IS IT FOOD?

Addressing Marine Mammal and Seabird Declines

Sea Lions

Numbers in Thousands

160
140
120
100
80
60
40
20

1960   1970   1980   1990

Workshop Summary
Alaska Sea Grant Report 93-01

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Workshop Summary

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PREFACE

Significant declines of pinnipeds and piscivorous seabirds in the northern Gulf of Alaska and Bering Sea have raised concerns among resource managers, environmentalists, Alaska Native subsistence communities, and also fishermen who fear that changes in these predators may signal changes lower in the ecosystem that may affect future harvests. The decline of Steller sea lions is so great that they have been listed as "threatened" under the Endangered Species Act. Further unexplained declines leading to a change of status to "endangered" could broadly affect uses of this ocean region. Some harbor seal populations have seen substantial declines as well, raising concerns for the health of their populations.

Since passage of the Magnuson Fisheries Conservation and Management Act the fisheries off Alaska have grown to account for nearly half of all U.S. landings. Although much of this "growth" in U.S. landings is a displacement of foreign fishing in the U.S. fishery conservation zone, there have been changes in fishing technique and in the species targeted over the past two decades. The expansion of the U.S. fleet off Alaska has been met with an expansion of research to meet the needs of fisheries managers. However, with respect to the overall ecosystem supporting populations of pinnipeds or seabirds, the data base is too thin and too short to provide an explanation of the current declines, or even to set the current substantial declines in a historical context. Data on the fatty feed fishes, which are important prey both to commercially important fish and to birds and mammals, is poor even over the past two decades because much of the fisheries assessment gear has too large a mesh to capture capelin, sand lance, and similar prey.

It was in this setting that scientists from the United States, Canada, Norway, England, Scotland, and the U.S.S.R. were invited to Fairbanks, Alaska, by the Sea Grant College Programs of the University of Alaska and University of Washington to address the question "Is food availability the key to declining marine mammal and seabird populations in the northern Gulf of Alaska and Bering Sea?" Recognizing at the outset that data alone would not answer the question, the participating scientists were asked to push themselves beyond data certainty and to bring their best scientific judgement, intuition, and knowledge of scientific principles to bear on the question. With a limited number of scientists at the workshop, the conveners hoped that a forceful and lively discussion could ensue. We were not disappointed.

Food availability seems to be the most plausible explanation for observed declines of pinnipeds and piscivorous birds in the region. Nesting birds and juvenile mammals, because of their limited forage range and capacity, seem to be especially vulnerable to local changes in the availability of quality prey. Although there was broad support for this conclusion at the workshop, the more detailed the explanation of the causes of reduced food availability, whether it be focused on climate change, ecosystem processes, or anthropogenic activity, the less unified was the support.

Because reputable scientists shared important ideas at the workshop, it would be wasteful to record only the broadest of those ideas that had consensus. Understanding this regional ecosystem to the point of explaining the observed declines of birds and mammals may well begin with the further exploration of ideas debated at this workshop. To preserve some of the flavor of this workshop discussion, the conveners opted to summarize the meeting through a series of authored reports, rather than a single consensus document.

There remain many interesting questions that were beyond the scope of this workshop. If food availability is indeed a key factor af-

fecting the decline of seabirds and pinnipeds, as it seems to be, is human activity playing a significant role affecting the availability of food? Or for that matter, can humans intervene to affect forage availability? Are these population declines unusual, or do they fall within historic limits? If human activity is not a significant factor, are the changes in seabird and mammal populations cyclical or do they reflect changes in the ecosystem that are not predictable?

The overview of the workshop by Warren Wooster and the authored reports coming out of the discussion groups may provide guidance and stimulus for the scientific community to further address these and other questions significant in our understanding fish, birds, and mammals in this region, an understanding that is so important to the users of the ocean environment and to the nation as well.

Ron Dearborn, Director
Alaska Sea Grant College Program

ABOUT THE WORKSHOP

The Is It Food? workshop was held on the University of Alaska Fairbanks campus March 11-14, 1991. Alaska Sea Grant director Ron Dearborn began the meeting by presenting the workshop plan to the participants. During the first half-day of the workshop, participants heard overviews on six subtopics.

Mammals . . . . Michael Castellini, University of Alaska Fairbanks
Seabirds . . . . Alan Springer, University of Alaska Fairbanks
Forage Fish . . . . Lowell Fritz and Vidar Wespestad, National Marine Fisheries Service
Physical Environment . . Joe Niebauer, University of Alaska Fairbanks
Fisheries . . . . Lee Alverson, Natural Resource Consultants
Modeling . . . . Ray Hilborn, University of Washington

After the information sessions, the participants divided into five interest groups for morning discussions: mammals, seabirds, fish, physical environment, and modeling. The reports in this book on fish, oceanography, and modeling came out of those discussions. The mammal and seabird contributions are the result of further interest group discussions. During the next two days all workshop participants joined seabird and mammal interest groups, where they discussed the importance of food in population declines of marine mammals and seabirds in Alaska. The session leaders then compiled the reports.

The following organizations supported the Is It Food? workshop:

Alaska Sea Grant College Program
School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
Fairbanks, Alaska

Washington Sea Grant College Program
University of Washington
Seattle, Washington

Pacific States Marine Fisheries Commission
Portland, Oregon

Center for Marine Conservation
Washington, D.C.

Minerals Management Service
United States Department of the Interior

IS IT FOOD? AN OVERVIEW

Warren S. Wooster
Institute of Marine Studies
University of Washington

Declines in the populations of some pinnipeds (Steller sea lions, fur and harbor seals) and seabirds have been observed during the last few decades, starting in the eastern Aleutians and spreading to the eastern Bering Sea and Gulf of Alaska, as well as to the western Aleutians and Kuriles. While the declines, particularly of pinnipeds, seem to be unequivocal, in the case of seabirds and sea lions at least, there are large uncertainties in the population estimates, and the shapes of the abundance curves are poorly known (i.e., data are insufficient to show whether the decline has been linear or has accelerated since the mid-1970s). Furthermore, except for fur seals, the time series of abundance estimates are short, so it is unknown whether there have been previous population changes of a similar magnitude.

During the period of these population declines, there has been a major growth of fishing activity in the region (Alverson 1991), and since both the pinnipeds and many of the seabirds are piscivorous, it is not surprising to find the declines attributed to fishery effects. Steller sea lions have decreased to the point where they have been listed as "threatened" under the Endangered Species Act, and on their behalf restrictions have been proposed and some have been imposed on fisheries, especially in the vicinity of key rookeries.

A case might be made for such restrictions as a way to determine the fishery effects, but it is not evident that the measures have been designed or are being implemented as an experiment. Instead, in the face of uncertainty and without evidence to the contrary, a conservative approach has been taken with the clear implication that the problem is fishery-generated.

However, the cause-effect relationship has been difficult to demonstrate. There has unquestionably been mortality directly associated with fishing activity, but this is not generally considered a sufficient explanation for the declines. On the other hand, a fishery-caused shortage of food resulting from direct competition for the same prey between fisherman and sea lions or seabirds is a possibility that must be evaluated.

The workshop examined the possibility that the declines were caused by shortages of food. While the evidence (based on energetic calculations, weight-at-age, and detection of starved individuals) is far from conclusive, it was generally accepted that these populations are ultimately limited by availability of adequate food. The question then is whether a decrease in food availability can be actually demonstrated and, if so, whether it can be attributed to fisheries.

There is no doubt that the abundance of fish species of commercial interest varies significantly. For example, estimates of abundance of eastern Bering Sea pollock have varied fourfold in the last 25 years. The decline of sea lions since the early 1970s coincides with a

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The author was asked to serve as general rapporteur for the workshop "Is it Food?" held in Fairbanks on 11-14 March 1991. Reports were prepared by several working groups and form the main body of the workshop report. I have drawn upon them in preparing this overview. There was no attempt at the workshop to obtain a general consensus, and this essay does not pretend to offer such a consensus. It is only the author's view of the matters dealt with at the workshop.

period of major increase in pollock abundance. Starting in the late 1970s, herring biomass also increased in both the eastern Bering Sea and the Gulf of Alaska.

In the case of pollock, large numbers of cannibalistic adults might be expected to reduce the abundance of juveniles (and of other species of appropriate size) that might otherwise be available for consumption by birds and pinnipeds. This suggests possible benefits from reducing the number of adults through a vigorous fishery. On the other hand, while the number of pollock juveniles certainly varies from year to year, there has been no reduction in the frequency of strong year classes in either region during the period of decline.

Important prey species such as capelin and sand lance are not subject to commercial exploitation in this region, so their populations are not well estimated. Furthermore, even for exploited species (e.g. pollock and herring), population estimates are only made for large areas, and little is known about local prey abundance and availability in the feeding areas which may not be correlated with large-scale abundance as estimated from population models. Even the locations and dimensions of feeding areas are in most cases poorly known. Furthermore, it is quite likely that in a given feeding area, the abundance, nutritional value and concentration, and species composition of forage differs significantly from one time to another, not only seasonally but over longer time scales.

There is a further complication, namely that the abundance of fish stocks is not solely, perhaps not even principally, a function of fishing. In most cases, natural variability is as large or larger than that induced by fisheries. Natural variability is not, as commonly believed, controlled solely by fluctuations in primary and secondary productivity. It reflects year-to-year differences in recruitment success, which may depend on the availability of suitable food for larvae at critical stages in their development, or on unusual coincidences of

larvae with aggregations of predators, or on the physical transport of larvae to or away from feeding grounds. Each of these factors is affected by environmental conditions. Because of differing life histories, conditions that favor one species may disfavor another so that the mix of species, for example of forage fish, in a given area is likely to change with time for natural as well as fishery-related reasons.

Thus concluding that populations of pinnipeds and seabirds are limited by food is not the same as concluding that fisheries such as that for pollock are the cause of the declines. An alternative hypothesis should also be considered: Long-term changes in oceanic conditions, perhaps of decade scale, and the consequent fluctuations in recruitment of the various fish stocks that make up the ecosystems of the Bering Sea and the Gulf of Alaska, could cause the carrying capacity for piscivores to vary with time, perhaps on time and space scales comparable to those of changes in pinniped and seabird populations. The dramatic changes in climate and ocean conditions (Kerr 1992; Hollowed and Wooster 1992) in the eastern North Pacific since the mid-70s may have affected not only fish (and shellfish) stocks but also the marine populations that consume them.

Thus the agenda for investigating the causes of pinniped and seabird declines should include not only studies of their feeding areas and their food requirements and food availability in those areas, but also of all the major causes of variability of the food supply.

ACKNOWLEDGMENT

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REPORT OF THE MARINE MAMMAL WORKING GROUP

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SUMMARY STATEMENT

1) The group felt that marine mammal population and feeding pattern data were insufficient for the period before the mid-1970s to formulate and test hypotheses as to the "cause" of the initial decline in pinniped populations in Alaskan and surrounding waters. Therefore, effort was instead focused on the continued decline of Steller sea lions, harbor seals, and northern fur seals since 1975, a period for which there are more extensive data sets.

2) While overall population trajectories in Steller sea lions and northern fur seals can be partially explained by decreased adult survival, age structure alterations in the populations are indicative of reduced juvenile survival. Time series of demographic data useful to test these theories do not exist for harbor seals.

3) Using comparative data from other populations of pinnipeds that have experienced known reduced food supplies, a matrix of diagnostic indicators of food limitation (for example, low pup birth weights, reduced adult body condition, and longer foraging times) was constructed. The working group found that many of these same indicators exist in the northern fur seal and Steller sea lion populations. Little information of this type is available for harbor seals.

4) The above conclusions suggest there might be a food availability problem for the pinniped populations in question. A simple model was constructed to test this idea for the Gulf of Alaska using known and estimated values for fisheries and pinniped interactions. Given what is known about the energy requirements and

population biology of pinnipeds and what is known about the biology of prey species, especially pollock, a food supply problem is not inconsistent with the data. Basically, the model suggests that there may not be enough young age class pollock in the Gulf to support the pinniped populations. However, alternate prey species of similar sizes, but of higher caloric values than pollock, also occur in the Gulf and Bering Sea. Depending on the availability of these species to marine mammals, a limitation in the amount of pollock available may or may not impact individual nutrition and population dynamics. Limited data suggest that these alternate prey stocks may currently be at low levels, which would enhance the importance of pollock in marine mammal nutrition.

5) Therefore, based on the changing population demographics of pinnipeds, the presence of diagnostic indicators of food limitation, and a possible shortage of the appropriate type of prey items, the working group concluded that food supplies are limited for pinnipeds in and around Alaska waters.

DETAILED REVIEW OF SUMMARY FINDINGS

Item 1. Availability of Pre-1975 Pinniped Data.

While there are substantial data showing that the decline of Steller sea lions and fur seals began before 1975, there is minimal information on the feeding habits of these pinnipeds for that period. From a limited study of eight Steller sea lions collected in the mid-1940s, it appeared that pollock was a dominant food item (Imler and Sarber 1947). On the

other hand, pollock did not appear to be a major food item from samples collected around 1960 (Mathisen et al. 1960, Fiscus and Baines 1966). The working group concluded that this sample size was too limited to draw any firm conclusions about food habits of Steller sea lions from this time period.

There was a great deal of work done on the diet of northern fur seals from 1958 to 1974 (for review, Perez and Bigg 1986, Lowry et al. 1989). In the Gulf of Alaska, pollock made up from 5% to 15% of northern fur seal diet for this time period, whereas in the Bering Sea, pollock increased in importance to about one third of the diet.

There is very little information available for harbor seal diets earlier than the 1970s. In a very limited sample in 1954 (Wilke 1957), pollock was found in only 1 of 7 stomach samples. Three seals collected at Unalaska in 1972 all had pollock in their stomachs (Lowry et al. 1979).

Overall, the data base on food items for Steller sea lions and harbor seals in the early years was considered too limited to draw major conclusions about dietary habits or shifts. The working group recognized that broad patterns were apparent in pre-1975 data, such as the correlation between the decline in Steller sea lions and the apparent increase in the biomass of pollock. However, it was the general consensus that such broad correlations could lead to any number of hypotheses about relationships between pinnipeds and their food supplies, and that these hypotheses could not be rigorously tested.

Since 1975, there has been much more extensive and rigorous sampling of both fisheries data and marine mammal food habits. On the basis of these arguments, all participants agreed to limit their discussions and models to data collected after 1975 and the rest of this report concerns only this time period.

A detailed review of the population trends and food habits of the species in question is given in Appendix 1.

Item 2. Juvenile Survival.

The population of Steller sea lions in the vicinity of Marmot Island has declined since 1975 at about 5% per year. Comparisons of fecundity and survival rates from two life tables made in 1975-78 and 1985-86 indicate that the average age of females older than 3 yr in this population has increased about 1.55 yr (SD = 0.35 yr) during this period. Possible causes of the population decline were modeled by perturbing the life tables and examining the short-term behavior of the population and age trajectories. The simplest explanation for the observed decline in numbers and increase in average age of females older than 3 yr was a 20% per year decrease in the survival of juveniles of age 0-3 yr (York, In Press). Broader models suggest that the only way to duplicate the overall decline in the population of Steller sea lions is to remove 3,000 to 3,500 females between the age 1 and 7 every year over the past 30 years (Blackburn 1990).

Based on these data and models, the working group concluded that while overall population trajectories could be simulated by reducing survival of adults, the change in age class structure was strong evidence for the reduced survival of juvenile Steller sea lions and that there might also be an increased reduction in survival of breeding females.

As with Steller sea lions, simulation models suggest that commercial female harvesting and a series of poor juvenile survival rates were responsible for causing and maintaining the observed decline in northern fur seal pup production on St. Paul Island from 1956 to 1970 (Trites and Larkin 1989). The more recent drop in pup production is also attributed to poor juvenile survival. Reductions in the fur seal food base and entanglement-related mortality contribute to the current decline. The available data are consistent with the view that per capita fish abundance is insufficient for the young fur seals during their migration through the Gulf of Alaska.

The working group noted that the evidence

for reduced juvenile survival was substantial in Steller sea lions and northern fur seals, but that no data exists for harbor seals.

Item 3. Diagnostic Indicators of Food Limitation on Pinnipeds.

The working group constructed a matrix of the known impacts of food limitation on pinniped populations (Fig. 1). This matrix consisted of demographic, behavioral and physiological impacts of food deprivation. The basic working premise of this section of the workshop was to compare this matrix with what was known about the biology of the pinniped species in the Gulf. The working group found that a substantial number of diagnostic indicators existed in the species being studied and concluded that there was therefore evidence of food limitation in these populations.

Not all indicators were found in the questioned species, just as not all indicators were found in each of the reference species. However, the appearance of a substantial number of the indicators was considered to be significant evidence for food limitation problems in pinniped populations. For example, in Steller sea lions, the observed indices of food limitation include a possible decline in birth rate, fewer breeding females, fewer pups, decreased adult

body condition, decreased juvenile survival, a change in population age structure, and overall population decline.

To better explain how food limitation would alter marine mammal physiology and result in the indices noted in the matrix, the working group also considered the theoretical physiological implications of food limitation on seals. A graphic tree of how food supply would impact immature individuals was constructed (Fig. 2). It should be noted that all of the following pathways have been observed in species that are food limited, although not every indicator has been recorded in every species.

As food becomes limiting, a juvenile seal or sea lion may have to increase search time to compensate, but at the price of increased probability of predation because of increased time at sea. They might also be able to keep foraging trips the same length, but have to work harder in each trip. If such efforts are not completely successful, then body condition will begin to decline. Decreased body condition leads to two basic options: either increased starvation rates or slower growth rates. Starvation leads directly to decreased juvenile survival, and therefore age class shifts in the population are due to reduced recruitment. Reduced growth itself leads to delayed maturity, and therefore longer generation times. This also

INDICATOR	Northern fur seals St. Paul	St. George	Gulf Stellers	Harbor seals	Antarctic fur seals	California sea lions	Galapagos fur seals	Harp seals
Decline in birth rate	NC	MAYBE	MAYBE		NC		NC	
Fewer breeding females/fewer pups	OBS	OBS	OBS	OBS	OBS		NC	
Lower birth rates					OBS		OBS	MAYBE
Feeding of pups [milk per trip]	NC	NC			NC			
Feeding of pups [milk consumption]	NC	NC			DECR	DECR	DECR	
Changes in attendance	NC	NC	NC		INCR		INCR	
Pup growth rates					DECR	DECR	DECR	
Changes in time to weaning					NC		INCR	MAYBE
Pre-weaning pup survival	INCR	INCR			DECR	DECR	DECR	NC
Adult/juvenile condition	INCR	INCR	DECR		DECR	DECR		DECR
Adult/juvenile survival	MAYBE	MAYBE	DECR		DECR		DECR	DECR
Changes in feeding areas					NC			OBS
Changes in feeding patterns					OBS	OBS		
Territorial male effects	OBS	OBS			NC		DECR	
Age at first reproduction					NC			
Age structure			OBS		NC		OBS	
Population decline	OBS	OBS	OBS	OBS	NA	OBS	OBS	OBS

NC = No change observed
Maybe = Not enough data
OBS = Effect seen
INCR = Increased

Figure 1. Impacts of food limitation on pinniped populations.

