CHAPTER 19

Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1991

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SUMMARY

(1) Between 1975 and 1991, a complex series of changes occurred in the southeastern Bering Sea marine ecosystem. Sea surface temperatures increased from the late 1970s to the mid-1980s, and then decreased. Over the same period, there were inter-annual variations in the water masses surrounding the Pribilof Islands, as judged by zooplankton species composition. Subsequent to the mid-1970s, there were changes in the abundance of capelin *Mallotus villosus* and 1-group walleye pollock *Theragra chalcogramma* as determined by trawl samples.

(2) The use of capelin by both black-legged kittiwakes *Rissa tridactyla* and red-legged kittiwakes *R. brevirostris* decreased at the Pribilof Islands subsequent to 1978, as did the use of 1-group pollock in the late 1970s. Based on their occurrence in the diets of black-legged kittiwakes, the availability of fatty fishes such as myctophids, capelin and sandlance decreased after the late 1970s.

(3) Beginning in the late 1970s, there was a decrease in the number of chicks produced per nest for both black-legged and red-legged kittiwakes nesting on the Pribilof Islands.

(4) Inter-annual variation in the availability of fatty fish was at least in part responsible for variations in the production of chicks by red-legged and possibly by black-legged kittiwakes.

(5) We do not know why these changes in forage fish availability occurred in the vicinity of the Pribilof Islands, but they may have been related either to changes in the biomass of predatory adult pollock or to changes in the marine climate.

Key-words: Bering Sea, forage fish, Pribilof Islands, *Rissa brevirostris*, *Rissa tridactyla*, sea surface warming, seabird foraging, seabird reproduction

INTRODUCTION

Since the early 1970s, the marine ecosystems of the North Pacific Ocean and Bering Sea have undergone major changes, with sea surface temperatures increasing and then decreasing (e.g. Royer 1993). Over roughly the same period, northern sea lion *Eumetopias jubatus* populations decreased by about 80%, and over the past three decades, northern fur seal *Callorhinus ursinus* populations at the Pribilof Islands decreased by about 50%, eventually stabilizing their numbers during the 1980s (Castellini 1993). Further, harbour seal *Phoca vitulina* populations in the Kodiak region of the Gulf of Alaska decreased severely between 1976 and 1984 (Castellini 1993). Populations of black-legged kittiwakes *Rissa tridactyla*, red-legged kittiwakes *R. brevirostris*, and Brünnich's guillemots (thick-billed murres) *Uria lomvia* on the Pribilof Islands have also decreased by 22% to 54% since 1976, and the reproductive outputs of both species of kittiwakes have decreased dramatically subsequent to the late 1970s (Climo 1993, Dragoo & Sundseth 1993).

A number of hypotheses have been advanced to account for these changes in marine mammal and seabird populations (e.g. Loughlin 1987, Anon. 1993). One of these hypotheses emphasizes the role of walleye pollock *Theragra chalcogramma* and the potential effects of the pollock fishery on the marine prey base. A second set of hypotheses emphasizes the potential role of changes in the distribution and abundance of fatty fish (compared to pollock), such as herring *Clupea harengus*, capelin *Mallotus villosus*, sandlance *Ammodytes hexapterus*, and lantern fish (Myctophidae) (Alverson 1991, Anon. 1993). Springer (1992) focused on the importance of pollock as a keystone predator that may have pervasive influence on the availability of prey to upper trophic levels in the Bering Sea. In contrast, Decker *et al.* (1995) and Hunt *et al.* (in press) have investigated changes in the diets of Pribilof Islands' seabirds in relation to fluctuations in the marine climate. The present paper focuses on changes in the diets of the two species of kittiwakes breeding on the Pribilof Islands, and the possible influence that changes in the abundance and availability of species of fatty fish may have had on kittiwake reproductive ecology.

METHODS

Data on food habits of seabirds nesting at the Pribilof Islands were obtained by collecting regurgitations from nestlings when they were handled for weighing, and by shooting adults near the island early in the season before chicks had hatched. Samples were stored in 80% ethanol, and prey in samples were identified to the lowest taxon possible in the laboratory. Data on prey obtained from adult and nestling kittiwakes were combined because adults regurgitate prey carried in their foregut to young. Data on the diets of adult and nestling murres were analysed separately because adult murres provision their young with bill-loads of prey that differ from the foods that they ingest for their own use. Otoliths were measured to the nearest 0.1 mm, and pollock size-classes were determined using published regressions of fish length versus otolith size. Details on methodology are available in Hunt *et al.* (1981, in press).

MARINE SETTING

The Pribilof Islands are located near the edge of the continental shelf ('shelf-break' hereafter) of the south-eastern Bering Sea (Fig. 19.1). The waters over the shelf are divided into discrete domains separated by fronts (Iverson *et al.* 1979, Kinder & Schumacher 1981). The middle domain of the shelf is dominated by a benthic food web, and the outer domain by a pelagic food web (Iverson *et al.* 1979, Walsh & McRoy 1986). Avian use of these domains reflects these differences in

