUE are evidence of a decline in the pollock population (Bakkala et al. unpubl.). Three methods used to model pollock stocks – cohort analysis, fishable biomass virtual population analysis and catch-age analysis – all indicate a decline in pollock biomass between 1971–79 similar in magnitude to the declines evident in the CPUE data (Bakkala et al. unpubl.). The model estimates further indicate a recovery during the early 1980's, resulting in large part from the growth of the exceptionally strong 1978 year class. However, repeated years of poor recruitment, continued fisheries pressure and the uncertainty of environmental conditions are now growing causes for concern as the aging breeding stock passes through the population.

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