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            ┌──────────────────────┐
            │  Immature Individuals │
            └──────────────────────┘
                       │
                       ▼
            ┌──────────────────────┐
            │    Decreased Food     │
            └──────────────────────┘
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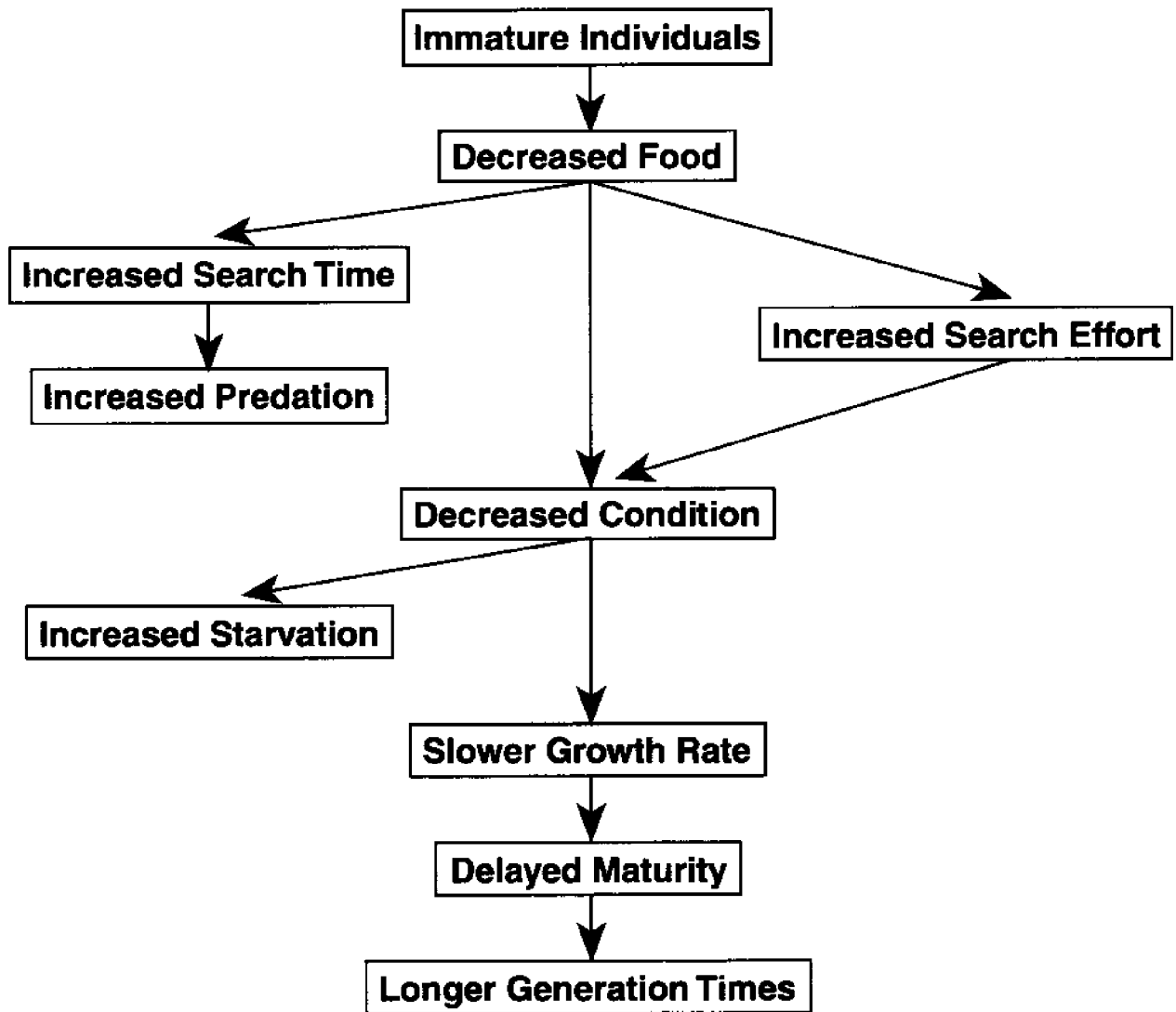
Figure 2. Impact of food supply on immature marine mammals.

leads to an age class shift in the population with the increase in the age of first birth.

The working group concluded that there were multiple indicators of food limitation in the questioned species and that therefore a problem with the supply of food was consistent with the available data.

Item 4. Gulf of Alaska Fisheries/Marine Mammal Model.

The following model is a calculation of the energy demands of pinnipeds for the Gulf of Alaska. There are many approximations in this model, but it was based on the most current information available to the working group. Rather than reference each of the points as they are presented, we included a basic annotated bibliography at the end of the section.

The approach of this model was to estimate the total number of northern fur seals, harbor seals, and Steller sea lions that live in or pass through the Gulf of Alaska, and then calculate the total food requirements of these populations. This was done by using known or estimated metabolic requirements of the concerned species.

Since the time of the workshop (March

Populations of pinnipeds for the Gulf of Alaska.

Steller sea lions: juveniles	25,000 including 9,600
Harbor seals: of juveniles)	50,000 (unknown number
Northern fur seals: months	50,000 juveniles for 12
	50,000 adults for 6 months

Energy requirements (units are expressed in kilojoules [kJ] where 4.184 kJ = 1 kcal)

Steller sea lions:	5.9×10^{11} kJ/year juveniles
	13.1×10^{11} kJ/year adults
	19.0×10^{11} kJ/year total
Harbor seals:	1.4×10^{11} kJ/year total
Fur seals:	4.7×10^{11} kJ/year juveniles
	3.5×10^{11} kJ/year adults
	8.2×10^{11} kJ/year total
Total:	10.6×10^{11} kJ/year juveniles
	28.5×10^{11} kJ/year all animals

Using an energy value of 1.1×10^3 kcal/kg of pollock, the total energy demand of 28.5×10^{11} kJ/year is equivalent to:

- 617,000 mt/year pollock equivalent taken by the total population of pinnipeds.
- 228,000 mt/year pollock equivalent taken by juveniles.

1991), there has been considerable scientific and legal discussion on the pollock biomass in the Gulf. The National Marine Fisheries Service in late spring *increased* the total allowable catch of pollock to over 100,000 mt. In response, Greenpeace sued the NMFS saying that the scientific basis for increasing the total allowable catch (TAC) was not valid. In October 1991, the court upheld the altered TAC. The estimate of total pollock biomass in the Gulf used by the NMFS was based on the statement that the 100,000 mt of pollock was 10% of the total biomass, or 10^6 mt (June 5, Biological opinion, NMFS report). Therefore, for the broad approximation of this model, the working group used 10^6 mt of pollock.

The working assumptions here are:

- 1,000,000 mt of pollock age 5+ exist in the Gulf
- 150,000 mt of pollock age class 1-2
- Energy demand of adult pollock: 1% of body mass/day
- 20% of adult pollock diet = juvenile pollock
- Therefore 750,000 mt/year of juvenile pollock are consumed by adult fish.

It is known that Steller sea lions consume younger age class pollock (over 60% of pollock taken are less than age class 2) and assuming that younger sea lions consume smaller fish than do adult sea lions, the energy requirements of juvenile pinnipeds (equivalent to 228,000 mt/year of juvenile pollock) are far outstripped by the energy requirements of adult pollock (equivalent to 750,000 mt/year of juvenile pollock).

These values are rough approximations, but the overall point is not changed substantially by more precise values: there would seem to be a limited food resource in terms of juvenile pollock in the Gulf that would be necessary to keep both the pinnipeds and adult pollock populations stable and pinnipeds would seem to require over half of the total adult population of pollock.

References and Working Assumptions for Gulf Model

Energy requirements of pinnipeds

Harbor seals: The metabolic requirement of an adult harbor seal is 2.5×10^6 kJ/year (Ashwell-Erickson and Elsner, 1981).

Northern fur seals: The metabolic requirement of juvenile and adult fur seals have been estimated at 1.3×10^7 kJ/year for 70 kg adults and 0.9×10^7 kJ/year for 40 kg juveniles (Costa 1991). This is approximately 12% of body mass/day.

Steller sea lions: There have been no direct measurements of metabolic rate in Steller sea lions. Therefore, values were assumed to be about 10% of body mass per day using the

values from Costa (1991) for fur seals and noting that the metabolic rate of Steller sea lions would be lower because of their increased body mass compared to fur seals.

These metabolic values for the concerned species are consistent with a multispecies model of marine mammal food requirements presented by Perez et al., 1990.

Energy densities of prey items

The energy density of adult pollock is 1.1 x 10^3 kcal/kg from Ashwell-Erickson and Elsner, 1981.

Population levels of pollock

NMFS stock synthesis model (Tabb9 SAFE 90-91) for average age class biomass of pollock (1988-1990 average) shows about 1,000,000 mt of adult pollock (beginning of year biomass, year class 5+) in the Gulf of Alaska, and 150,000 mt of pollock age class 1-2.

RECOMMENDATIONS

The working group on marine mammals felt that some very basic recommendations could be made based on the findings of the workshop. These suggestions are attempts to define realistically attainable goals that would most directly impact the populations of marine mammals in Alaska waters.

It was felt that these recommendations would be the most straightforward and promising approach to take to best understand the nature of the declining populations of pinnipeds in Alaska waters.

Approach Plan

1. Attempt to ensure the availability of small and/or young age class fish for pinniped prey.
2. Monitor the resident populations of pinnipeds to test the impact of increasing the available biomass of prey as suggested in

item 1 by:

2.1. Locating the feeding grounds (by season, geographic area, and foraging depth) of pinnipeds in Alaska waters, especially juveniles.

2.2 Examining the available food base in these areas of pinniped foraging.

2.3 Expanding studies of dietary analysis in pinnipeds in the questioned areas.

2.4 Monitoring resulting pinniped demographic data:
2.4.1 Population size trends.
2.4.2 Age class structure changes.
2.4.3. Condition indices.

3. Expand fisheries sampling to better monitor non-commercial groundfish that are potential prey items for pinnipeds.

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APPENDIX 1. POPULATION STATUS TREND OF STELLER SEA LIONS, HARBOR SEALS, AND NORTHERN FUR SEALS

The number of sea lions, harbor seals, and fur seals in the Bering Sea, Aleutian Islands, and Gulf of Alaska has been declining. The types of data that have been collected and the intensity and regularity of sampling have not been equal for the three species.

Counts and estimates of the number of fur seal pups born on the Pribilof Islands are available beginning in 1912. In that year there were about 67,000 pups born on St. Paul Island and 12,000 on St. George. Fur seal numbers increased greatly, and by 1950 it was estimated that over 450,000 pups were born on St. Paul.

Numbers began to decline in the late 1950s and continued to do so through 1980 (Table A). Since 1981 there has been no significant trend in pup births at St. Paul, but pup production on St. George has continued to decline at about 6% per year (York and Kozloff 1987; A. York, personal communication). Estimates of the total stock size indicate a peak of about 2.2 million animals in the mid-1950s, followed by a decline to about 877,000 in 1983 (Briggs and Fowler, 1984)

The abundance of Steller sea lions has been indexed by counts of animals on rookeries and haulouts during the breeding season. Aerial surveys in the late 1950s gave a count of about 140,000 animals in the region from the central Gulf of Alaska to the central Aleutian Islands. However these surveys were not designed specifically to enumerate sea lions, and the reliability of counts is uncertain. Subsequent counts using standardized methodology designed for sea lions have shown a major decline that has continued through at least 1989 (Table A). The decrease was first noted in the eastern Aleutian Islands in the mid-1970s (Braham et al. 1980), then appeared to spread eastward to the Kodiak Island area in the late 1970s and early 1980s, and westward to the central and western Aleutian islands during the early and mid-1980s

Table A. Trends in numbers of Pribilof fur seals, Steller sea lions, and harbor seals in parts of the Gulf of Alaska and Bering Sea.

Year	Pribilof fur seal[1]	Steller sea lion[2]	Harbor seal[3]
1950	451,000		
1955	461,000		
1960	320,000	140,115	
1965	253,768		
1970	230,485		
1975	278,261	103,976	
1976	298,000		6,919
1977	235,200		6,617
1978	247,100		4,839
1979	245,932		3,836
1980	203,825		
1981	179,444		
1982	203,581		1,575
1983	165,941		
1984	173,274		1,390
1985	182,258	67,617	
1986	167,656		1,270
1987	171,422		
1988	202,300		1,014
1989	171,530	24,953	
1990	201,310	27,860	960

[1] Number of pups born at St. Paul Island; from York and Kozloff (1987) and NMFS (unpublished data).

[2] Index counts of adults and juveniles on rookeries and haulouts from the Kenai Peninsula to Kiska Island; from Loughlin et al. (1990) and Merrick et al. (1987, 1991).

[3] Mean counts of seals hauled out on Tugidak Island during the fall molt; from Pitcher (1990) and ADF&G (unpublished data).

(Merrick et al. 1987, Byrd 1989). Sea lion numbers in the eastern Gulf of Alaska, from Prince William Sound through southeast Alaska, have remained relatively stable during this time (D. Calkins, personal communication). Pup counts conducted in these areas corroborate the general trend in overall numbers (Merrick et al. 1987 and 1991). At the rookery on Walrus Island in the Pribilof Islands, the number of animals has declined from 4,000-5,000 in 1960 (Kenyon 1962) to about 600 in 1982 (Loughlin et al. 1984).

Harbor seal population trend has been indexed by counts of animals hauled out during either the pupping or molting period. Counts are usually made in relatively small areas where the major haulout sites are known. The best information available is for Tugidak Island, in the central Gulf of Alaska south of Kodiak Island (Table A). Index counts made at Tugidak, which used to support one of the largest concentrations of harbor seals in the world, declined 86% from 1976 to 1990 (Pitcher 1990 and unpublished). Data for other areas are much more limited. Comparisons of counts made in 1984 and 1988 showed no significant change in southeast Alaska near Ketchikan, but a decline of 41% in Prince William Sound (Pitcher

Table B. Importance of various prey in the diets of Pribilof fur seals, Steller sea lions, and harbor seals the Gulf of Alaska and Bering Sea.

Ranking	Pribilof fur seal[1]	Steller sea lion[2]	Harbor seal[3]
1	Squids (33.3)	Pollock (58.3)	Pollock (21.4)
2	Capelin (30.6)	Squids (4.2)	Octopus (18.3).
3	Pollock (25.1)	Herring (20.6)	Capelin (10.4)
4	Atka mackerel (3.5)	Capelin (7.4)	Eulachon (11.6).
5	Herring (2.9)	Pacific cod (0.9)	Herring (6.4).
6	Bathylagidae (2.9)	Salmon (5.1)	Pacific cod (3.2).
7	Salmon (1.1)	Octopus (<0.1)	Shrimps (3.3)
8	Flatfishes (0.6)	Sculpins (1.3)	Flatfishes (2.6).
9	Sablefish (0.2)	Flatfishes (0.3)	Salmon (4.4).
10	Sand lance (0.2)	Rockfishes (0.8)	Squids (1.6)

[1] Rankings based on modified volume, numbers in parentheses are modified volumes; from Perez and Bigg (1981).
[2] Rankings based on combination rank index, numbers in parentheses are percent of total sample volume; from Pitcher (1981).
[3] Rankings based on modified index of relative importance, numbers in parentheses are percent of total sample volume; from Pitcher (1980).

1989). Counts made at large harbor seal haulouts on the north side of the Alaska Peninsula in 1975-77, 1985, and 1990 indicate an overall decline in numbers of about 44% (NMFS and ADF&G, unpublished data).

Food Habits

The predominant items in the diet of fur seals, harbor seals, and Steller sea lions are small to medium-sized fishes and cephalopods. The data available on diet composition has come from examination of stomach contents, which may bias evaluations of prey importance.

Sampling has generally been spatially and temporally restricted, which limits its utility for making comparisons and correlations.

Perez and Bigg (1981) analyzed food remains in stomachs of 1,749 fur seals collected pelagically in the Bering Sea in June-October 1958-74. Principal prey items were squids, capelin, and walleye pollock (Table B). Data collected from other regions indicated a generally similar diet. There has been little information collected on fur seal foods in recent years (Loughlin and Livingston 1986).

Pitcher (1981) reported on the stomach contents of 153 Steller sea lions collected in the Gulf of Alaska during 1975-78. The prey items of greatest importance were pollock, herring, capelin, salmon, and squids (Table B). In 74 stomachs examined from the Kodiak area in 1985-86 the principal prey were pollock, octopus, flatfishes, and sand lance; 14 animals collected in southeast Alaska had eaten mostly pollock and Pacific cod (Calkins and Goodwin 1988). Limited data available for the Bering Sea indicate that pollock is a major food (Lowry et al. 1982 and 1989, NMFS and ADF&G unpublished).

Pitcher (1980) described the diet of harbor seals in the Gulf of Alaska based on the contents of 269 stomachs from animals collected during 1973-78. Principal prey were pollock, octopus, capelin, eulachon, and herring (Table B). No stomach samples have been collected in the Gulf since the mid-1970s. Limited data available for the Bering Sea and Aleutian Islands indicate that the harbor seal diet is generally similar to that in the Gulf of Alaska (Lowry et al. 1982, ADF&G unpublished).

In the Gulf of Alaska the pollock eaten by both sea lions and harbor seals included a wide

range of sizes (Pitcher 1981). On average sea lions ate pollock that were considerably larger (29.8 cm long versus 19.2 cm). For the Bering Sea, Frost and Lowry (1986) also found a wide overlap in the range of sizes eaten, but on average smaller pollock in harbor seals (mean length 24.5 cm) than in sea lions (mean 29.3 cm). In a collection made in the central and western Bering Sea, sea lions 1-4 years old ate significantly smaller pollock than did older animals (mean lengths 22.4 cm versus 26.9 cm) (Frost and Lowry 1986).

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REPORT OF THE SEABIRD WORKING GROUP

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INTRODUCTION

A precipitous decline in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska during the past 15-20 years and the listing of sea lions as threatened under the Endangered Species Act, plus declines of harbor seals (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*), and fish-eating seabirds on the Pribilof Islands have focused renewed attention on ecosystems of the Bering Sea and Gulf of Alaska. Numerous hypotheses have been advanced to explain these events, with the most compelling probable cause being food shortage (e.g., Springer 1992, Trites 1992). A panel of distinguished scientists was convened at the University of Alaska during March 10-14, 1991 to examine the question "Is it food?", or the lack thereof, that is responsible for the changing abundance of marine mammals and birds. The following report presents evidence, conclusions, and recommendations for future studies drawn from discussions of the working group on seabirds.

BACKGROUND

Systematic studies of seabirds in Alaska were undertaken at only one colony, Cape Thompson in the eastern Chukchi Sea (Swartz 1966) (Fig. 1), prior to the mid-1970s and the initiation of the Outer Continental Shelf Environmental Assessment Program (OCSEAP). With the beginning of OCSEAP in 1975, however, numerous projects were initiated at colonies around the state and information on seabirds grew rapidly. Several colonies have now been visited for many years (Table 1). The emphasis of most studies has been on monitor-

ing numbers and productivity of the more accessible, cliff-nesting species, particularly Northern Fulmars (*Fulmarus glacialis*), Common and Thick-billed Murres (*Uria aalge* and *U. lomvia*), and Red-legged and Black-legged Kittiwakes (*Rissa brevirostris* and *R. tridactyla*). Dietary studies of these species and of Horned and Tufted Puffins (*Fratercula corniculata* and *F. cirrhata*) have been undertaken with varying frequency through the years.