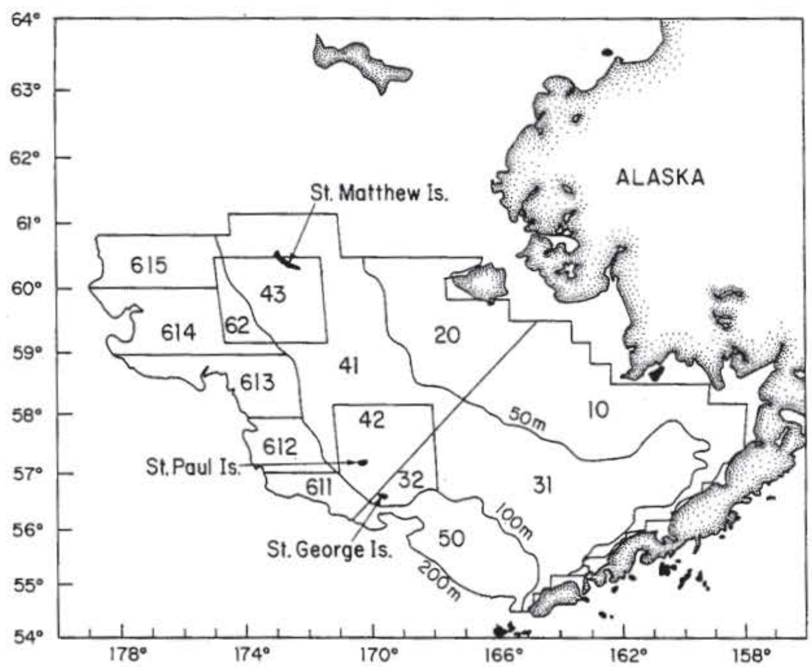

Fig. 19.1. Location of the Pribilof Islands with respect to the sampling strata used by the National Marine Fisheries Service in their bottom trawl survey of walleye pollock. The inner domain is inshore of the 50 m isobath, the middle domain between the 50 and 100 m isobaths and the outer domain between the 100 and 200 m isobaths.

food web structure (Schneider *et al.* 1986). Data from the 1970s show that the species composition of nesting seabirds and their diets on St. Paul and St. George Islands also reflect differences in the proximity of these islands to the outer domain (Hunt *et al.* 1981, Schneider & Hunt 1984).

SEA SURFACE TEMPERATURE

Sea surface temperatures vary at seasonal, annual, and longer timescales. Royer (1989) identified low-frequency fluctuations in the sea surface temperature of the northeastern North Pacific Ocean and the Bering Sea, which he estimated had a period of approximately 20 to 30 years. More recently, Miller *et al.* (1994), Trenberth & Hurrell (1994), and Royer (1993) documented a marked shift in the climate of the northeastern North Pacific Ocean characterized by a warming of surface waters in the late 1970s. In the Bering Sea, Decker *et al.* (1995) obtained monthly mean sea surface temperatures for a 5° latitude by 10° longitude grid surrounding the Pribilof Islands that encompassed a major portion of the foraging areas used by Pribilof Islands' seabirds. These data show a similar fluctuation in surface temperatures to those found by Royer (1989) (Fig. 19.2). In the early to mid-1970s, water temperatures were considerably below the long-term mean; 1977 was the first of several years of above average sea surface temperatures. From 1979 to 1983, temperatures were near or above the average, with temperatures generally shifting to below the average after 1984.

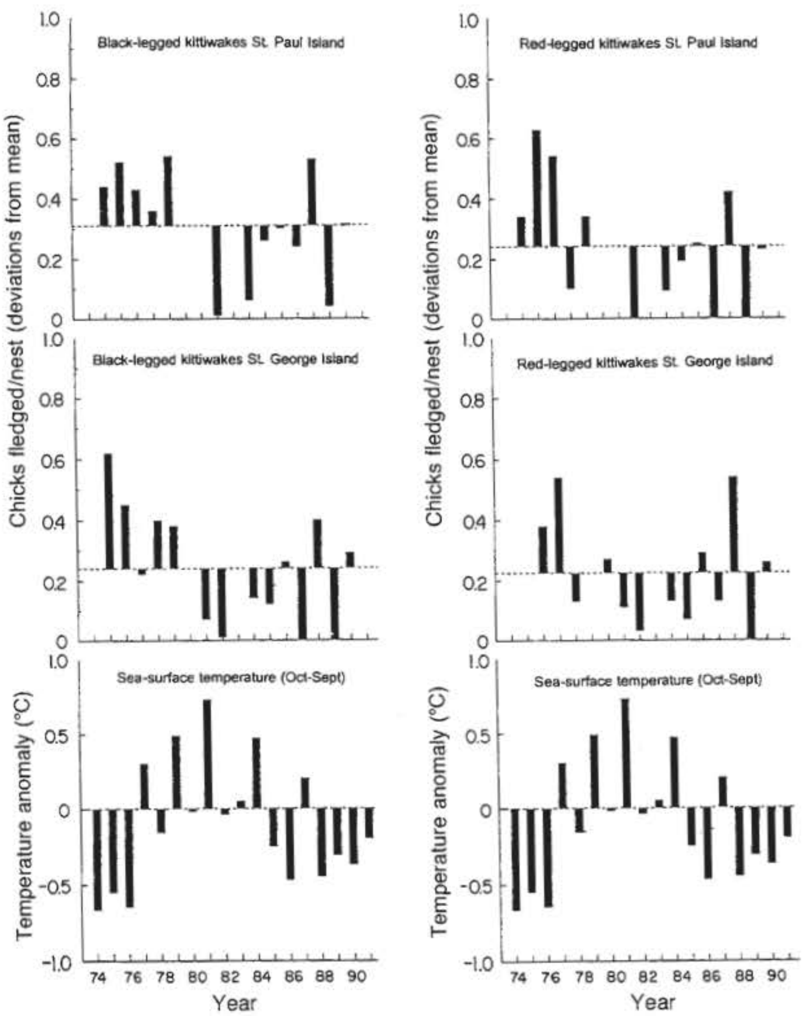

Fig. 19.2. Changes in production of young by black-legged and red-legged kittiwakes on St Paul and St. George Islands and variations in the sea surface temperature with respect to the long-term mean (1950 to 1991). After Decker *et al.* (1995), with permission.