Fulmars, murres, kittiwakes, and puffins are all primarily piscivorous. There are additionally several species of planktivorous seabirds in Alaska, but unfortunately much less is known about trends in their abundance or productivity because they all nest underground and are more difficult to study. The principal exceptions are on St. Lawrence Island and St. George Island (Pribilof Islands). Censuses and studies of the breeding biology and diets of Least, Crested, and Parakeet Auklets (*Aethia*
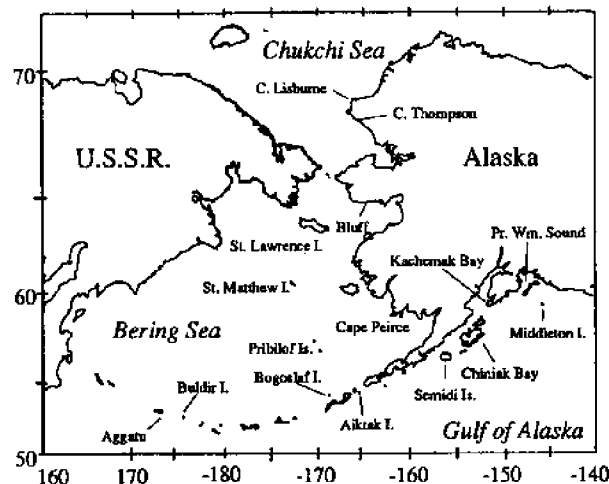

Figure 1. Seabird colonies and other locations in Alaska discussed in this report.

pusilla, *A. cristatella*, and *Cyclorrhynchus psittacula*) were carried out in the mid-1960s, mid-1970s, and early and mid-1980s on St. Lawrence Island and in the mid-1970s and early to mid-1980s on St. George Island. Although present concerns center on fish-eating species, particularly murres and kittiwakes, knowledge of the planktivores can be useful in understanding community relationships and ecosystem processes important to both seabirds and marine mammals.

OBSERVATIONS

Northern Bering Sea

St. Lawrence Island has some of the largest concentrations of breeding seabirds in Alaska (Sowls et al. 1978) because of its location next to a major ocean current that enriches the region with abundant nutrients, phytoplankton, and zooplankton from off the continental shelf (Springer et al. 1987, Springer et al. 1989, Walsh et al. 1989). Three censuses of murres (*Uria* spp.) on sample plots in 1972, 1976, and 1981 suggested that no long-term changes occurred during that time (Roseneau et al. 1985). Unfortunately, the same plots were not counted during the most recent work on the island in 1987 (Piatt et al. 1988).

Because the intervals between studies at St. Lawrence Island have been long, there is no information on trends in productivity of murres or kittiwakes. All that is known is that productivity varies between high and low levels and appears in general to track productivity at other colonies in the northern Bering Sea and eastern Chukchi Sea (Searing 1977, Roseneau et al. 1985).

Murres and kittiwakes on St. Lawrence I. feed on a variety of fishes, including primarily arctic cod (*Boreogadus saida*) and sand lance (*Ammodytes hexapterus*) (Fig. 2), with lesser amounts of saffron cod (*Eleginus gracilis*), pollock (*Theragra chalcogramma*), and capelin (*Mallotus villosus*) (Springer et al. 1987, Piatt et al. 1988).
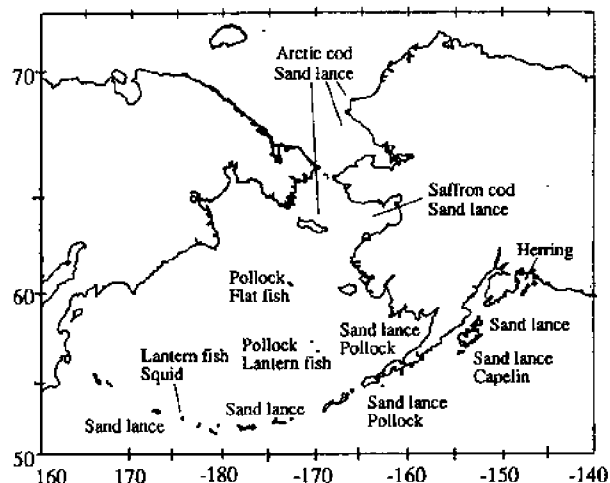

Figure 2. Principal prey of murres and kittiwakes in Alaska.

Least and Crested Auklets on western St. Lawrence Island have increased by an average of about 75% since the mid-1960s (Fig. 3). Two hypotheses have been advanced to explain the change: (1) reduced predation pressure by foxes and humans (Piatt et al. 1990) and (2) an increase in prey abundance (Springer 1992). Least Auklets feed nearly exclusively on large calanoid copepods during summer,
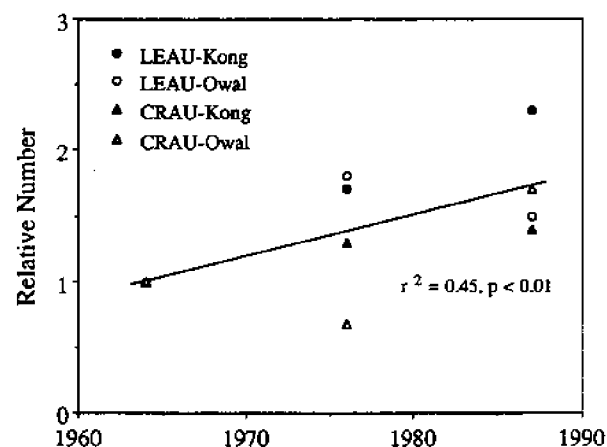

Figure 3. Trends in numbers of auklets at St. Lawrence Island. Data from summary by Piatt et al. (1990). LEAU = Least Auklet; CRAU = Crested Auklet; Kong = Kongkok Bay colony; Owal = Owalit Mountain colony.

Table 1. Information obtained at major seabird colonies in the Bering Sea and Gulf of Alaska.

Parameter	Usefulness	Bluff 1975-90 BLKI, COMU	Pribilof Is. 1975-82, 84-90 RLKI, BLKI, TBMU	Cape Peirce: 89-90 BLKI, COMU	Semidi Is. 1976-81, 85-87, NOFU, BLKI, COMU, TBMU, HOPU, TUPU
Abundance of prey species	10		Pollock		
Die-offs	5	BLKI: 1984	RLKI, BLKI: 1983, 1987		PECO, BLKI-1983, 1989
Adult behavior	7		All: all years		All: all years
Phenology	4	Both: all years	All: all years	Both: all years	All: 1976-81, 89-90
Clutch size	10	Both: all years	All: all years	Both: all years	All: 1976-81, 89-90
Productivity	8	Both: all years	All: all years	Both: all years	NOFU, BLKI: 1976-81, 89-90 COMU: 1979-81, 89-90 TBMU: 1977-81, 89-90
Colony attendance	5	Both: all years	All: 1976, 82, 84-90	Both: 1984-90	All: 1976-81, 89-90
Laying success	9	BLKI: all years	RLKI, BLKI: all years		All: 1976-81, 89-90
Diet composition					
Adults	10	Both: 1978-90	All: 1975-78, 84-88	Both: 1982, 84	BLKI, COMU: 1987, 90
Chicks	10		All: 1975-78, 87-88		HOPU, TUPU: 1979, 85-87
Body condition					
Adult mass	6	Both: 1978-90	All: 1975-78, 84-88	Both: 1982, 84	BLKI, COMU: 1987, 90
Chick growth rate	10	BLKI: 1978-90	All: 1975-78, 84, 87-88		
Chick fledging weight	10		All: 1975-78		
Additional needs					
Population age structure	10				
Population cohort change	10				
Physiological parameters					
Haematology	10				
Fat	10				
Protein	10				
At-sea behavior indexes					
Trip length	10				
Chick feeding rates	10				
Egg size	7				

Notes: NOFU=Northern Fulmar; PECO=Pelagic Cormorant; BLKI=Black-legged Kittiwake; RLKI=Red-legged Kittiwake; COMU=Common Murre; TBMU=Thick-billed Murre; HOPU=Horned Puffin; TUPU=Tufted Puffin. Usefulness values 1-10 = little-great.

Table 1. (continued)

Middleton I. 1972, 76, 78, 81-90 PECO, BLKI, COMU, HOPU, TUPU	Pr. Wm. Sound 1972, 84-90 BLKI	Barren Is. 1975-83, 89-90 BLKI, TBMU, HOPU, TUPU	Buldir I. 1974-76, 88-90 RLKI, BLKI, TBMU, HOPU, TUPU	Agattu I. 1979, 88-90 BLKI, COMU, HOPU, TUPU
COMU: 1972		BLKI: 1983, 1989		
BLKI: 1970s, 1980s	1980s			
All: 1976, 78, 81-90	Late 1980s	Both: 1975, 89-90	All: 1976, 88-90	Both: 1979, 88-90
All: 1976, 78, 81-90	Late 1980s	Both: 1975, 89-90	All: 1976, 88-90	Both: 1979, 88-90
BLKI: 1976, 78, 81-90	1984-90	Petrels: 1980s	All: 1988-90	Both: 1988-90
BLKI: 1976, 78, 81-90	1972, 84-90	Both: 1976-78, 89-90	All: 1974, 76, 88-90	Both: 1979, 88-90
PECO, BLKI: 1978	1988-90		RLKI, BLKI: 1988-90	BLKI: 1988-90
PECO, BLKI, HOPU, TUPU: 1987, 89-90	1989-90		All: 1988-90	Both: 1988-90
PECO, BLKI, HOPU, TUPU: 1978, 87, 89-90	1989-90	HOPU, TUPU: 1976-79, 90	HOPU, TUPU: 1975, 88-90	HOPU, TUPU: 1988-90
PECO, BLKI, HOPU, TUPU: 1987, 89-90	1989-90		All: 1988-90	Both: 1988-90
	1988-90	HOPU, TUPU: 1980-82, 90	RLKI, BLKI: 1988	HOPU, TUPU: 1988-90

while Crested Auklets feed on copepods, euphausiids, and hyperiid amphipods (Bedard 1969, Hunt et al. 1981, Springer and Roseneau 1985). Auklets compete for zooplankton with fishes, including particularly juvenile pollock, as well as arctic cod, sand lance, and capelin.

One of the most thorough, long-term studies of a seabird colony in Alaska has been made at Bluff in Norton Sound. Numbers of Common Murres apparently fell rapidly during the late 1970s then stabilized during the 1980s (Fig. 4); Thick-billed Murres nest only in very small numbers in Norton Sound. There has been no long-term change in the abundance of Black-legged Kittiwakes, although numbers have fluctuated considerably between years apparently in response to changes in prey availability (Murphy et al. 1991).

The productivity of murres and kittiwakes at Bluff has varied widely and in parallel between years, and is positively correlated with air temperature, and presumably water temperature, in Norton Sound (Murphy et al. 1986 and 1991). Murres and kittiwakes there depend on saffron cod and sand lance for the bulk of their diets, and the abundance of these fishes is greater in warm years than in cold years (Springer et al. 1984 and 1987). However, a
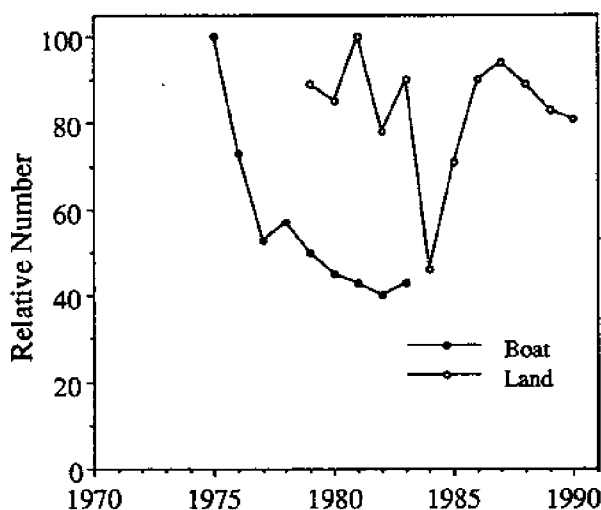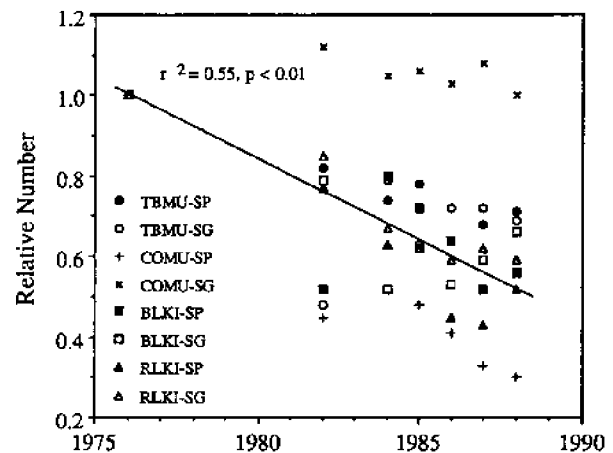

Figure 5. Trends in numbers of murres and kittiwakes on the Pribilof Islands. Data from Byrd (1989), Craighead and Oppenheim (1985), Hickey and Craighead (1977), Johnson (1985), and A. Sowls (unpubl. data).

numerical simulation of the murre population at Bluff indicated that the decline in numbers could not be explained by changes in productivity associated with patterns of environmental temperature, thus implicating factors during winter that affect survival of juvenile or adult birds (Murphy et al. 1986).

Southeastern Bering Sea

The greatest number of Thick-billed Murres in the Pacific Ocean and the greatest number of Red-legged Kittiwakes in the world nest on St. George Island (Sowls et al. 1978, Byrd and Gibson 1980). Since 1976 the abundance of Thick-billed and Common Murres and Red-legged and Black-legged Kittiwakes has declined by an average of about 40% on the Pribilofs, except that the number of Common Murres on St. George I. apparently has not changed (Fig. 5). No changes in numbers of murres or kittiwakes were detected on St. Matthew-Hall islands during work there in the early to mid-1980s (Murphy et al. 1987).

The productivity of murres and kittiwakes has varied greatly between years on the Pribilofs, but in general it followed a pattern of decline during the late 1970s and early 1980s

Figure 4. Trends in the number of Common Murres at Bluff. Data from Murphy et al. (1986) and E. Murphy (unpubl. data).

with a subsequent recovery (Fig. 6). Productivity of kittiwakes on St. Matthew Island also was very low in 1982-83 and increased somewhat by 1985-86.

Kittiwake productivity is negatively correlated with the overall biomass of pollock (r^2 = 0.45, p < 0.01). This could be interpreted to mean that large pollock have a negative effect on the birds by depressing the abundance of critical prey such as juvenile pollock, sand lance, or capelin. For example, Black-legged

Kittiwake productivity on the Pribilofs has never been as high, even at its highest level in the mid-1970s, as at colonies where sand lance is abundant. Kittiwake productivity is also negatively correlated with sea surface temperature (r^2 = 0.37, p < 0.05), which could occur if water temperature affects prey abundance or just its availability, for example by changing its vertical or areal distribution. The correlation between kittiwake productivity and pollock biomass is somewhat stronger than that
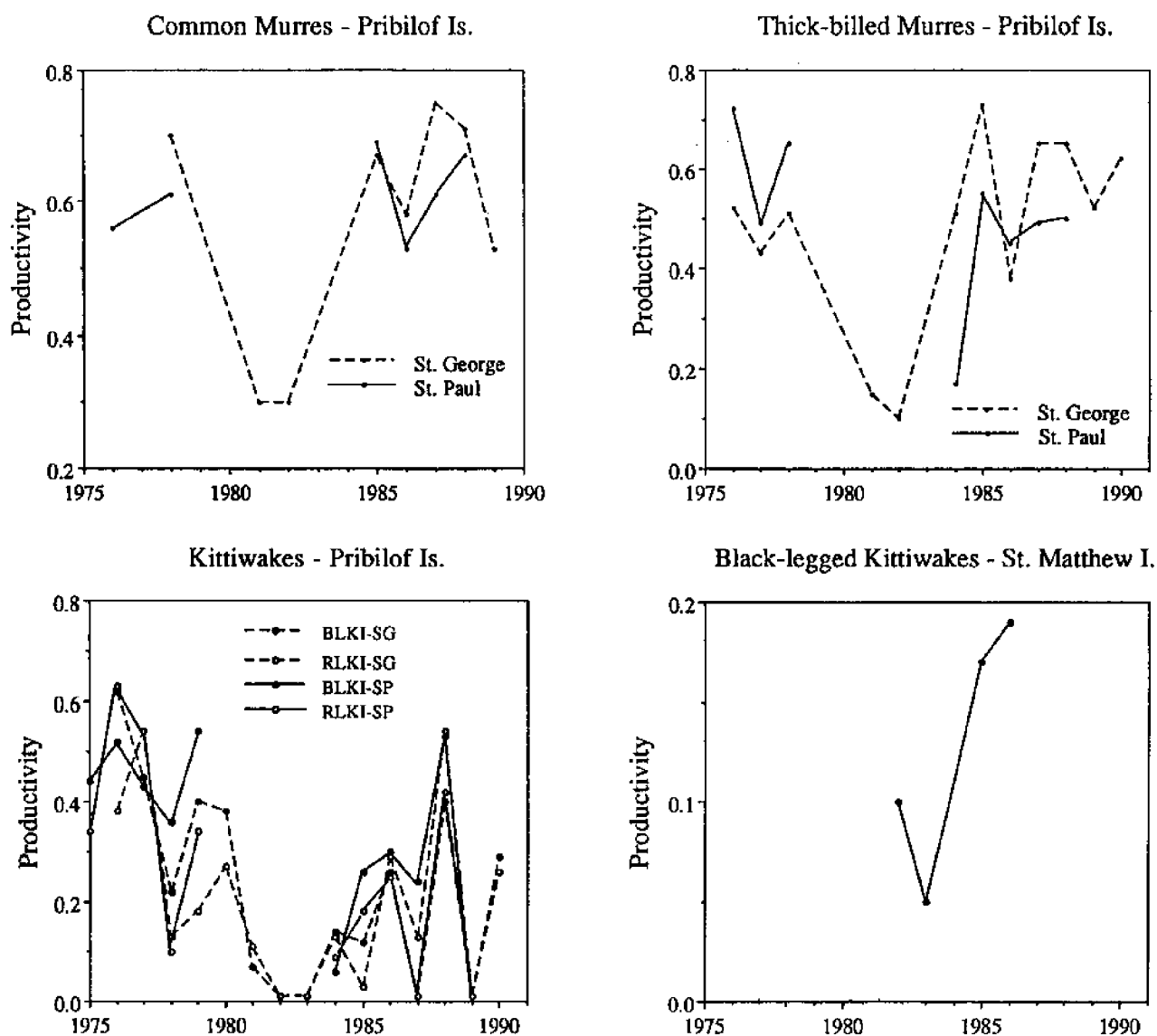

Figure 6. Trends in productivity of murres and kittiwakes on the Pribilof Islands and St. Matthew Island. Pribilof data from summary by Dragoo et al. (1989); St. Matthew data from summary by Murphy et al. (1987).
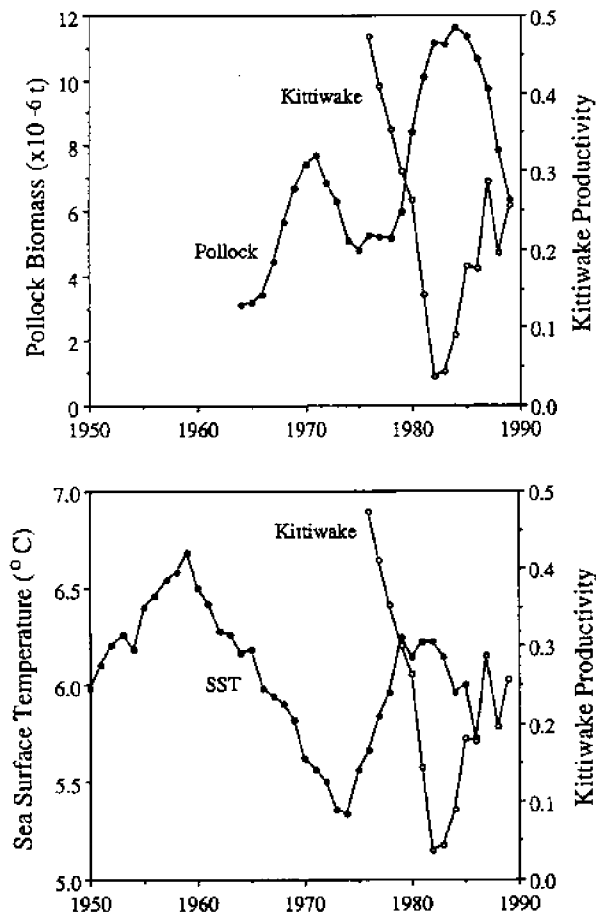
Figure 7. Relationship between kittiwake productivity on the Pribilof Islands and pollock biomass and sea surface temperature in the eastern Bering Sea. From Springer (1992).

between productivity and water temperature, but that might be misleading. That is, kittiwake productivity began to decline at least four years before the recent increase in pollock and, although its low point coincided with the early years of peak biomass, productivity began to rise before pollock biomass began to fall (Fig. 7). In contrast, the decline in kittiwake productivity and warming water temperature corresponded much more closely in time, as did the rise in productivity and the cooling of temperatures.

Murres and kittiwakes on the Pribilofs and on St. Matthew-Hall islands feed on a variety of prey, but the most important species is juve-

nile (age 0-1) pollock (Hunt et al. 1981, Springer et al. 1986, Murphy et al. 1987, D. Dragoo 1991). Pollock comprises about 60%-70% of the diets of murres and Black-legged Kittiwakes and 30% of the diets of Red-legged Kittiwakes on the Pribilofs, and about 70%-90% of murre and Black-legged Kittiwake diets on St. Matthew-Hall islands. Juvenile pollock apparently have declined since the early 1970s, notwithstanding the exceptionally strong 1978 year class and above average 1977 and 1982 year classes (Fig. 8). There is a strong positive correlation between the mean abundance of murres and kittiwakes on the Pribilof Islands and the abundance of age 1 pollock in the eastern Bering Sea (Fig. 9).

At Cape Peirce and Nunivak Island, numbers of Common Murres and Black-legged Kittiwakes have been stable since the early to mid-1970s (Haggblom 1991; McCaffery 1989, unpubl. data). However, kittiwake productivity at Cape Peirce and nearby Round Island has
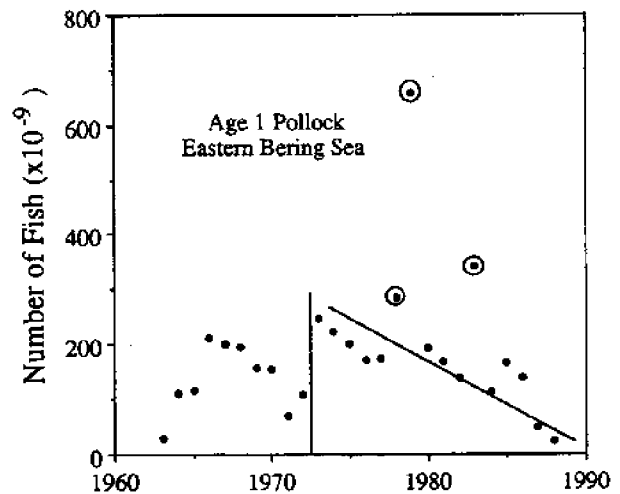

Figure 8. Trend in abundance of age 1 pollock in the southeastern Bering Sea. Regression line fitted by hand. The three circled values are departures from the overall trend since 1973. The correlation between year and abundance is not significant if all values are used, but is significant if the highest value (1979) is omitted ($r^2 = 0.35$, $p < 0.05$) and is highly significant if the two highest values (1979, 1983) are omitted ($r^2 = 0.66$, $p < 0.01$). Data are from Quinn and Collie (1990); figure is from Springer (1992).
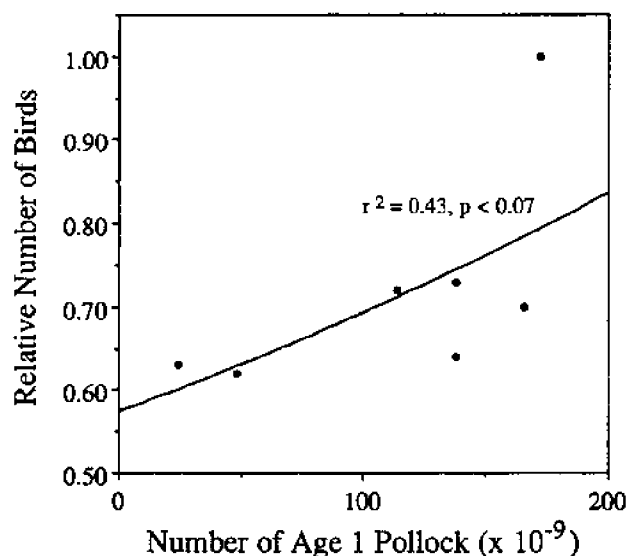
Figure 9. Relationship between the mean abundance of Common and Thick-billed Murres and Red-legged and Black-legged Kittiwakes on the Pribilof Islands and the abundance of age 1 pollock in the eastern Bering Sea. Exponential fit of data.

been generally poor (Fig. 10). Kittiwakes apparently feed primarily on sand lance at Cape Peirce, while common murres feed on sand lance, saffron cod, and pollock (Lloyd 1985, unpubl. data; V. Mendenhall unpubl. data). The consistently low productivity of kittiwakes during both the 1970s and 1980s contrasts with patterns at other colonies in the Bering Sea, and might indicate that factors, such as avian predators, are additional important causes of egg and chick mortality (e.g., Haggblom and Mendenhall 1991).

Auklets apparently have declined considerably in this century on St. George Island due to the loss of nesting habitat as vegetation encroached on the talus fields of the island (Roby and Brink, 1986). But, Least Auklets apparently increased in number on both St. George Island and St. Paul Island (Pribilof Is.) between 1976-82, while Crested Auklets and Parakeet Auklets either increased or remained stable (Craighead and Oppenheim 1985). A third census in 1984 failed to indicate further gains (Johnson 1985). Still, there is no indication of

declining populations like those of the piscivores.

Aleutian Islands

There is little information on population trends of seabirds in the central or eastern Aleutian Islands and there is no evidence of changing numbers. Counts of murres on Bogoslaf Island in 1984 were similar to 1973, and Tufted Puffin burrow counts on Aiktak Island in 1990 were about the same as in 1980 (Byrd et al. 1992).

Conditions in the western Aleutian Islands, however, appear to have been very good for seabirds during the past 15-20 years. Murres and kittiwakes on Buldir Island have increased by an average of nearly 400% since the mid-1970s and Common Murres have doubled on Agattu Island (Fig. 11). Numbers of Black-legged Kittiwakes at Agattu Island do not show such a clear trend. Common Murres nest in relatively small numbers at Buldir, Thick-billed Murres are uncommon at Agattu, and Red-legged Kittiwakes do not nest at Agattu. Productivity of kittiwakes has been variable since 1988 (Williams and Byrd 1992).
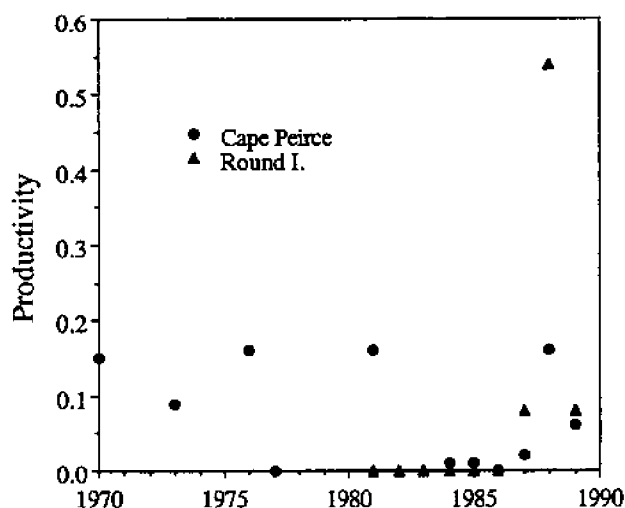
Pollock apparently is not important to sea-

Figure 10. Productivity of Black-legged Kittiwakes at Cape Peirce and Round Island. From data summarized by Hatch et al. (1992).
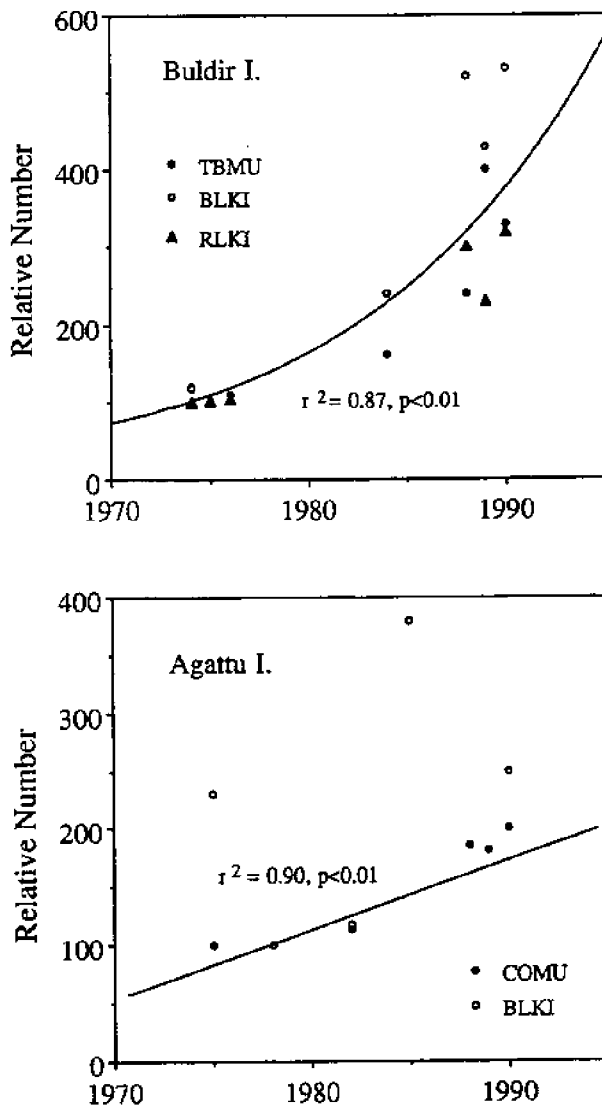
Figure 11. Trends in numbers of murres and kittiwakes on Buldir and Agattu islands (western Aleutian Islands). Exponential fit of Buldir data, linear fit of Common Murre data at Agattu. Data are from Byrd and Douglas (1989) and V. Byrd (unpubl. data). TBMU = Thick-billed Murre; BLKI = Black-legged

birds as prey in the western Aleutians (Whele 1976, Springer 1991). On Buldir, Thick-billed Murres and both species of kittiwake feed primarily on lanternfish (e.g., *Stenobrachius leucopsarus*), squids, greenling (e.g., *Pleurogrammus* spp.), and some sand lance, while on Agattu, Common Murres and Black-legged Kittiwakes feed almost entirely on sand lance. Sand lance also is important to seabirds

at other islands in the central Aleutians (Springer 1991) and probably the eastern Aleutians, and juvenile pollock is important prey fed to Tufted Puffin chicks in the eastern Aleutians (Sanger and Hatch 1987).

Sand lance is an essential prey species of piscivorous seabirds throughout most of the Bering Sea (Springer 1991). The rather infrequent occurrence of sand lance at Buldir Island has been attributed to the lack of shallow water surrounding it compared to other islands in the Aleutian chain, such as the neighboring Near Islands, which have relatively expansive shallows and where sand lance is by far the most important prey of seabirds (Springer 1991). Judging from the small number of sand lance in seabird diets on the Pribilofs and St. Matthew Island, they are uncommon in both places in spite of an extent of shallow water around them similar to that around many of the Aleutian Islands where sand lance are common. One important difference between the Aleutian Islands and the Pribilofs and St. Matthew Island, though, is the abundance of pollock, which is insignificant in the Aleutians compared to the shelf around the Pribilofs and St. Matthew Island. The paucity of sand lance might be related to the surfeit of pollock.

Gulf of Alaska

Twenty-three species of seabirds regularly breed at colonies in the Gulf of Alaska, of which murres, kittiwakes, puffins, fulmars, and storm-petrels (*Oceanodroma* spp.) are the most abundant (Sowls et al. 1978). Those species and others were investigated in some detail during the mid-late 1970s (Baird and Gould 1986, DeGange and Sanger 1986). Monitoring programs were continued or have been reactivated in the 1980s in a few areas, including Prince William Sound (Irons et al. 1987), Middleton Island (Nysewander et al. 1986), and the Semidi Islands (Dragoo and Bain 1990). There is no evidence of downward trends in the populations or productivity of murres or puffins (Hatch and Hatch 1989, Byrd et al.

1992), fulmars (Dragoo and Bain 1990, Hatch and Hatch 1990), or cormorants (*Phalacrocorax* spp.) (Nysewander et al. 1986, Hatch and Hatch 1990). Populations of Glaucous-winged Gulls and Pelagic Cormorants (*P. pelagicus*) at Middleton Island (Nysewander et al. 1986, S. Hatch unpubl. data) and Northern Fulmars at the Semidi Islands (Hatch 1992) might be increasing.

In contrast to most species in the Gulf of Alaska, Black-legged Kittiwakes show signs of a population under increasing stress. The mean productivity of kittiwakes at outer coast colonies (Semidi Is., Chiniak Bay, and Middleton I.) declined in the 1980s to about half the mean levels observed in the 1970s, and the frequency of colony failures (fewer than 0.1 young/pair fledged) has increased (Fig. 12). Six of eight years observed at Middleton Island since 1983 have been total or near-total breeding failures, as have six years observed at

the Semidi Islands over the same period. This pattern does not exist at inner coast colonies (Kachemak Bay and Prince William Sound), however, suggesting that the two regions are affected by different physical or biological processes.

The evidence of overall population trends in kittiwakes is equivocal. A decline of 50% has occurred in the large colony on Middleton Island since 1981, whereas smaller colonies in Chiniak Bay (Kodiak I.) have shown marked increases since the late 1970s (Hatch et al. 1992). Between 1976 and 1990, there was relatively little change at the Semidi Islands, in spite of poor productivity during the 1980s (Hatch and Hatch 1988, Dragoo and Bain 1990), or at several other colonies in the northern Gulf of Alaska and Prince William Sound (Irons et al. 1987, Nysewander and Dipple 1992).

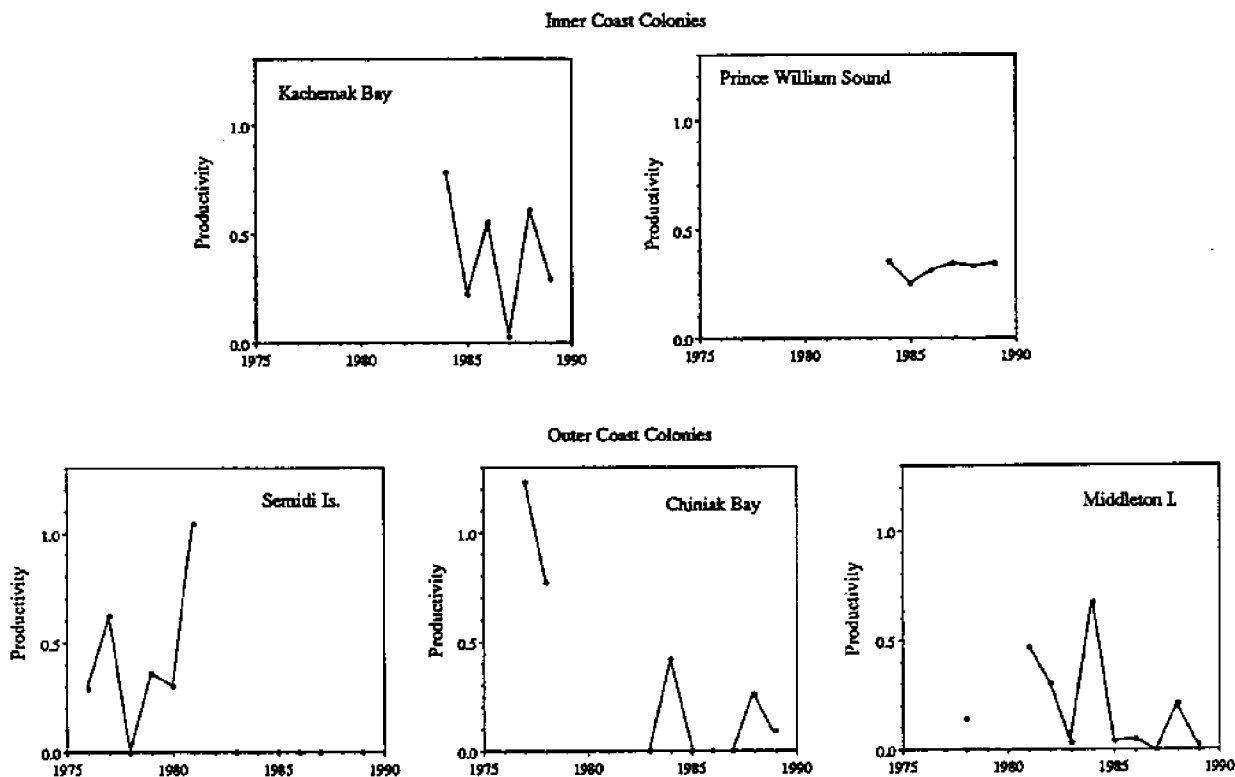Overall, sand lance appears to be the most important summer prey of murres, kittiwakes,

Figure 12. Productivity of Black-legged Kittiwakes in the Gulf of Alaska. From data summarized by Hatch et al. (1992).

and other piscivorous seabirds in the Gulf of Alaska (Sanger 1987). Capelin was important in kittiwake diets around Kodiak Island in the late 1970s, but there are no recent data from that area. Kittiwakes took mainly lanternfish in April-May at Middleton Island in 1990 (B. Fadely and S. Hatch unpubl. data). A few pollock were consumed later in the season at Middleton Island, but sand lance was the main prey in mid-summer.

Heavy use of walleye pollock by Tufted Puffins has been documented at colonies in the western Gulf of Alaska (Sanger and Hatch 1987). Diets of puffin chicks consisted of up to 75% pollock (age 0) in those areas in 1986 and 1987, whereas sand lance and capelin predominated at colonies in the central and eastern Gulf, including the Semidi Islands and Middleton Island. The pollock fed to puffin chicks in the western Gulf probably originated in Shelikof Strait, and the east to west gradient of increasing importance of juvenile pollock is probably proportional to their development time and local current speeds.

The initial period of decline in kittiwake productivity at outer coast colonies in the Gulf of Alaska coincided with an apparent rise in pollock biomass during the late 1970s and early 1980s (Fig. 13). Pollock biomass peaked in 1982-83 and has been declining since, and kittiwake productivity has continued to decline. Kittiwake productivity in the Gulf is related to water temperature in a similar way as on the Pribilof Islands—that is, productivity fell as temperature rose between 1975-85. Water temperature is now cooling, which might lead to a reversal of kittiwake fortunes if temperature affects the availability of prey.