Sea surface temperature may be a proxy variable for a variety of physical and biological changes that coincide with fluctuations in the properties of surface water. For example, Cooney & Coyle (1982) and Vidal & Smith (1986) found that in the middle domain of the Bering Sea, more of the primary production was captured in the pelagic food web during a warm-water year than in a cold-water year. The difference was determined by the rate at which the copepod grazers developed, which was temperature dependent. Similarly, atmospheric conditions that lead to sea surface warming may also displace currents and their associated fronts (T.C. Royer, personal communication), and the position of the domains may shift with respect to the Pribilof Islands. Diet data from least auklets *Aethia pusilla* show that copepod species composition varied inter-annually and support the hypothesis that St. Paul Island was within outer domain waters in 1975 and 1976, but it was surrounded by middle domain waters in 1978 and 1989 (Hunt *et al.*, in press). It is unknown if there was a long-term shift in the location of the domains subsequent to 1977, but changes in access to a particular domain or the fronts separating domains could influence the availability of prey to seabirds nesting at the Pribilof Islands.

KITTIWAKE REPRODUCTION

Both black-legged and red-legged kittiwakes showed diminished reproductive output in the 1980s as compared to the 1970s (Fig. 19.2). Reproductive output was significantly lower after 1978, but there was no significant correlation between the production of young and sea surface temperatures (Decker *et al.* 1995).

PREY AVAILABILITY

Information on the availability of prey to seabirds is difficult to obtain. In some instances, independent samples of the abundance of prey species in the vicinity of breeding colonies exist (e.g. Baird 1990, Hatch & Sanger 1992, Monaghan *et al.* 1989, in press, Wright & Bailey 1993). In the southeastern Bering Sea, National Marine Fisheries Service bottom trawl surveys provide some information on the abundance of walleye pollock and, less satisfactorily, of capelin, but these surveys do not address the question of the availability of these prey. As an alternative approach, we employed variations in the use of a prey species by a generalist predator (black-legged kittiwake) as an index of the availability of that prey relative to other prey taken. We reasoned that a generalist predator would change prey types freely with respect to their availability, and that a specialist predator, such as the red-legged kittiwake, might be slower to switch to an alternative prey when its preferred prey became less available.

During the mid-1970s, 1-group pollock were a small but important part of the diets of kittiwakes and murres on the Pribilof Islands (Hunt *et al.*, in press). Between 1979 and 1982, the numbers of 1-group pollock estimated by trawl surveys to be present in the vicinity of the Pribilof Islands and along the shelf edge to the west of the islands dropped precipitously (Hunt *et al.*, in press) (Fig. 19.3). Similarly, west and south of the

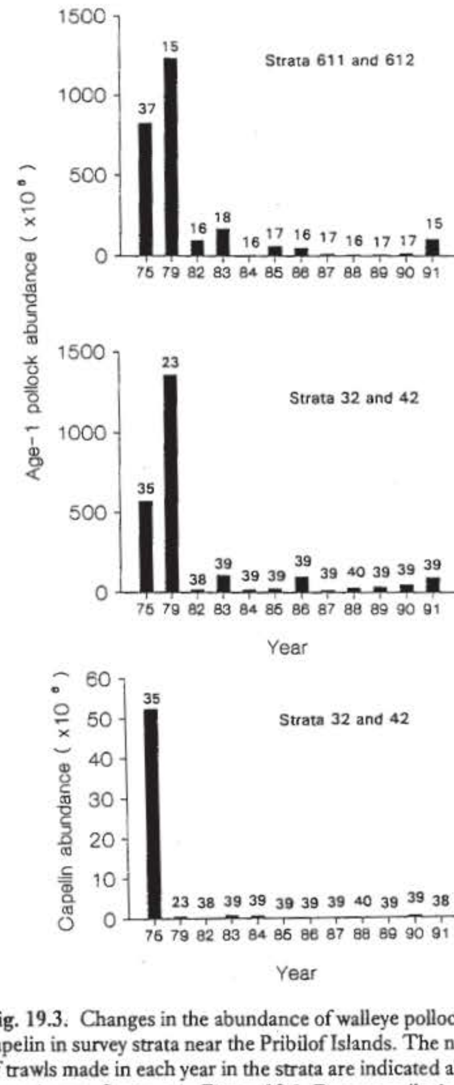

Fig. 19.3. Changes in the abundance of walleye pollock and capelin in survey strata near the Pribilof Islands. The number of trawls made in each year in the strata are indicated above the columns. Strata as in Figure 19.1. Data on pollock redrawn from Hunt *et al.* (in press), with permission.