There have been instances of widespread mortality of adult and juvenile seabirds during summer (late July-September) in the Gulf of Alaska during the 1980s. Kittiwakes and Short-tailed Shearwaters (*Puffinus tenuirostris*) were most prominent among the affected species, but others included fulmars, cormorants, and puffins. The most severe event in 1983 was not confined to the Gulf, however, but included
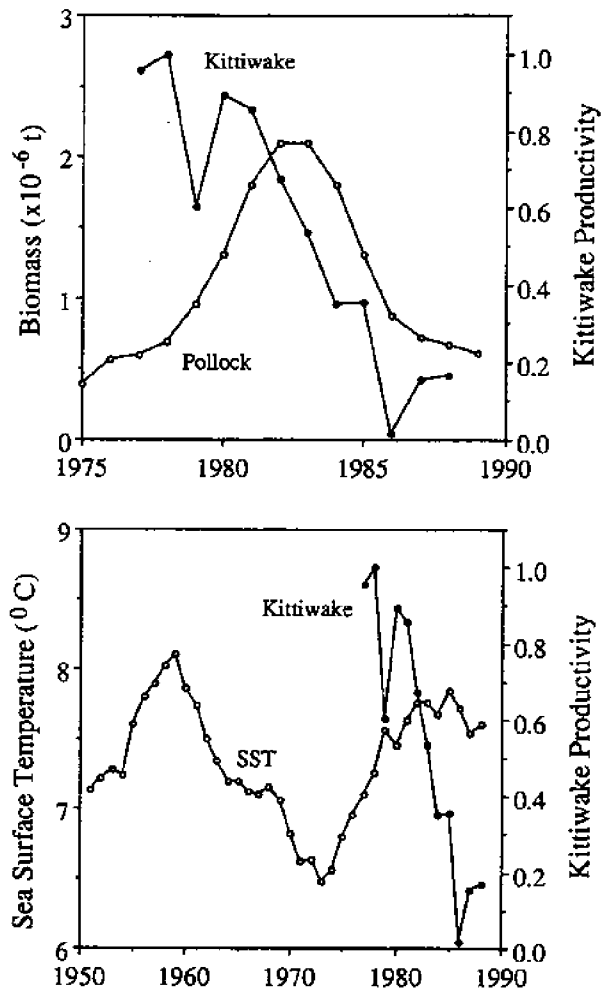

Figure 13. Relationship between kittiwake productivity at outer coast colonies and pollock biomass and sea surface temperature in the Gulf of Alaska. Three-year running mean of productivity at the Semidi Is., Chiniak Bay, and Middleton I.

the eastern and western Bering Sea and eastern Chukchi Sea (Nysewander and Trapp 1984); a lesser event, apparently unrelated to the oil spilled from the *Exxon Valdez*, was documented in 1989 (Piatt et al. 1990). Autopsies of dead birds have indicated that starvation was the most likely cause of death, since most carcasses were extremely emaciated (Nysewander and Trapp 1984).

Energetics Considerations

An energy budget was calculated for seabird populations of the Pribilof Islands, for

which moderately good census estimates exist and about which present concerns are greatest. Field metabolic rates (FMR) were measured at the Pribilofs by G. Gabrielsen and B. Flint using doubly-labeled water, except for fulmars and Horned Puffins, which were assumed to have field metabolic rates of 3x basal metabolic rates (BMR) as predicted from published allometric equations.

In addition to breeding seabirds, G. Hunt found large numbers of Short-tailed Shearwaters in the area of St. Paul Island in 1987 and 1988. The mean density he recorded was 150 birds/km over an area estimated at 15,400 km^2. These 2,300,000 birds, which weigh about 350 g each, have a predicted BMR of 160 kJ/d. Assuming a FMR of 3x BMR and that the birds are present from June-September, their food requirement would be 1.8×10^{11} kJ. This can be compared with a total for Pribilof breeding seabirds of 7×10^{11} kJ. The overall food requirement from the area of nearly 9×10^{11} kJ can be converted to about 100,000 t of prey. Much of this is euphausiids, but in the order of 50,000 t could be pollock, since pollock is an important food of murres and kittiwakes.

Wiens (1984) estimated that Pribilof seabird breeding populations took 53,600 t of food each year during the 4-month breeding season. If a calorific value of 8 kJ/g is assumed for prey, that total is equivalent to 4.5×10^{11} kJ. Given the tentative nature of the data, Wiens' total and this one are essentially the same. That the present estimate is slightly higher can be attributed to FMR values for Pribilof seabirds being higher than those found in many other seabird studies. The high FMRs may be taken to reflect food stress—Pribilof seabirds appear to have to work harder than seabirds in most other regions and so the community energy demands are raised.

CONCLUSIONS

The evidence presented at the conference strongly supports the hypothesis that food limitation is the cause of the declining bird popula-

tions on the Pribilof Islands. Energetics studies of seabirds on the Pribilofs and observations of dying chicks there in many years indicate that birds are food stressed. There was a lack of consensus on the importance of the roles played by pollock versus other prey species in the natural histories of the declining populations, except it was agreed that changes in the abundance and biomass of pollock are important clues to discovering the cause of insufficient prey. For example, juvenile pollock have been the single-most important prey of seabirds on the Pribilof Islands since the mid-1970s. Numbers of murres and kittiwakes on the Pribilof Islands and numbers of juvenile pollock in the southeastern Bering Sea have declined during that time. These observations support the hypothesis that seabird abundance on the Pribilofs is proportional to the abundance of *juvenile* pollock. On the other hand, adult pollock are cannibals as well as predators and trophic competitors of small forage fishes. Overall pollock biomass, and thus their total food requirement, increased substantially during the period of the greatest decline in seabird abundance (Springer 1992), which supports the hypothesis that seabird numbers on the Pribilofs are inversely proportional to the *overall* biomass of pollock because of a depressing effect that pollock have on populations of more suitable forage fishes.

The productivity of murres and kittiwakes on the Pribilofs is negatively correlated with sea surface temperature (SST) and with pollock biomass. The correlation between productivity and SST implies that SST has a depressing effect on the abundance of important prey or on the availability of prey.

Numbers of murres and kittiwakes in the western Aleutian Islands have been increasing dramatically during the time that those on the Pribilofs have been falling. Lanternfish, sand lance, squid, and greenling are the main prey of piscivorous seabirds in the western Aleutians, but pollock is not important as prey. The increasing numbers of birds supports the hypothesis that prey availability in the western

Species	Number of Individuals	Days at Colony	Field Metabolic Rate (kJ d^{-1})	Population Energy Intake (kJ x 10^{-10})
Black-legged Kittiwake	103,000	135	800	1.5
Red-legged Kittiwake	222,200	135	900	3.6
Common Murre	193,900	120	1,870	5.8
Thick-billed Murre	1,610,000	120	2,080	53
Least Auklet	273,000	120	533	2.3
Fulmar	70,700	200	942	1.8
Parakeet Auklet	184,000	120	533	1.6
Horned Puffin	32,400	150	915	0.6

Aleutians has risen in recent years.

Kittiwakes on Middleton Island in the Gulf of Alaska have declined by about half since 1981, but they have increased or remained stable at other colonies. Sand lance and capelin have been the primary prey of kittiwakes, and other piscivorous seabirds, at the colonies where population numbers have been monitored, including Middleton Island. Pollock is important to seabirds in the western Gulf only. Therefore, the situation in the Gulf of Alaska might not be the same as that in the Bering Sea.

The abundance of planktivorous auklets on the Pribilofs apparently has been stable or increasing since the mid-1970s and has increased considerably since the mid-1960s on St. Lawrence I. These trends support the hypothesis that the overall production potential, or "carrying capacity," of the Bering Sea or Gulf of Alaska has not declined in recent years because of depressed primary and secondary production (bottom-up control). An alternative hypothesis (top-down control) is that something changed at a higher level in the food web that has had deleterious effects at similar trophic levels in certain regions (e.g., Pribilofs) but positive effects in others (e.g., western Aleutians).

RECOMMENDATIONS

1. In view of the high energy demand of the Pribilof seabird community, the continuing decline in numbers of murres and kittiwakes (the Red-legged Kittiwake being a relatively scarce species with the bulk of its world population nesting on the Pribilofs), the apparent food stress affecting these seabirds, and the recent changes in breeding success, continue studies of the diets, breeding success, and numbers of kittiwakes and murres on the Pribilofs in order to determine the important food linkages.

2. The contrasting trend of rapidly increasing abundance of murres and kittiwakes in the western Aleutians indicates that very different environmental (physical or biological) conditions are present there than around the Pribilofs. Therefore, continue parallel studies of seabird diets, productivity, and abundance on the Near Islands and Buldir Island.

3. Conduct similar work annually on Middleton Island, Kodiak Island, and the Semidi Islands in the Gulf of Alaska. Additional emphasis should be placed on the

monitoring of numbers, productivity, and diets of important indicator species such as Common Murres, Black-legged Kittiwakes, and Tufted Puffins.

4. Monitor numbers, productivity, and diets of auklets in the Bering Sea. Appropriate sites would be the Pribilofs and St. Matthew Island. If the decline in piscivorous species has been caused by major food web changes, then measurable changes should be occurring in populations of planktivores as well.

5. Initiate feeding experiments to examine the relative nutritional value to seabirds of prey species such as pollock, sand lance, and capelin.

6. Define "critical habitat" for seabirds and monitor forage fish populations in critical areas.

7. Initiate studies to determine the movements of juvenile seabirds and the causes and levels of mortality after they leave the colonies.

8. Adopt a top-down interdisciplinary approach to ecosystem studies. There is no doubt that the upper trophic level species are indicating important areas of research.

9. Incorporate a restoration and conservation philosophy into marine ecology and resource management.

10. Develop consistent and reliable funding sources.

ACKNOWLEDGMENTS

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DISTRIBUTION AND ABUNDANCE TRENDS
OF FORAGE FISHES IN THE
BERING SEA AND GULF OF ALASKA

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INTRODUCTION

This report is written with respect to a hypothesis concerning declines in marine mammal and seabird populations observed since the mid-1970s:

H_0: Food limits the survival and natality of marine mammals and seabirds.

This first hypothesis is too general to be refutable; therefore, for the purpose of this study we dissect it into four sub-hypotheses listed below. Because of data limitations, we will only examine the period since the mid-1970s:

H_a: Overall prey abundance has declined.

H_b: Prey species composition has changed.

H_c: The size composition of important prey species has changed.

H_d: The temporal/spatial distribution of prey species has changed.

The hypothesized changes in fish distribution and abundance could result from fishing and/or environmental changes. We are primarily concerned with documenting the abundance of forage species, and secondarily with explaining the cause of any changes.

Following the remainder of this introduction we discuss separately the commercially exploited forage fish resources of the Bering Sea/Aleutian Islands region and the Gulf of Alaska because each of the two areas is assessed and managed under a separate Fishery Management Plan. The next part summarizes relative abundance and distributional information on non-exploited forage species in both areas. Finally we summarize the information with respect to the above hypotheses.

Forage species are generally defined as small schooling fish and squid that serve as prey for marine mammals, seabirds, and other fish. In the Bering Sea and Gulf of Alaska, forage fish species include juvenile walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), rainbow smelt (*Osmerus mordax*), eulachon (*Thaleichthys pacificus*), Pacific sand lance (*Ammodytes hexapterus*), and lanternfishes (family Myctophidae). Forage squid species include *Berryteuthis magister*, *Onychoteuthis borealijaponicus* and *Gonatopsis borealis*.

What—if anything—is known about recent trends in abundance and the general distribution of forage species? Our information is summarized largely from three sources: the proceedings of a conference on Forage Fishes of the Southeastern Bering Sea (Minerals Management Service 1987), Stock Assessment and

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Fishery Evaluation (SAFE) Reports for the Bering Sea/Aleutian Islands Region and the Gulf of Alaska as projected for 1992, and data collected by observers aboard commercial trawl vessels in the eastern Bering Sea and Gulf of Alaska.

Since the mid-1970s, observers aboard fishing vessels in the eastern Bering Sea and Gulf of Alaska have obtained detailed catch records for commercial groundfish and non-commercial species (such as forage fish), on a haul-by-haul basis. Data recorded with each haul include the haul duration, catch weight of each species encountered in a sub-sample of the total catch scaled up to total haul weight, and location and date of each haul. This large data set has been explored for trends in the distributions and abundances of non-target species, most of which serve as prey for a variety of marine mammals, birds, and other fish.

Data from all observed, sampled hauls in the Bering Sea, Aleutian Islands region, and Gulf of Alaska were summarized for the years 1980-1989, by quarter (months 1-3, 4-6, 7-9 and 10-12), by 2° latitude x 4° longitude blocks (14,400 square miles) and for 13 species and species-groups. Data consist of date and location codes, the total weight of each species caught and the duration of all hauls in each time/area cell. Species catch weights were divided by the total haul duration to estimate catch per unit effort (CPUE), or relative abundance, for each time/area cell for each of the following species/groups: Pacific herring, capelin, eulachon, other smelts, Pacific sand lance, lanternfish, and squid. There was little information in the observer database on catches of capelin, other smelts, Pacific sand lance, and lanternfish; these fish are less vulnerable to capture by groundfish trawls due to their small size, pelagic distribution, and/or relatively shallow water habitats. Interpretation of the squid CPUE data, especially with regard to relative abundance, is confounded by the fact that it was a target species of the foreign fleets fishing in the Bering Sea in the early 1980s but is

no longer commercially sought. Ancillary catches of Pacific herring (used only to determine seasonal distribution of bycatch) and eulachon (used both in seasonal distribution and for determination of abundance trends) were large and frequent enough for further analysis. However, the non-standardized sampling regime, and the large number and wide variety of gear types, vessels, and fishing practices employed, forces us to treat with caution any conclusions based on these analyses—especially those regarding abundance trends in eulachon. Eulachon abundance trends should be considered as relative abundance indices, not absolute biomasses.

EASTERN BERING SEA FISHERY RESOURCES

Of the 300 or so fish species in the eastern Bering Sea, 20 are commercially exploited. Total annual harvests of fish and shellfish from the eastern Bering Sea have ranged from 1 to 2 million t since the early 1970s. Most of the commercially exploited species have been studied extensively for at least 10 years, so a reasonably good data base has been assembled on these species.

The outer continental shelf and slope is the most productive area. Here, the walleye or Alaska pollock (*Theragra chalcogramma*), a gadoid, is the dominant species. It constitutes over 67% of the total eastern Bering Sea groundfish biomass (average exploitable biomass, 1977-88: 9 million t). Since the mid-1960s this fish has made up the major portion of the catch (Fig. 1). Deep-water flatfish, Greenland halibut (*Reinhardtius hippoglossoides*), arrowtooth flounder (*Atheresthes stomias*), rockfish (*Sebastes* sp.), and sablefish (*Anoplopoma fimbria*) also occur on the outer continental shelf, but their biomass in aggregate is about 300,000 tons, 66% of which is arrowtooth flounder.

On the middle and inner shelf, flatfish (with an aggregate biomass of approximately 4 million t in 1989) and crabs predominate. The

yellowfin sole (*Limanda aspera*) is the dominant species in this group with a biomass of about 2 million t (Fig. 2). Rock sole is the second most abundant at 1 million t. Other less important species are Alaska plaice (*Pleuronectes quadrituberculatus*) and flathead sole (*Hippoglossoides elassodon*). Red king crab (*Paralithodes camtschatica*) and two species of tanner crab (*Chionoecetes bairdi* and *C. opilio*) also occur. The crab species provide an average harvest of 54 thousand t, but their abundance is highly variable (Otto 1981).

The coastal domain shoreward of the middle shelf has been studied less intensively than the middle and outer shelf regions. Along the Alaska Peninsula, the coastal region is utilized by migrating Pacific salmon (*Onchorhynchus* sp.) and herring (*Clupea pallasii*). This is a major feeding area for Pacific cod (*Gadus macrocephalus*). Cod and herring move from wintering areas on the outer shelf to coastal waters for summer feeding, while salmon migrate across the inner shelf on their way to or from freshwater spawning grounds. Herring, the dominant commercial species of the coastal domain, was heavily fished by foreign fleets during the 1960s-70s (Fig. 1). As a consequence of fishing and year-class variation the stock was rapidly reduced in the early 1970s. Subsequent strong recruitment in the late 1970s led to the stock's recovery in the early 1980s
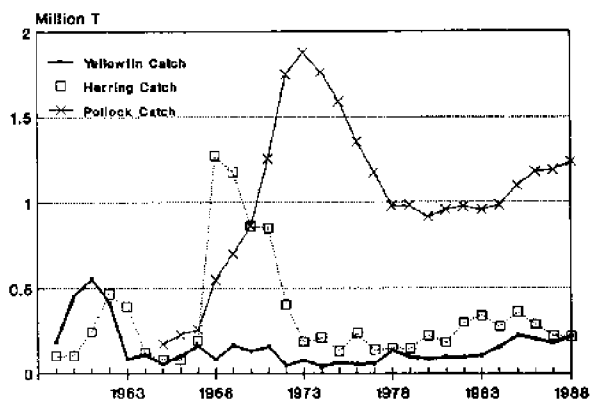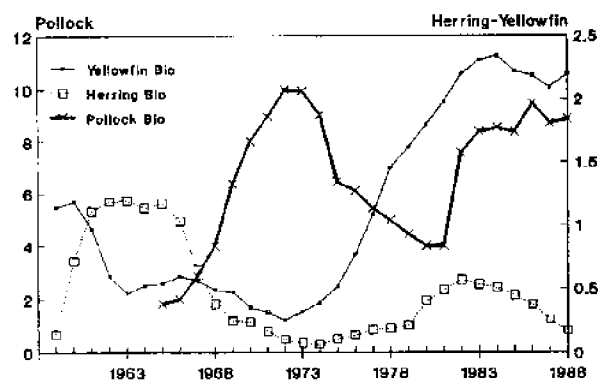

Figure 2. Biomass, in millions of metric tons, of pollock, herring and yellowfin sole in the eastern Bering Sea, 1959-88.

(Fig. 2 and 3).

The variation in the biomass of the principal commercial fish species in the eastern Bering Sea is primarily due to recruitment variation. Fishery removals have generally been low relative to biomass (Fig. 4). Excessive removals—greater than 40% of the exploitable biomass—occurred in yellowfin sole harvests in the late 1950s and in herring and yellowfin sole in the early to mid-1970s. However, exploitation of pollock has been low, rarely exceeding 20% (Fig. 4).

Walleye Pollock

Pollock is a semi-demersal species, primarily pelagic during the first few years of its life and becoming increasingly demersal with age. Pollock are found in coastal regions throughout the north Pacific, from Japan, through the Bering Sea and Gulf of Alaska, and south to central California on the North American coast. The species is greatest in abundance along the outer continental shelf and slope at depths ranging from 100-500 m. Young-of-the-year pollock, however, can be concentrated in relatively shallow coastal embayments along the Alaska Peninsula and around Kodiak Island (Smith et al. 1984; Spring and Bailey 1991). Older pollock can range pelagically into deep waters of the Aleutian Basin.

Pollock, one of the most abundant fish spe-

Figure 1. Catch of pollock, herring and yellowfin sole in the eastern Bering Sea, 1959-88.

cies in the north Pacific Ocean, supports large commercial fisheries along the Asian coast, in the Bering Sea and in the Gulf of Alaska. Although pollock spawn intermittently year-round, most spawning in the eastern Bering Sea and Gulf of Alaska occurs in winter and early spring (Kendall and Picquelle 1990). Pollock undergo seasonal movement associated with feeding and spawning. Large assemblages of spawning pollock near Bogoslof Island, on the southeastern Bering Sea shelf, and in Shelikof Strait have been the basis of roe fisheries since the early 1980s.

Eastern Bering Sea pollock abundance is estimated with cohort analysis and catch-at-age analysis, calibrated with trawl survey data (Wespestad and Dawson 1991). Information on discards was incorporated in the 1991 stock assessment. Discard rates were 8% in 1990 and 13% in 1991. Discards include both large and small pollock. When the directed fishery started in the 1960s, exploitable biomass (age 3+) was low (Fig. 2). Since then there have been two periods of high biomass: 1969-1975 and 1982 to present. Since 1988, biomass has decreased, to 7.3 million t in 1990 and an estimated 6.6 million t in 1991. This remains above the level expected to produce long-term MSY (6 million tons).
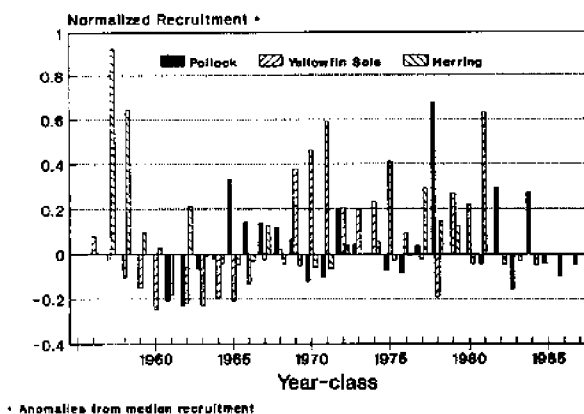
Abundance estimates for the Aleutian Is-

Figure 3. *Recruitment trends for pollock, yellowfin sole, and herring in the eastern Bering Sea by year-class.*
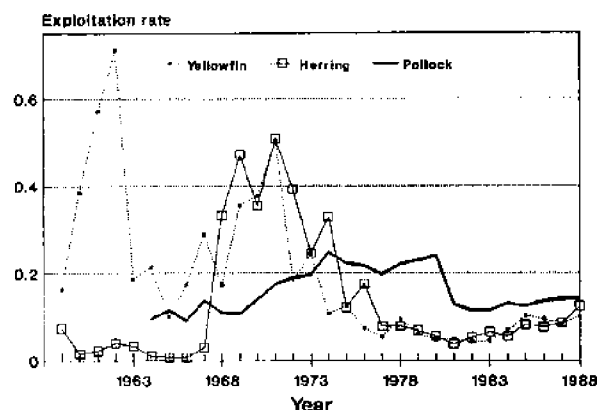

Figure 4. Rates of exploitation for pollock, herring, and yellowfin sole in the eastern Bering Sea, 1959-88.

land pollock stock come from periodic bottom trawl surveys. The 1991 estimate of exploitable biomass was 180,000 t, down from the 1986 survey. Pollock harvested in the Bogoslof Island fishery are generally older than those taken on the eastern Bering Sea shelf. These pollock, part of the Aleutian Basin stock, have been reduced in abundance from about 2 million tons to 0.6 million tons in 1991 (Wespestad and Dawson 1991).

Changes in pollock biomass stem from the underlying recruitment variability (Fig. 3). Pollock are partially recruited to the trawl fishery at age 2 (28 cm) and fully recruited by age 4 (40 cm). Strong pollock year-classes originated in 1965-69, 1972, 1978, 1982, and 1984. The large biomass prevalent in the 1980s was fueled by the exceptionally large 1978 year-class; this has been followed by the strong 1982 and 1984 cohorts. Preliminary survey data suggest that the 1989 year-class may be strong.

In the 1960s, a series of above-average year-classes entered the population (Figs. 2 and 3), causing an increase in abundance that was part of a wide-spread phenomenon in the North Pacific Ocean at that time. For instance, Kachina and Sergeyeva (1981) show evidence of an increase in the west Kamchatka shelf population (one of the largest populations of pollock in the North Pacific).

In the eastern Bering Sea, pollock recruit-

ment positively correlates with temperature (Fig. 5). The fact that in the 1960s pollock abundance increased throughout much of the North Pacific Ocean suggests that large-scale climatic events, with concurrent temperature increases, brought about the enhanced pollock production. Another large increase in abundance occurred in the late 1970s, also a warm period. The cold period of 1970-76 resulted in a decline in abundance during the mid-1970s. An exception was the 1972 year-class, spawned in a cold year, but one of the most abundant year-classes observed.

Pacific Herring

The Pacific herring is a common pelagic species in the Bering Sea and in coastal embayments of the Gulf of Alaska. In the Bering Sea, herring migrate seasonally from offshore wintering areas to inshore spring and summer spawning and feeding areas (Fig. 6). This migratory behavior was also observed in the seasonal patterns of herring bycatch by the groundfish fisheries (Funk 1990). The location of the wintering area, while generally northwest of the Pribilof Islands between 57-59° latitude, shifts in relation to the severity of the winters: in mild winters, herring concentrate farther north and west, while in severe winters, farther south and east (Shaboneev 1965). The primary
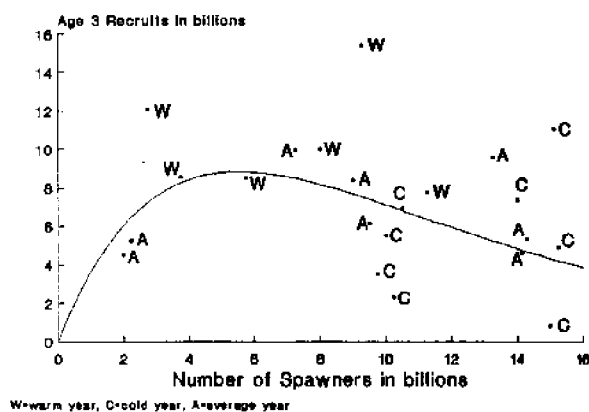

Figure 5. *Eastern Bering Sea pollock spawner-recruit relationship and relative temperature condition during the first year for each year-class.*

spawning areas for herring in the Bering Sea are Togiak Bay and Norton Sound, while other areas along the coasts of the Bering and Chukchi seas are of lesser importance (Fig. 7; Wespestad 1991).

Over the last 30 years, Pacific herring biomasses have fluctuated widely, due to both variability in recruitment and fishing pressures (Fig. 8; Wespestad 1991). Cohort analyses of populations in both the Bering Sea and the Gulf of Alaska indicate that the herring populations in both areas were low during the 1970s, but increased during the early 1980s. Assessments in the Bering Sea indicate that recent recruitment has been poor (Fig. 3), as evidenced by the declining biomass since 1982-83 (Fig. 8).

Herring in the eastern Bering Sea are less abundant (the mean biomass is about 475,000 t) than in other comparable areas such as the North and Barents seas. The frontal structure resulting from winter ice over the Bering Sea shelf may pose a physical limit on herring abundance by preventing herring from utilizing large areas of the middle shelf. A NWAFC survey across the middle shelf front found that herring were more prevalent on the warm side of the front and appeared to prefer 4°C waters. Interannual variation in abundance may be controlled by climatic factors. Wespestad and Gunderson (1991) found that the size of eastern Bering Sea herring year-classes was affected by water temperature and wind-driven transport. Favorable year-classes occur in years of light on-shore winds and warm water temperatures. Aside from inducing variability in recruitment, oceanographic structure in the eastern Bering Sea may limit herring habitat.

GULF OF ALASKA FISHERY RESOURCES

The Gulf of Alaska has a much narrower continental shelf than the eastern Bering Sea and supports a correspondingly smaller groundfish biomass. Overall, the groundfish stocks in the Gulf of Alaska are at a relatively high level
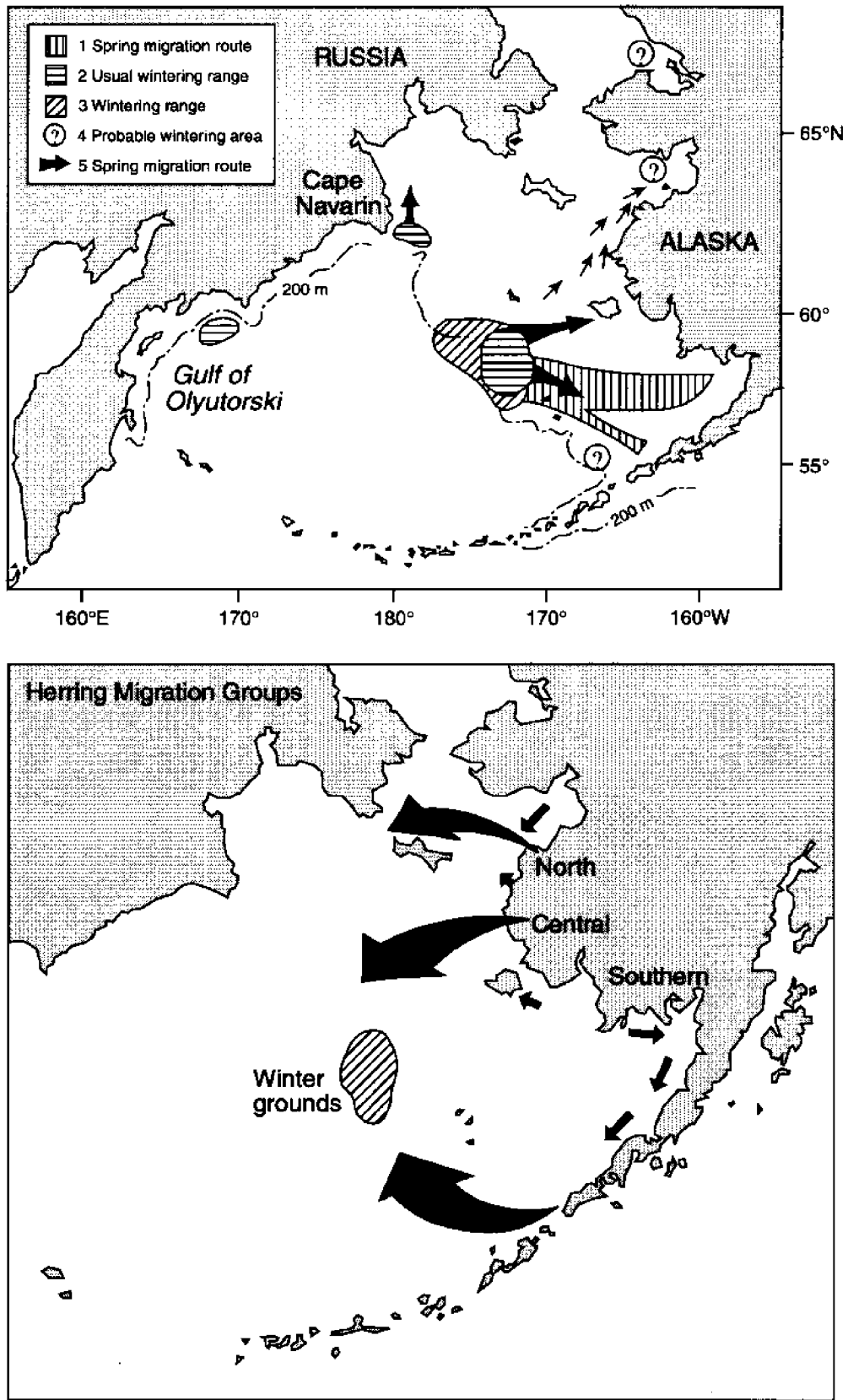
Figure 6. Migration routes of Pacific herring from wintering grounds to spawning areas (top; from Barton and Wespestad 1980) and to wintering grounds (bottom; from Wespestad 1991) in the eastern Bering Sea.
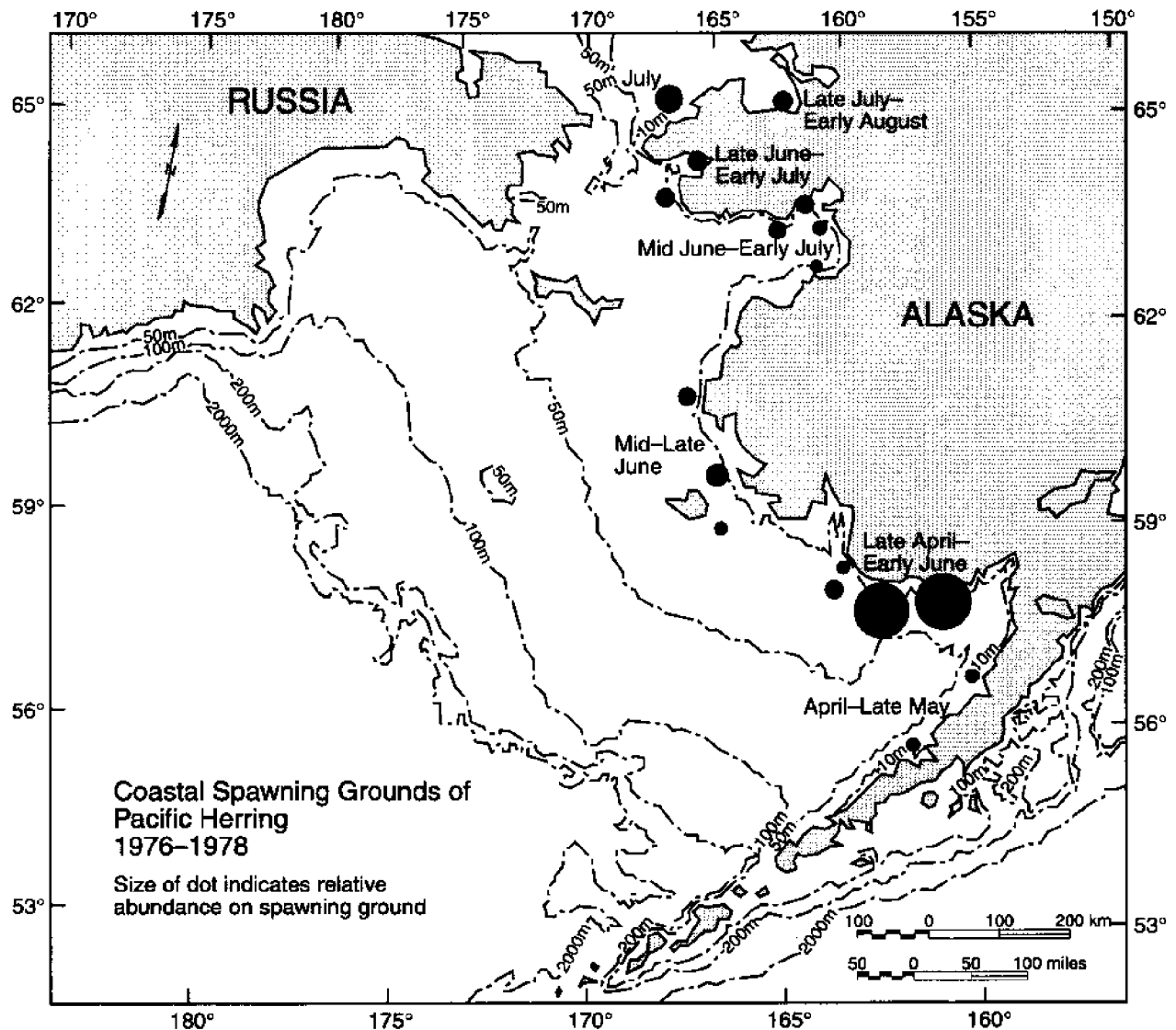
Figure 7. Major coastal spawning areas of Pacific herring in the eastern Bering Sea (from Wespestad 1991).

of abundance. The abundances of Pacific cod, sablefish, and most flatfish species are high; pollock is at an intermediate abundance level; rockfish abundance is low. The total allowable catch of groundfish is increasingly constrained by halibut bycatch caps, particularly in the flatfish fisheries.

Walleye Pollock

Pollock abundance, as estimated with the stock synthesis model (Hollowed et al. 1991), is much smaller in the Gulf of Alaska than in the Bering Sea. The model incorporates age-specific data from the commercial catch, annual hydroacoustic surveys, and triennial bottom-trawl surveys. Two important additions to the 1991 assessment are the inclusion of discard information and historical length-frequency data. Pollock may be discarded either because they are the wrong size for fillet machines or because they are taken as bycatch during a period when the pollock fishery is closed. Two years of discard data were presented in Table 6 of the 1991 SAFE document. The weighted discard rates, as a percentage of

total pollock removals, were approximately 14% in 1990 and 12% in 1991.

Strong pollock year-classes originated in 1962, 1972, 1975-1979, 1984, and 1988 (Fig. 9). The influence of these strong year-classes is reflected in the biomass time series. Alton et al. (1985) presented survey data that indicated a substantial increase in abundance of pollock in the Gulf of Alaska between 1961 and the early 1970s. Biomass peaked in the early 1980s and has declined since then to pre-1980 levels (Fig. 10). Current exploitable biomass (843,000 t in 1991) is above the level estimated to produce long-term MSY. The lowest level of spawner biomass that produced a strong

Figure 9. Relative year-class strength of walleye pollock in the eastern Bering Sea and Gulf of Alaska, 1962-1988/89. Data are results from cohort analyses (Bering Sea; Wespestad and Dawson 1991) and stock-synthesis analyses (Gulf of Alaska; Hollowed et al. 1991) of the pollock populations in each area.
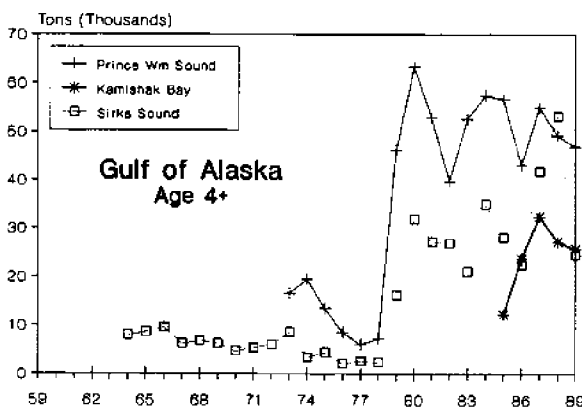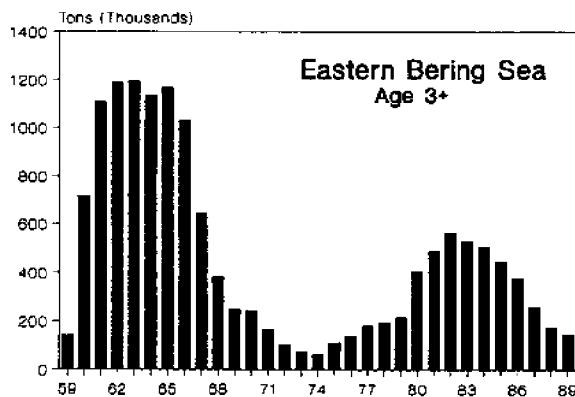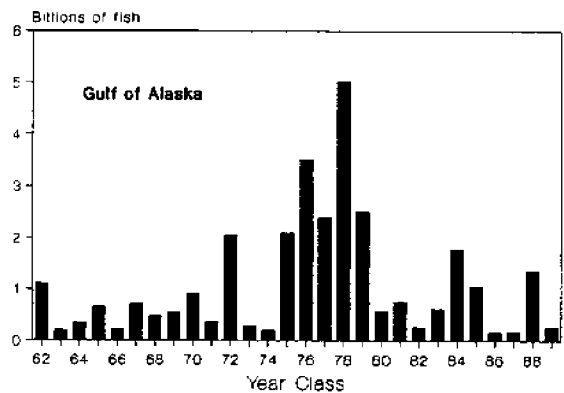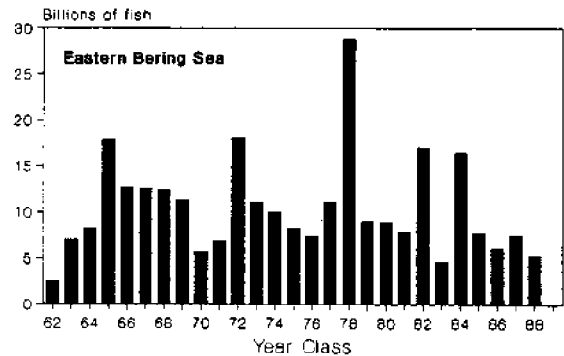
Figure 8. Biomass estimates from cohort analyses of Pacific herring in the eastern Bering Sea (Wespestad 1991) and several stocks in the Gulf of Alaska (F. Funk, ADF&G, pers. comm.).

year-class was 691,000 t for the 1975 cohort; current spawning biomass is above this level. The smallest spawning biomasses produced some of the strongest and weakest year-classes, suggesting that environmental changes are partially responsible for variations in the supply of young pollock, and in particular for the strong 1975-1979 year-classes.