Pribilof Islands along the shelf break, 1-group pollock numbers decreased after 1982, and remained low at least until 1991. Elsewhere on the shelf, numbers of 1-group pollock fluctuated, but showed no obvious trend, except that in most areas the unusually large 1978 year class created an obvious spike in abundance. Springer (1992) estimated population sizes for 1-group pollock for the entire eastern Bering Sea, and found no significant change in the number of 1-group pollock as a function of year when all values for the period 1973 to 1988 were used. However, there was a significant decrease when the large year classes from 1978 and 1981 were excluded. Data from both surface foraging kittiwakes and subsurface foraging guillemots breeding on the Pribilof Islands showed marked decreases in the use of 1-group pollock after the mid-1970s, with few fish of this age class taken after 1979 (Fig. 19.4). Information on the use of 1-group pollock by guillemots is included because the decrease in 1-group pollock in guillemot diets reinforces the conclusion that the change was not just in the vertical position of these fish in the water column. In sum, the available evidence shows that 1-group pollock became less available after the late 1970s, particularly in the vicinity of the Pribilof Islands. As of 1991, these fish had not returned to their former abundance near the Pribilof Islands.

During July and August, 0-group pollock are a significant component of the diets of several species of seabird breeding at the Pribilof Islands (Hunt *et al.*, in press). No measures of their abundance in the vicinity of the Pribilof Islands, independent of seabird diet samples, are available. The presence of juvenile pollock in the diets of seabirds at the Pribilof Islands decreased in the 1980s compared to the 1970s (Fig. 19.5). Most of this change is attributable to a decrease in the amount of 0-group pollock taken, as these were the principal age class of pollock taken starting in late July (Hunt *et al.* 1981).

Capelin also decreased in abundance in the vicinity of the Pribilof Islands. Limited data from the National Marine Fisheries Service bottom trawl surveys recorded many capelin near the Pribilof Islands in 1979, but few to none in subsequent years (Fig. 19.3). Similarly, capelin disappeared from the diets of both surface foraging kittiwakes and subsurface foraging Brünnich's guillemots at the Pribilof Islands after 1978 (Fig. 19.6) (see also Decker *et al.* 1995). It is not known why capelin left the vicinity of the Pribilof Islands, but it may have been in response to increasing sea water temperatures, decreases in annual sea ice extent (Fritz *et al.* 1993), or possibly competition with young pollock for prey (Springer 1992).

There are no data independent of seabirds on the abundance or availability of myctophids (lantern fish) in the vicinity of the Pribilof Islands. Myctophids are the principal prey of the primarily nocturnally-foraging red-legged kittiwake, a relatively specialized forager. They are a secondary prey of the primarily diurnally-foraging black-legged kittiwake, a relatively generalized forager, which forages for myctophids at night (Hunt *et al.* 1981, Decker *et al.* 1995). Myctophids were less used by black-legged kittiwakes on St. George Island in 1984 and 1988 than in the 1970s, although there was no apparent change in their use by red-legged kittiwakes between the decades (Fig. 19.7). We interpret these data as an indication that the availability of myctophids

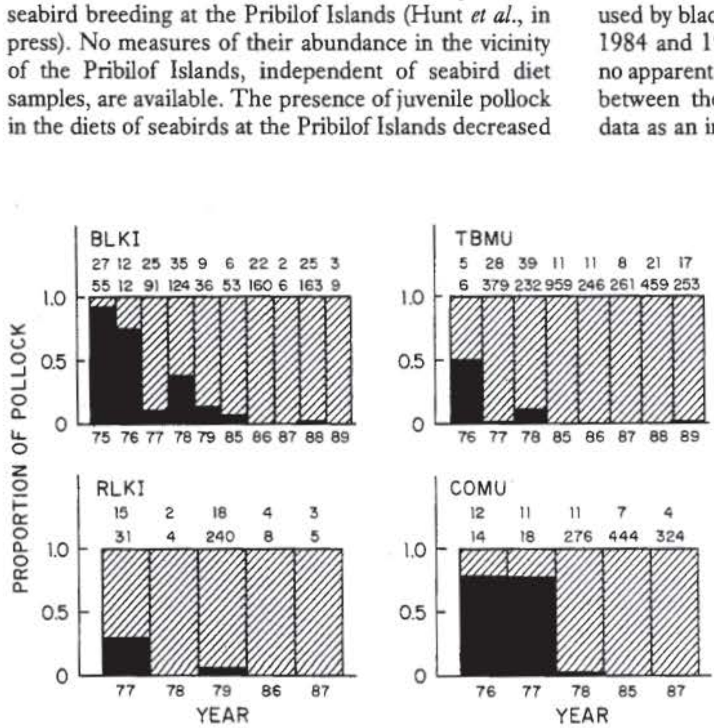

Fig. 19.4. Changes in the relative proportions of 0-group (diagonal fill) and 1-group walleye pollock (solid fill) in the diets of black-legged kittiwakes (BLKI), red-legged kittiwakes (RLKI), Brünnich's guillemots (thick-billed murres TBMU) and guillemots (common murres COMU) on the Pribilof Islands, 1975 to 1989. The top number above each column is the number of stomach samples examined; the number beneath is the number of pollock obtained from samples in a given year. From Hunt *et al.* (in press), with permission.