Variability in year-class strength since the early 1960s appears to be greater in the Gulf of Alaska than in the Bering Sea (Fig. 9). From 1962-1988, the range in sizes of year-classes (assessed as 2-year-olds) in the Bering Sea (maximum: 1978 YC = 28.8 billion fish; minimum: 1962 YC = 2.5 billion; range = 26.3
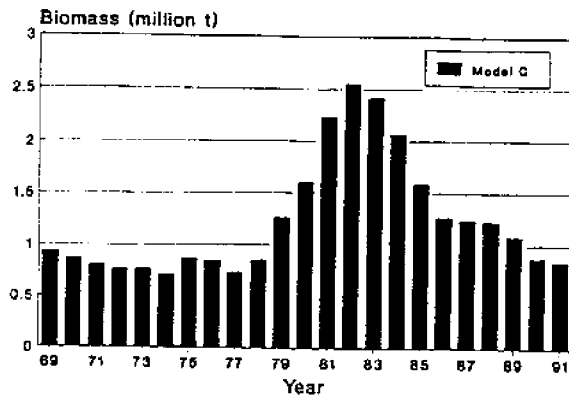
Figure 10. Biomass of pollock in the Gulf of Alaska as estimated with the stock synthesis model (from Hollowed et al. 1991).

billion) has been approximately three times the median year-class size of 8.8 billion fish. By contrast, in the Gulf of Alaska, the range is approximately eight times the median year-class size (maximum: 1978 YC = 5 billion fish; minimum: 1986 YC = 0.2 billion; range = 4.8 billion; median = 0.6 billion). There is some degree of recruitment synchrony between eastern Bering Sea and Gulf of Alaska pollock; the 1972, 1978 and 1984 year-classes were strong in both stocks.

Pollock exhibit wide annual variability in the distribution of juvenile (ages 0, 1, and 2 years) individuals. Surveys along the Alaska Peninsula and on the Kodiak archipelago (Smith et al. 1984; Spring and Bailey 1991) have shown that the abundance of juvenile fish in individual embayments fluctuated widely between years; reasons for these differences in distribution are unknown.

In 1990 the pollock TAC was divided into four equal quarterly allocations. To protect Steller sea lions, three management measures were implemented in 1991, distributing pollock fishing effort in the Gulf of Alaska in both time and space. These measures were:

1. Allocation of the pollock TAC to each of three management areas west of 147°W longitude in proportion to the biomass distribution of the most recent bottom trawl

survey;

2. Stipulation that re-allocation of unharvested amounts not exceed 150% of the initial quarterly allowance; and

3. Prohibition of fishing with trawl gear within 10 nautical miles of sea lion rookeries.

Pacific Herring

Pacific herring in the Gulf of Alaska are characterized by several more-or-less discrete stocks segregated by the location of their spawning aggregations. Principal herring stocks in the Gulf spawn in Kamishak Bay (mouth of Cook Inlet), Prince William Sound, and in Sitka Sound in southeast Alaska (F. Funk, ADF&G, pers. comm.). Abundance in the Gulf of Alaska has been estimated for several regions, for various time periods. Wespestad used cohort analysis to reconstruct the abundance of herring in the southeast Alaska reduction fishery from 1929-1966. The reduction fishery harvested a mixture of herring stocks; most of the herring were probably from the Sitka Sound stock. There were two periods of high abundance: from 1929-1934 and from 1954-1961 (Fig. 11).

Since 1959, the Alaska Department of Fish and Game has monitored the abundance of Sitka herring with an index of miles of spawn; catch-at-age analysis has been performed on data since 1971 (Collie 1991). Abundance was low during the 1970s and increased in 1979 with recruitment of the strong 1976 year-class. Since then biomass has remained at relatively high levels with the infusion of a strong cohort every four years. However, current biomass in Sitka is only about 10% of the peak biomass levels estimated for all southeast Alaska in the 1930s and 1950s. Recruitment from 1971 to 1990 was positively correlated with sea-surface temperature (SST) in Sitka sound and negatively correlated with along-shore winds (Zebdi 1991). Fluctuations in biomass correspond roughly to cycles in SST (Fig. 11).

Prince William Sound herring have an abundance pattern remarkably similar to Sitka Sound (Fig. 8). Biomass in Prince William Sound is
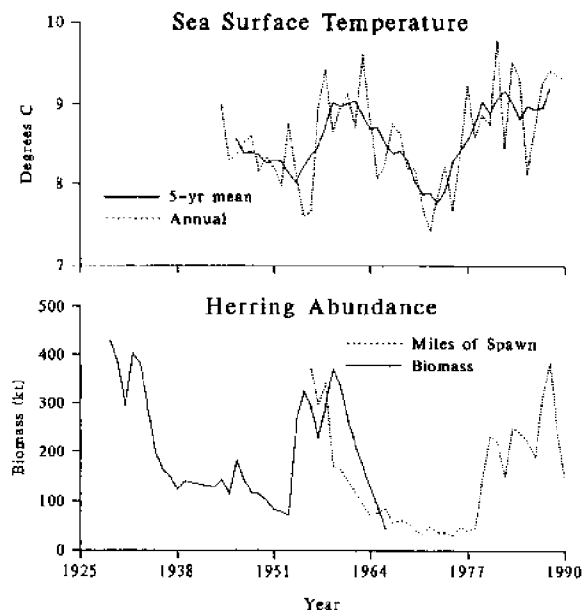
Figure 11. Sea surface temperature and herring abundance trends in southeast Alaska. Top: Sitka Sound sea surface temperature. Bottom: herring biomass estimated with cohort analysis for southeast Alaska reduction fisheries, 1929-66. Miles of spawn in Sitka Sound, 1955-90.

also at a high level compared with the 1970s. Limited data exist on other herring stocks in the Gulf of Alaska; five years for Kamishak Bay, for instance. Fritz Funk is performing catch-at-age analysis on data from other Alaska stocks, but results are still preliminary. In summary, herring in the Gulf of Alaska is currently at a high abundance level relative to the 1970s, but still much lower than the peak abundances estimated for earlier periods.

ABUNDANCE AND DISTRIBUTION OF NON-EXPLOITED FORAGE FISH SPECIES

Smelts (Capelin, Rainbow Smelt and Eulachon)

Smelts (family Osmeridae) are slender schooling fishes that can be either marine (such as capelin) or anadromous (rainbow smelt and

eulachon). Based on data collected by NMFS summer groundfish trawl surveys and by fisheries observers, a generalized distribution of these three smelt species in the southeastern Bering Sea (Fig. 12) can be drawn.

Capelin are distributed along the entire coastline of Alaska and south along British Columbia to the Strait of Juan de Fuca. In the North Pacific, capelin can grow to a maximum of 25 cm at age 4. Most capelin spawn at age 2-3, when they are only 11-17 cm (Pahlke 1985). Spawning occurs in spring in intertidal zones of coarse sand and fine gravel—especially in Norton Sound, northern Bristol Bay, and Kodiak. Very few capelin survive spawning. The age of maturity of capelin in the Barents Sea has been shown to be a function of growth rate, with fast-growing cohorts reaching maturity at an earlier age than slow-growing cohorts. Thus, it is possible to have slow and fast-growing cohorts mature in the same year, resulting in large spawning biomasses one year preceded and potentially followed by small spawning biomasses.

In the Bering Sea adult capelin are only found near shore during the months surrounding the spawning run. During other times of the year, capelin are found far offshore in the vicinity of the Pribilof Islands and the continental shelf break. The seasonal migration may be associated with the advancing and retreating polar ice front, as it is in the Barents Sea. In the eastern Bering Sea, winter ice completely withdraws during the summer months. If migration follows the ice edge, the bulk of the capelin biomass in the Bering Sea could be located in the northern Bering Sea, beyond the area worked by the groundfish fisheries and surveys. Very few capelin are found in surveys, yet they are a major component of the diets of marine mammals feeding along the winter ice edge (Wespestad 1987), and of marine birds, especially in the spring. In the Gulf of Alaska, which remains ice free year round, capelin overwinter in the bays of Kodiak Island and in Kachemak Bay. Little is known
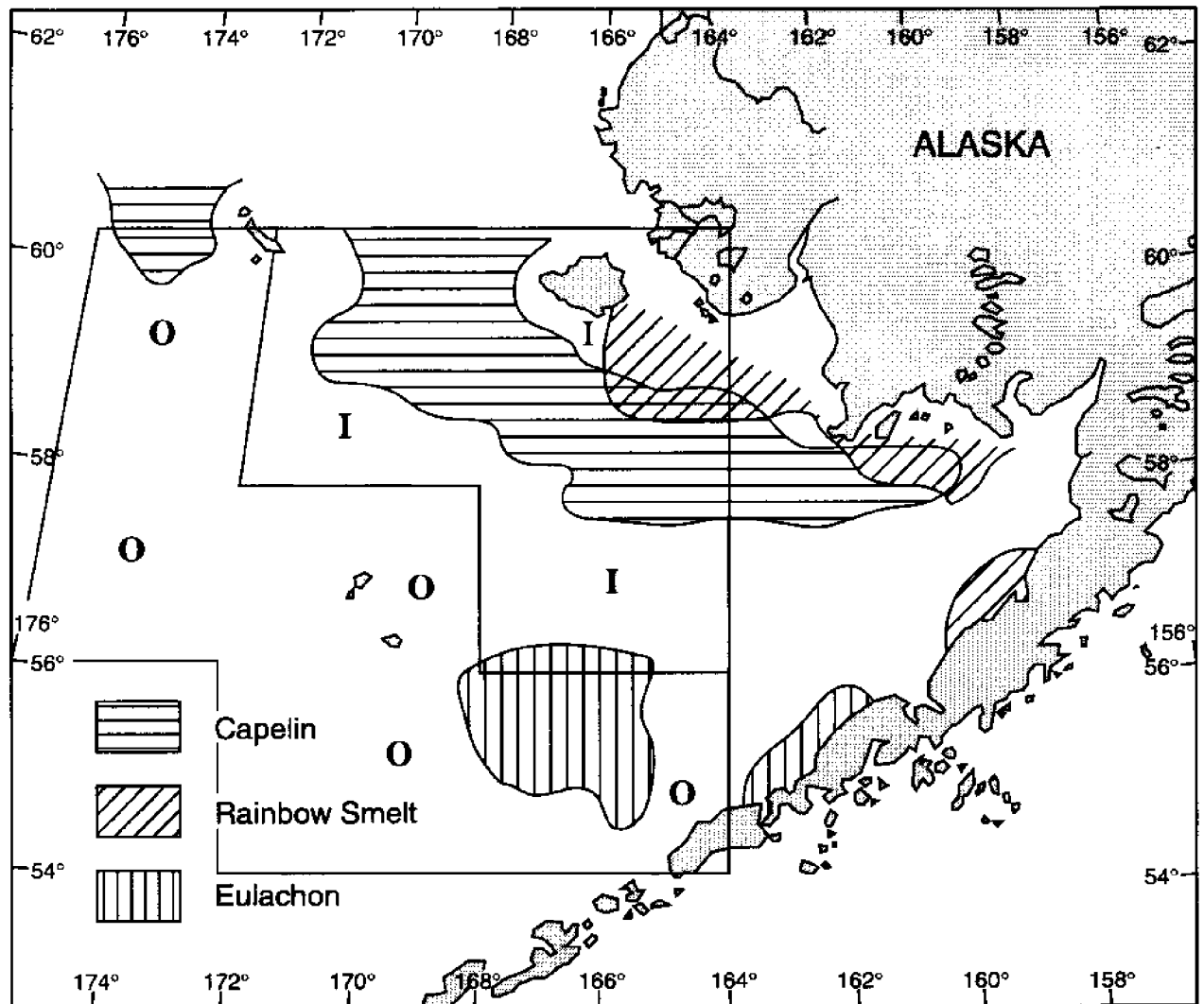
Figure 12. Generalized distribution of smelts in the eastern Bering Sea based on NMFS groundfish trawl surveys and fisheries observer data. Area marked with "O"s and "I"s represent outer and inner shelf areas, respectively, over which fisheries observer data pooled for analysis of eulachon abundance trends (Figure 13).

about trends in capelin abundance, except that fluctuations are common (Pahlke 1985).

Rainbow smelt ascend rivers to spawn in spring shortly after the breakup of the ice. After spawning, they return to the sea to feed. Surveys have found concentrations of rainbow smelt off Kuskokwim Bay, Togiak Bay, and off Port Heiden (Fig. 12), but they also probably occur in many nearshore areas near river mouths. Rainbow smelt mature at ages 2-3 (19-23 cm), but can live to be as old as 9 years and as large as 30 cm. Little is known about trends in abundance of this species.

Eulachon also spawn in spring in rivers of the Alaska Peninsula, and possibly other rivers draining into the southeastern Bering Sea. Eulachon live to age 5 (and grow to 25 cm), but most die following first spawning at age 3. Eulachon are consistently found by groundfish fisheries and surveys between Unimak Island and the Pribilof Islands in the Bering Sea, and in Shelikof Strait in the Gulf of Alaska (Fig. 12).

To determine if any trends existed, fisheries observers' catch-per-unit-effort data (kg eulachon per hour trawled) were pooled, by

year, for outer shelf and inner shelf areas of the eastern Bering Sea (Fig. 13). In both the outer and inner shelf areas, CPUE of eulachon declined from the early 1980s through 1989. Effort (hours of sampled trawls) during the same time period increased through the mid-1980s and has been lower since then. These data suggest (given all the cautions noted above in interpreting the data) that eulachon abundances have declined in the eastern Bering Sea during the last decade.

Data from recent groundfish trawl surveys in the eastern Bering Sea also hint at declining

eulachon abundances. Biomass estimates for the eastern Bering Sea and statistical area 517 (between Unimak Island and the Pribilof Islands and onto the southeastern Bering Sea shelf west of 165° longitude and south of 56°30' latitude) were higher in 1979 and 1984 and lower since 1985 (Fig. 14). Three-year moving averages (Fig. 14) reveal a general declining trend since 1982-84. These data should be interpreted with caution: these surveys are not designed to sample small pelagic fishes such as eulachon. Causes of the decline, if real, are unknown, but may be related to variability in year-class strength as noted for capelin.

Pacific Sand Lance

Because they do not possess air bladders, Pacific sand lance are negatively buoyant. They are usually found on the bottom, at depths between 0-100 m except when feeding (pelagically) on crustaceans and zooplankton. Spawning is believed to occur in winter. Sand lance mature at ages 2-3 years and lengths of 10-15 cm. Little is known of their distribution and abundance; they are rarely caught by trawls. In the Bering Sea, sand lance are common prey of salmon, northern fur seals, and many species of marine birds. Thus, they may be abundant in Bristol Bay, along the Aleutian Islands and Alaska Peninsula. In the Gulf of Alaska, sand lance are prey of harbor seals, northern fur seals, and marine birds, especially in the Kodiak area and along the southern Alaska Peninsula. Given the sand lance's short life span and the large number of species that prey on it, mortality, fecundity, and growth rates of Pacific sand lance are probably high.

Squid and Lanternfishes

Oceanic squids (families Gonatidae and Onychoteuthidae) constitute varying proportions of the diet of northern fur seals, harbor seals, Steller sea lions, sperm whales, and marine birds in the Bering Sea and Gulf of Alaska. Two species, *Berryteuthis magister* and
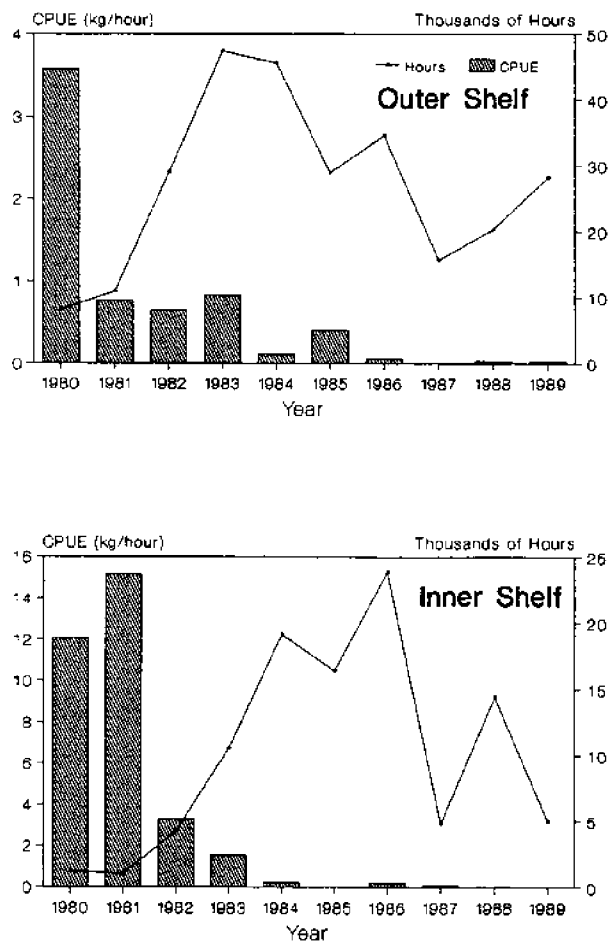

Figure 13. Trends in CPUE (catch per unit effort) of eulachon from fisheries observer data in outer and inner shelf areas of the eastern Bering Sea (see Fig. 12). Hours represent total duration of sampled trawls in region for each year.
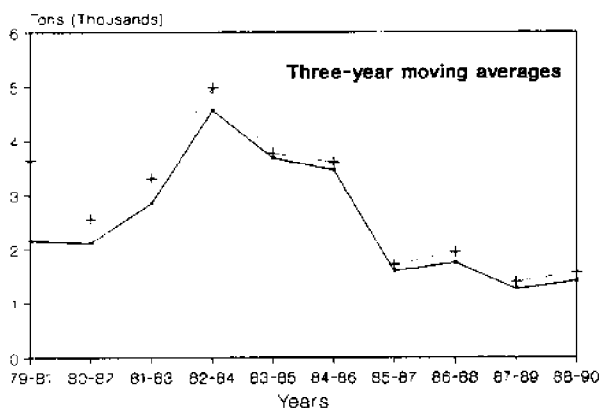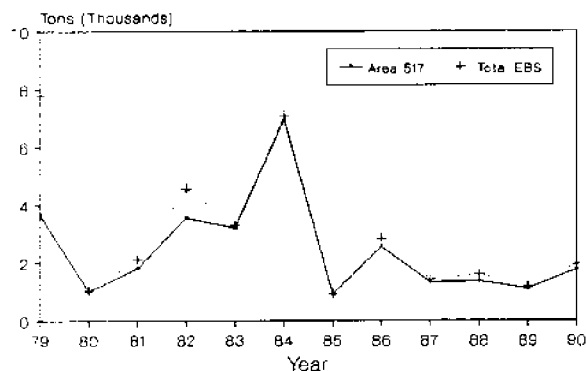
Figure 14. Eulachon biomass estimates for statistical area 517 (see text) and the eastern Bering Sea from NMFS groundfish bottom trawl surveys, 1979-1990. Top: annual biomass estimates. Bottom: Three-year moving average of annual biomass estimates.