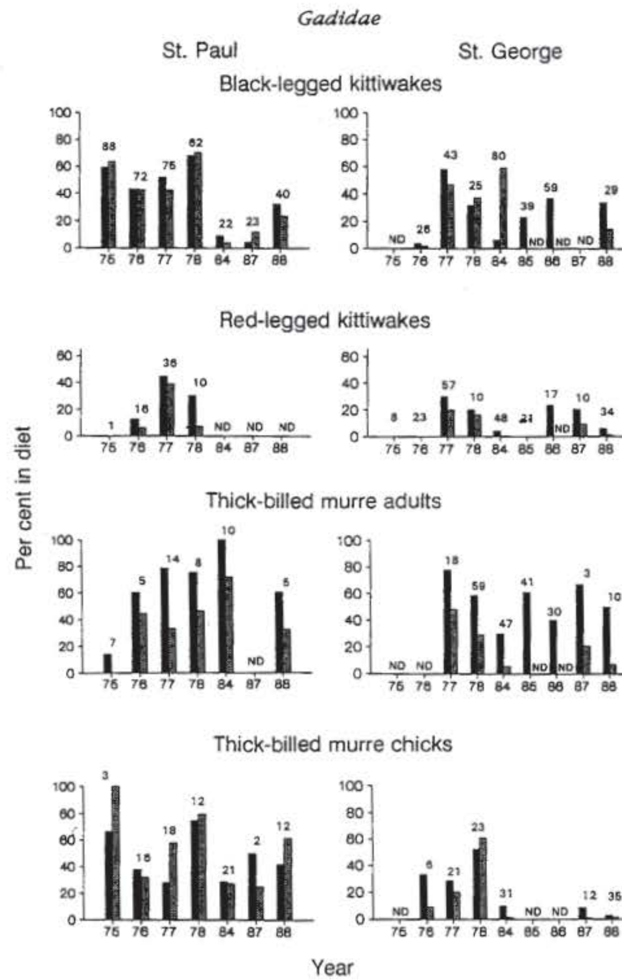

Fig. 19.5. Use of gadids, mostly walleye pollock, by kittiwakes and Brünnich's guillemots (thick-billed murres) on the Pribilof Islands. Solid filled bars represent percentage occurrence, diagonal filled bars percentage volume. Numbers at the tops of columns are the numbers of stomach samples or food loads examined. Redrawn from Decker *et al.* (1995), with permission.

decreased in the 1980s and that red-legged kittiwakes on St. George Island continued to seek myctophids, whereas black-legged kittiwakes there gave up foraging for them and turned to alternative prey in 1984 and 1988. The data from St. Paul Island are more difficult to interpret. We cannot determine, on the basis of these data alone, whether myctophids became less available to black-legged kittiwakes, or if some other prey, such as sandlance, became more available (see below). Guillemots did not use myctophids to an appreciable extent.

In contrast to the decreases in availability of some prey types, sandlance appeared to become more available in the 1980s than in the 1970s. Although there were no measures of their availability independent of seabirds, consumption of sandlance at both St. Paul and St. George Islands increased in the two seabird species, black-legged kittiwake and Brünnich's guillemots, which preyed upon them (Fig. 19.8).

PREY USE AND SEABIRD REPRODUCTIVE PERFORMANCE

Springer (1992) found negative correlations between the average annual productivity of kittiwakes on the Pribilof Islands and both the total biomass of pollock and the abundance of 1-group pollock in the eastern Bering Sea between 1976 and 1990. At a smaller spatial scale, Decker *et al.* (1995) failed to find a significant positive correlation between the annual variability in numbers of 1-group pollock in the vicinity of the Pribilof Islands and the reproductive performance of seabirds nesting there. Further, they found no significant positive

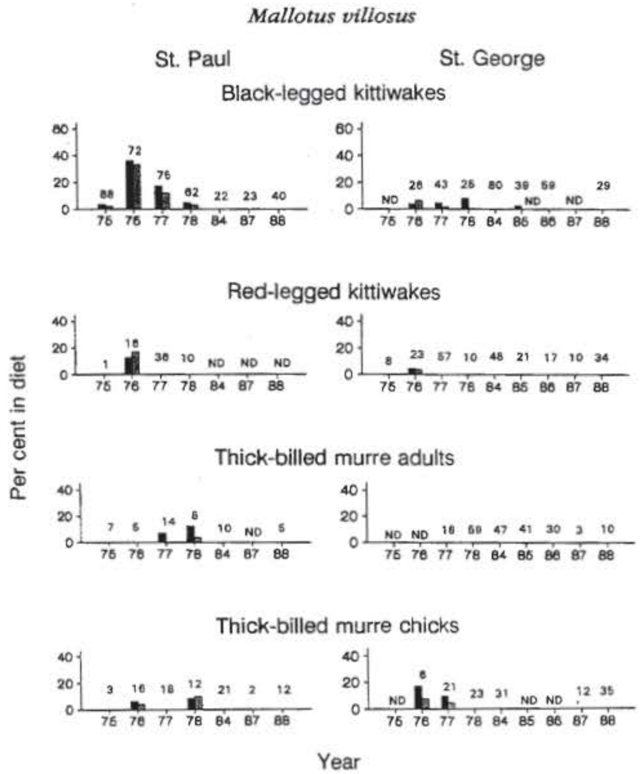

Fig. 19.6. Use of capelin by kittiwakes and Brünich's guillemots (thick-billed murres) on the Pribilof Islands. Solid filled bars represent percentage occurrence, diagonal filled bars percentage volume. Numbers at the tops of the columns are the numbers of stomach samples or bill loads examined. Redrawn from Decker *et al.* (1995), with permission.

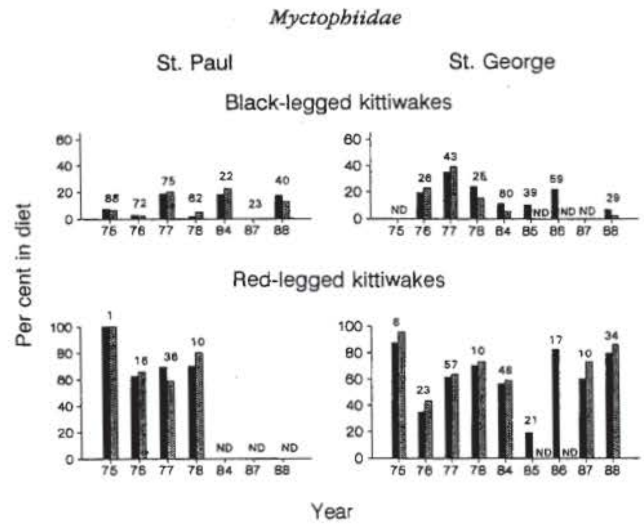

Fig. 19.7. Use of myctophids (lantern fish) by kittiwakes on the Pribilof Islands. Solid filled bars represent percentage occurrence, diagonal filled bars percentage volume. Numbers at the tops of columns are the number of stomach samples examined. Redrawn from Decker *et al.* (1995), with permission.

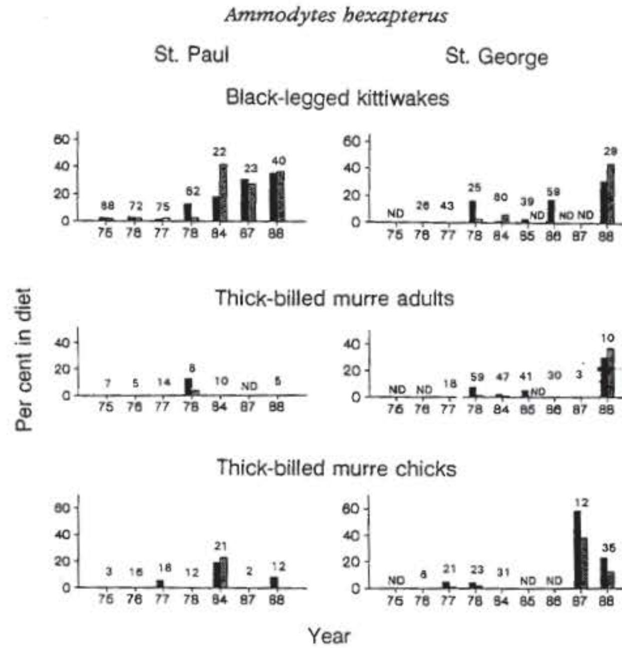

Fig. 19.8. Use of sandlance by black-legged kittiwakes and Brünnich's guillemots (thick-billed murres) on the Pribilof Islands. Solid filled bars represent percentage occurrence, diagonal filled bars percentage volume. Numbers at the tops of columns are the number of stomach samples or bill loads examined. Redrawn from Decker *et al.* (1995), with permission.

correlations between the percentage of pollock in seabird diets and reproductive success. There was, however, a significant negative relationship between the total amount of pollock in the diets of black-legged kittiwakes nesting on St. George Island and their production of young; separate examination of the role of 1-group pollock also showed no significant correlation with reproductive output (Hunt *et al.*, in press). On the basis of these findings, Hunt *et al.* concluded that variation in the abundance of walleye pollock in the vicinity of the Pribilof Islands was not the direct cause of interannual variation in seabird reproduction at the Pribilof Islands.

To examine the importance of fatty fish (myctophids, sandlance and capelin) to kittiwake reproductive performance, we compared inter-annual variation in the use of these fish to the number of chicks produced by each species of kittiwake on each island, but found no statistically significant relationships. We then examined the possibility that variations in the availability of fatty fish influenced the production of young by making the parents work harder to get these prey, even if the proportion of these fish in the diets might not correlate with reproductive output. We assumed that the proportion of fatty fish in the diets of generalist black-legged kittiwakes was an index of the availability of these fish to both species of kittiwakes at the Pribilof Islands. The proportion of fatty fish in the diets of black-legged kittiwakes on St. George Island was a significant predictor of the reproductive performance of red-legged kittiwakes on St. George Island ($r = 0.962$, $n = 5$, $p = 0.009$) (Fig. 19.9A). The use of fatty fish by black-legged kittiwakes on St. George Island also appeared to have been positively correlated with the production of young by black-legged kittiwakes on St George Island ($r = 0.639$, $n = 5$, $p = 0.246$) (Fig. 19.9B) and the production of young by red-legged kittiwakes on St. Paul Island ($r = 0.723$, $n = 5$, $p = 0.168$) (Fig. 19.9C), although these correlations were not statistically significant due to the small sample sizes involved.

Use of fatty fish by black-legged kittiwakes on St. Paul Island was not a useful predictor of either red-legged kittiwake ($r = 0.048$, $n = 7$, $p = 0.919$) or black-legged kittiwake ($r = -0.403$, $n = 6$, $p = 0.370$) reproductive performance there (Fig. 19.9D). If in the latter test the value for 1984 is removed, the strength of the relationship between use of fatty fish and reproductive performance for black-legged kittiwakes on St. Paul Island is similar to those obtained on St. George Island (Fig. 19.9B).

Fatty fish consumption by black-legged kittiwakes on St. George Island was a more useful predictor of red-legged kittiwake reproductive performance on both St. Paul and St. George Islands than was fatty fish consumption by black-legged kittiwakes on St. Paul Island. This discrepancy is probably a result of differences in

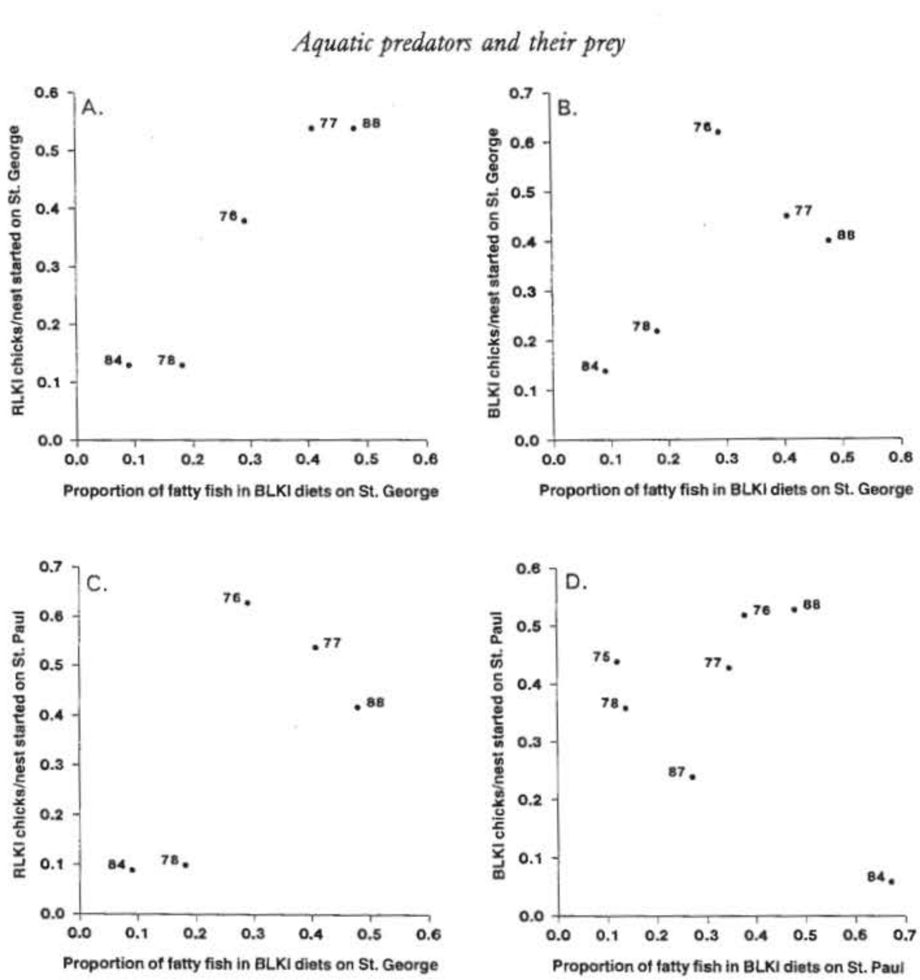

Fig. 19.9. Relationships between the proportion of fatty fish in the diets of black-legged kittiwakes (BLKI) and the production of chicks by black-legged and red-legged kittiwakes (RLKI) on the Pribilof Islands during the 1970s and 1980s. Sample sizes vary depending on the available data. The use of fatty fish by black-legged kittiwakes on St. Paul Island was not a useful predictor of the reproductive output of red-legged kittiwakes, and this relationship is not illustrated here.

the foraging areas used. Black-legged kittiwakes on St. Paul Island tend to forage north of the region used by red-legged kittiwakes from St. George Island, which forage primarily south and west of the island, often near the shelf edge (Hunt *et al.* 1981, Schneider and Hunt 1984). Red-legged kittiwakes fly south from St. Paul Island and forage in areas used by birds from St. George Island. Springer and Byrd (1989) have commented on the strong correlations between the reproductive performances of red-legged and black-legged kittiwakes on the two islands. In fact, the strongest correlation of chick production was between black-legged kittiwakes on St. George Island and red-legged kittiwakes on St. Paul Island (Pearson $r = 0.95$, $n = 12$, $p < 0.001$). We interpret these results as further evidence that the two species of kittiwakes from St. George Island and red-legged kittiwakes from St. Paul Island share a common foraging ground.

The species composition of the fatty fish taken by black-legged kittiwakes changed over the course of the study (Table 19.1). The primary fatty fish used shifted from myctophids to sandlance. This shift is compatible with the interpretation that the availability of myctophids may have decreased over the course of the study period, and could account for the relatively low level of reproduction of red-legged kittiwakes in the 1980s as compared with the 1970s (Decker *et al.* 1995). The year 1988 was an exception to the rest of the 1980s; both red-legged and black-legged kittiwakes took myctophids (Fig. 19.7), and both kittiwake species reproduced

Table 19.1. Principal types of fatty fish used by black-legged kittiwakes breeding on the Pribilof Islands, by percent volume.

Year	St. Paul Island		St. George Island	
	Fatty fish	% by vol.	Fatty fish	% by vol.
1975	Myctophids	8.0	No data	
	Capelin	2.4		
1976	Capelin	33.4	Myctophids	22.7
	Myctophids	2.4	Capelin	6.3
1977	Myctophids	20.3	Myctophids	39.2
	Capelin	11.8	Capelin	1.6
1978	Sandlance	5.6	Myctophids	15.3
	Myctophids	5.2	Sandlance	2.6
1984	Sandlance	44.2	Sandlance	8.6
	Myctophids	20.9	Myctophids	0.4
1987	Sandlance	27.3	No data	
1988	Sandlance	36.3	Sandlance	43.8
	Myctophids	12.7	Myctophids	2.3

successfully (Decker *et al.* 1995) (Figs 19.5 and 19.6). Although the availability of sandlance may have increased, they were not taken by red-legged kittiwakes.

DISCUSSION

This paper presents evidence that changes in access to fatty fishes may have played a more important role in the decrease in the reproductive output of kittiwakes on the Pribilof Islands than did changes in the availability of juvenile pollock. Other authors have suggested that because fatty fish are higher in energy content than pollock, a decrease in the availability of fatty fish could have resulted in decreases in seabird populations (Springer 1992, Anon. 1993). Similar arguments have been proposed to explain the decreases in fur seals and northern sea lions, and limited data support this hypothesis (e.g. Alverson 1991).

It is not clear why changes in the use by black-legged kittiwakes on St. George Island of all species of fatty fish combined should be a better predictor of red-legged kittiwake reproductive output on the Pribilof Islands than black-legged kittiwake use of myctophids. The principal fatty fish used by black-legged kittiwakes was sandlance, whereas red-legged kittiwakes, that specialize on myctophids, did not use sandlance. The most likely explanation is that conditions in the upper water column that draw foraging myctophids to the surface also are favourable for sandlance foraging. For example, in years with cool surface waters, copepod development may be slowed (Vidal & Smith 1986), and it is possible that larger numbers of copepods and other fish prey remain at the surface late into the summer as compared to years with warmer water. In the California Current, Roemmich and McGowan (1995) found a long-term negative relationship between sea surface warming and zooplankton biomass. They hypothesized that the 80% decline in zooplankton stocks was the result of decreased vertical flux of nutrients depressing primary production. Whatever the mechanism, it seems likely that the connection between the two species of kittiwakes involves not only their joint use of myctophids, but also a connection mediated by a broad variation in the foraging conditions experienced by their shared prey.

Although evidence from trawl surveys corroborates data from kittiwakes that 1-group pollock and capelin decreased in abundance near the Pribilof Islands between the 1970s and the 1980s, we have no data independent of the seabirds that indicate whether myctophids or sandlance changed in abundance or availability. Springer (1992) suggested that increased numbers of pollock may have preyed upon or competed with fish such as myctophids, capelin and sandlance, thereby reducing their availability to seabirds. Decker *et al.* (1995) provide limited data that argue against control of sandlance and capelin populations by pollock, but there is insufficient evidence to resolve the issue. Additionally, changes in sea surface temperatures and locations of the domains and fronts may have influenced the horizontal or vertical distribution of prey (Springer 1992, Decker *et al.* 1995, Hunt *et al.*, in press). A change in the vertical migration patterns of myctophids that resulted in their not approaching the sea surface at night would have had immediate effect on the diets of both species of kittiwakes, which are confined to foraging in the upper 25–50 cm of the water column.

Our ability to examine rigorously the importance of fatty fishes to the kittiwakes was severely diminished by the lack of a complete time series of seabird diets, and by the lack of independent data on the abundance and distribution of fatty fish. As efforts to develop multispecies models of fisheries interactions progress, our lack of knowledge about the ecology and population biology of these small forage fishes will become more critical. These fishes may be a key to the population regulation of marine bird and mammal populations. They may also play an important role in energy transfer to predatory fishes. The rapid decrease in some populations of marine birds and mammals in the northeast Pacific Ocean, and the potential or perceived threat to commercial fisheries if greater control measures are imposed when species of birds and mammals are declared threatened or endangered, should encourage investment in knowledge of forage fish biology.

ACKNOWLEDGEMENTS

We thank G.V. Byrd, P. Hunt, E. Woehler, and two anonymous referees for helpful comments on a previous draft of the manuscript. Research on the Pribilof Islands in the 1970s was supported by Bureau of Land Management, National Oceanographic and Atmospheric Administration Outer Continental Shelf Assessment Program contracts to G. Hunt. Studies in the 1980s were supported by a National Science Foundation Grant DPP-8521178 to G. Hunt. Data on seabird productivity in the 1980s and 1990s were provided by the Alaska Maritime National Wildlife Refuge. M.B. Decker was supported by a National Aeronautics and Space Administration Fellowship in Global Change Research.

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Aquatic Predators and their Prey

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First published 1996

Set in Ehrhardt 9/10.5 pt
by Best-set Typesetter Ltd. Hong Kong
Printed and bound in Great Britain by
The University Press, Cambridge.

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ISBN 0-85238-230-8