Onychoteuthis borealijaponicus predominated in commercial catches along the outer continental shelf/slope in the Bering Sea and Aleutian Islands, respectively (Bakkala 1991). Fisheries observer data show that incidental catches of squids in groundfish trawls have occurred primarily on the outer continental shelf and slope in both the Bering Sea and Gulf of Alaska, and primarily on Petrel Bank, Bowers Ridge, and near the Rat Islands in the Aleutians. Little is known of squid population dynamics or recent trends in abundance.

Lanternfishes (myctophids) are distributed pelagically in the deep sea throughout the world's ocean, where they occur at depth dur-

ing the day and migrate to near the surface to feed (and be fed upon) at night. The northern lampfish (*Stenobrachius leucopsarus*), which occurs in the Bering Sea and Gulf of Alaska, has a maximum length of approximately 13 cm. Myctophids have been found to be important forage fishes for marine birds and northern fur seals. Because they are rarely caught in survey or fishery trawls, little is known of recent trends in their abundance.

CONCLUSIONS

Available data on forage fishes in the Gulf of Alaska and Bering Sea permit only weak tests of the hypotheses listed in the introduction. Hypothesis (a), that overall prey abundance has declined, can be conditionally refuted. Overall prey abundance may have declined in both systems since the early to mid-1980s. However, these declines were preceded by large increases in pollock and herring biomasses in the late 1970s and early 1980s. Consequently, the available data suggest that prey availability on a system-wide basis increased significantly during the same period that some pinniped (particularly the Steller sea lion) and marine bird populations were declining. Limitations in the data, however, preclude determinations of changes in localized prey availability, or the small-scale distribution of system-wide fish biomasses, which could affect foraging efficiency of marine mammals and birds.

With respect to hypothesis (b), species composition has changed in the past three decades. In the Bering Sea, pollock biomass has peaked twice since the late 1960s, once in the early 1970s followed by a decline through the late 1970s, and again in the early-mid 1980s (Fig. 2). Pollock biomass was low in the Gulf of Alaska in the 1970s, increased during the 1980s, and is now declining slowly (Fig. 10). Herring biomass in the Bering Sea was very high in the 1960s, low in the 1970s and moderately high in the 1980s (Figs. 2 and 8). The patterns in pollock and herring abundance are caused mainly by recruitment variation and partly by

exploitation history. The abundance of eulachon in the Bering Sea apparently has decreased during the 1980s (Figs. 13 and 14) along with herring. The effects of observed changes in species composition on marine mammal and bird foraging success are unknown. Marine mammals and birds are, within certain ranges, usually more limited by the size rather than the classification of their prey. Therefore, a series of years with poor forage fish recruitment, which decreases the availability of small fish, may have greater impact on piscivores than a change in species composition.

Hypothesis (c) pertains to variability in the size composition of forage fish species, particularly pollock, which is consumed as a forage species mainly during the first few years of life. Age 2 is the earliest at which year-class strength can be assessed (Fig. 9). The supply of young pollock is highly variable from year to year, and may be even more variable in the Gulf of Alaska than in the Bering Sea. Over the three decades of data no long-term trend is apparent. Strong year-classes appear every 4-6 years; an exceptionally strong year-class has occurred only once in 30 years (1978). The one period that could be considered different is the late 1970s, when from one to five strong year classes recruited to the pollock populations in the Gulf of Alaska and Bering Sea. The effects of these strong pollock cohorts on the recruitment of other forage fish are largely unknown. Thus, the available data suggest that hypothesis (c), that size composition of important prey species has changed, cannot be refuted. However, the availability of small pollock on a system-wide basis may have been higher during the period of marine mammal and bird declines (during the late 1970s and early 1980s) than prior to it.

With respect to hypothesis (d), there is qualitative information relating the distributions of forage species to the ice edge in the Bering Sea, which itself is highly correlated with sea surface temperature (Niebauer and Day 1989). During warm periods (such as during the 1980s) some forage species may move to the northern Bering Sea beyond the feeding range of some marine mammals (particularly Steller sea lions) and seabirds breeding along the Alaska Peninsula and Aleutian Islands. Unfortunately there is little quantitative information to test this speculation.

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SPECULATIONS ON THE CONNECTION OF ATMOSPHERIC AND OCEANIC VARIABILITY TO RECRUITMENT OF MARINE FISH STOCKS IN ALASKA WATERS

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ABSTRACT

In this paper, we qualitatively compare variations in ocean conditions with recruitment variations of several commercially important marine fish. We demonstrate that strong shifts in atmospheric circulation patterns occurred in the late 1970s. These changes in the atmosphere resulted in warmer winter ocean conditions in the early 1980s. In the Bering Sea, shifts in ocean temperature appear to be linked to the location and intensity of the Aleutian Low pressure cell and may have origins in El Niño Southern Oscillation (ENSO) events which exhibit strong extra-tropical effects. The late 1970s shift in ocean conditions appears to be initiated by the moderate 1976 ENSO event. Many stocks in the North Pacific Ocean and Bering Sea exhibited strong year classes during the transition period between cool and warm ocean conditions from 1976 to 1978. Several explanations for this increase in the production of marine fish are presented.

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INTRODUCTION

In the Gulf of Alaska and Bering Sea, sea surface temperature (SST) of coastal waters over the continental shelf and slope oscillate between periods of warm and cool conditions of 6 to 12 year duration (Hollowed and Wooster 1992). In the Gulf of Alaska the periods of warm near-surface ocean conditions appear to be associated with an eastward displacement and intensification of the Aleutian Low and downwelling in coastal waters (Emery and Hamilton 1985; Wooster and Hollowed, in review). The origin of these large-scale shifts in ocean temperature has been linked to two mechanisms: El Niño Southern Oscillation (ENSO) events (Niebauer 1983; Hamilton 1988; Wooster and Hollowed, in review) and the luni-solar tidal cycles (Royer 1993).

In the mid-1970s, an ENSO event coincided with the maximum rate-of-change in the luni-solar tide cycle, during the same period winter SSTs in the Bering Sea and Gulf of Alaska changed from "cold" to "warm" (Wooster and Hollowed, in review). In this paper, we describe the potential connection between this recent shift in atmospheric conditions and observed changes in ocean conditions in the Bering Sea. We also speculate on

the implications of recent changes in ocean conditions on marine fish populations in the Gulf of Alaska and Bering Sea.

PHYSICAL CHANGES IN THE BERING SEA

Extraordinary interannual variability in ice cover, air and SSTs, and surface winds in the eastern Bering Sea have been observed over the past few decades (Niebauer 1980, 1983, and 1988) (Fig. 1). To investigate the causes of this interannual variability, long-term (20-40 years) time series of air temperature, ice, and ocean parameters from the Bering Sea were cross-correlated with the Southern Oscillation Index (SOI), an index of ENSO events in the tropical Southern Hemisphere (Fig. 2). With use of linear regression, up to 30% of the interannual variability in the Bering Sea data sets is explained by the SOI when the data sets lag the SOI by a year or more (Fig. 2). For comparison, up to 50% of the variability in the SST in the major upwelling regions of the Southeast Pacific Ocean can be explained by the SOI. Positive anomalies in the SOI and anti-El Niño events which often precede ENSO events, were found to precede cooling periods in the Bering Sea. Significant correlation persisted for up to 20 months (Fig. 2).

The mechanism for the connection between ENSO events and Bering Sea interannual variability in ocean conditions is probably atmospheric in nature because the ocean flow on the southeast Bering Sea shelf is sluggish and because the eastern Bering Sea is cut off from the North Pacific by the Aleutian Islands chain. Shifts in SST and sea ice distributions are associated with the winter position and intensity of the Aleutian Low. The Aleutian Low was intensified and eastward of normal in association with ENSO events causing more southerly air flow over the Bering Sea (i.e., warm events). When the Aleutian Low is weaker and westward of its normal location, a more northerly flow over the Bering Sea causes cool events.

The period from 1973 to 1979 (Fig. 1) is a good example (although probably an extreme case) of an ENSO event affecting the Bering Sea. From 1973 to 1975, the SST and air temperatures around the Pribilof Islands were about 2°C and 5°C below average, respectively. In 1976, an ENSO event occurred that exhibited strong extra-tropical effects in the North Pacific (Hamilton 1988, Emery and Hamilton 1985). The Aleutian Low was intense during the winter of 1976-1977 (Emery and Hamilton 1985). Ice extent was up to 10% above normal while northerly air flow was about 1.4 m/sec above normal for October 1976-April 1977. By the winter of 1979, the SST and air temperatures were 1.5°C and 6°C above normal, respectively, while ice extent was almost 15% below normal. During this period, surface winds were from the south averaging 0.3 m/sec which translates to a 1.8 m/sec anomaly. In the Bering Sea the maximum extent of annual sea ice cover retreated about 400 km northward between 1976 and 1979 (Fig. 1). This amounts to about 40% of the mean annual ice extent in the eastern Bering Sea.

IMPACT ON MARINE FISH POPULATIONS

Our results, and those of other researchers (Ebbesmeyer et al. 1991, Trenberth 1990) indicate that dramatic changes in ocean conditions in the North Pacific and Bering Sea occurred in the late 1970s. In this section, we speculate that the recent shift in ocean conditions influenced recruitment of the region's dominant groundfish stocks.

Following Hollowed and Wooster (1992), we identified recruitment events as years of synchronous strong year classes of marine fish stocks. Years of synchronous strong year classes are particularly interesting because they might identify unique ocean conditions that are favorable to recruitment of several stocks throughout the Gulf of Alaska and Bering Sea.

Time series of recruitment indices for 15 groundfish stocks were examined for evidence of synchronous strong year classes (Table 1).
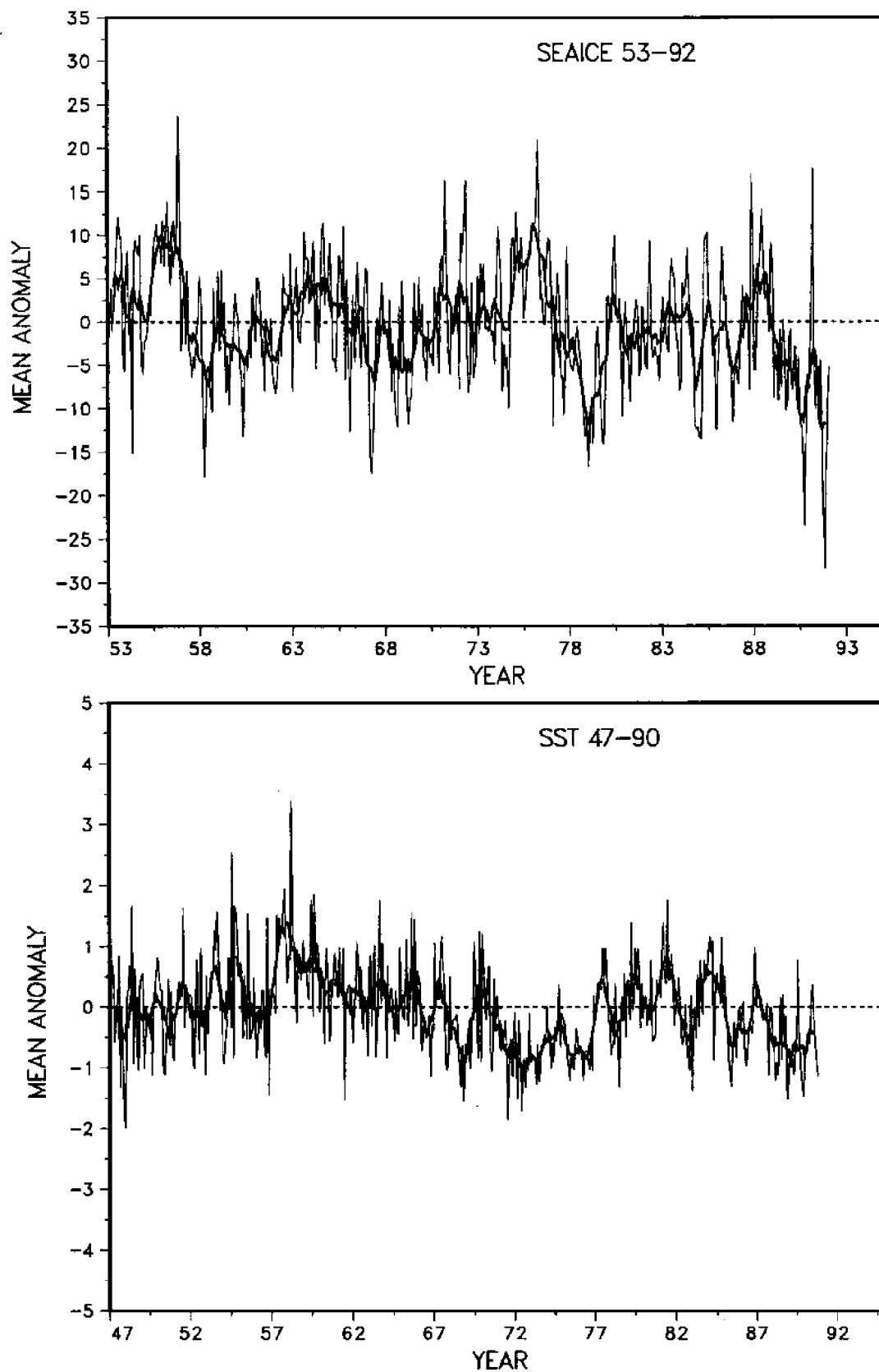
Figure 1. Deviations from monthly mean ice cover, sea surface temperature, and air temperature from the eastern Bering Sea, and Southern Oscillation Index (SOI) from the South Pacific.
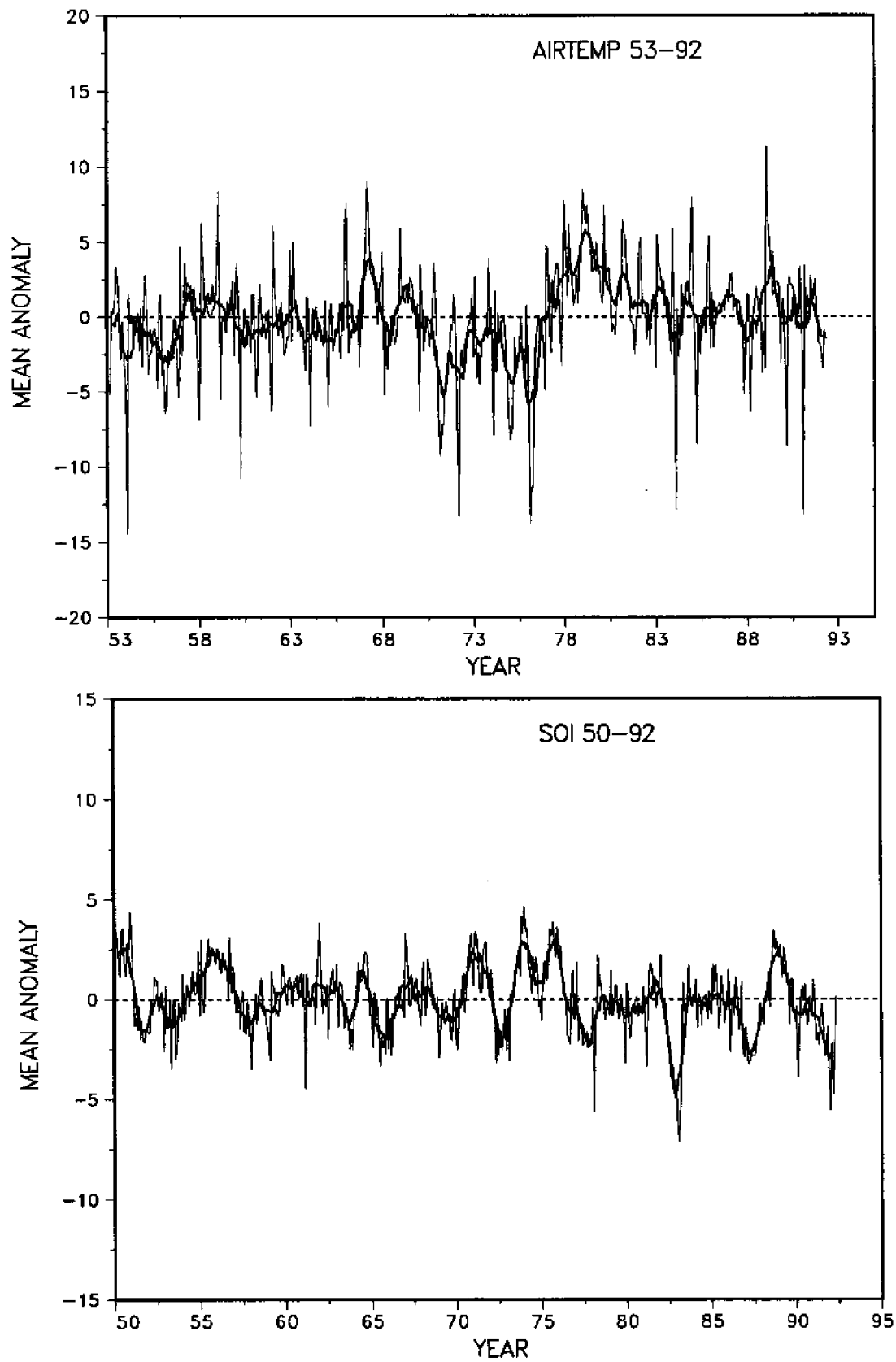
Figure 1 (cont.). The light lines are the actual monthly deviations from the mean while the heavy lines are a 9-month running mean (after Niebauer 1988).
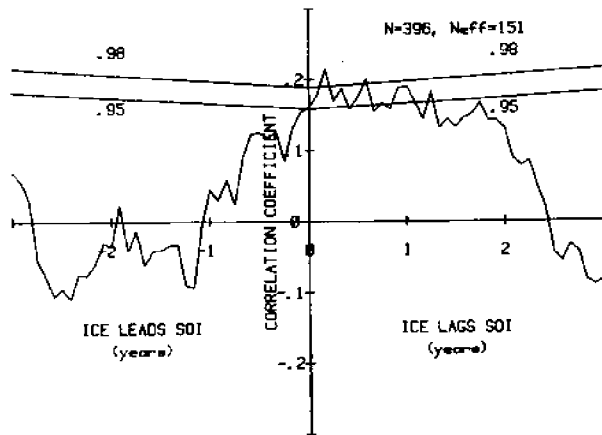
Figure 2. Cross-correlation plot of the Southern Oscillation Index versus ice cover in Figure 1. The x-axis is the time lag between data sets. N is the number of data points, while Neff is the number of effective or independent data points available for use in calculating the confidence levels (from Niebauer 1988).

Strong year classes were identified as described in Hollowed et al. (1987), and Hollowed and Wooster (1992). Synchronous strong year classes were defined as years when 50% or more of the groundfish stocks had strong year classes.

RECRUITMENT EVENTS

Widespread synchrony of strong year classes of groundfish occurred in regions from California to the Gulf of Alaska in 1961, 1970, 1977, and 1984 (Fig. 3). Each of these years coincided with warm ocean temperature conditions, and in at least three years, a strong Aleutian Low (Table 2). The Aleutian Low pressure index was developed by McFarlane and Beamish (1992). This index represented the area of the North Pacific Ocean less than 100 kPa atmospheric pressure at sea surface as
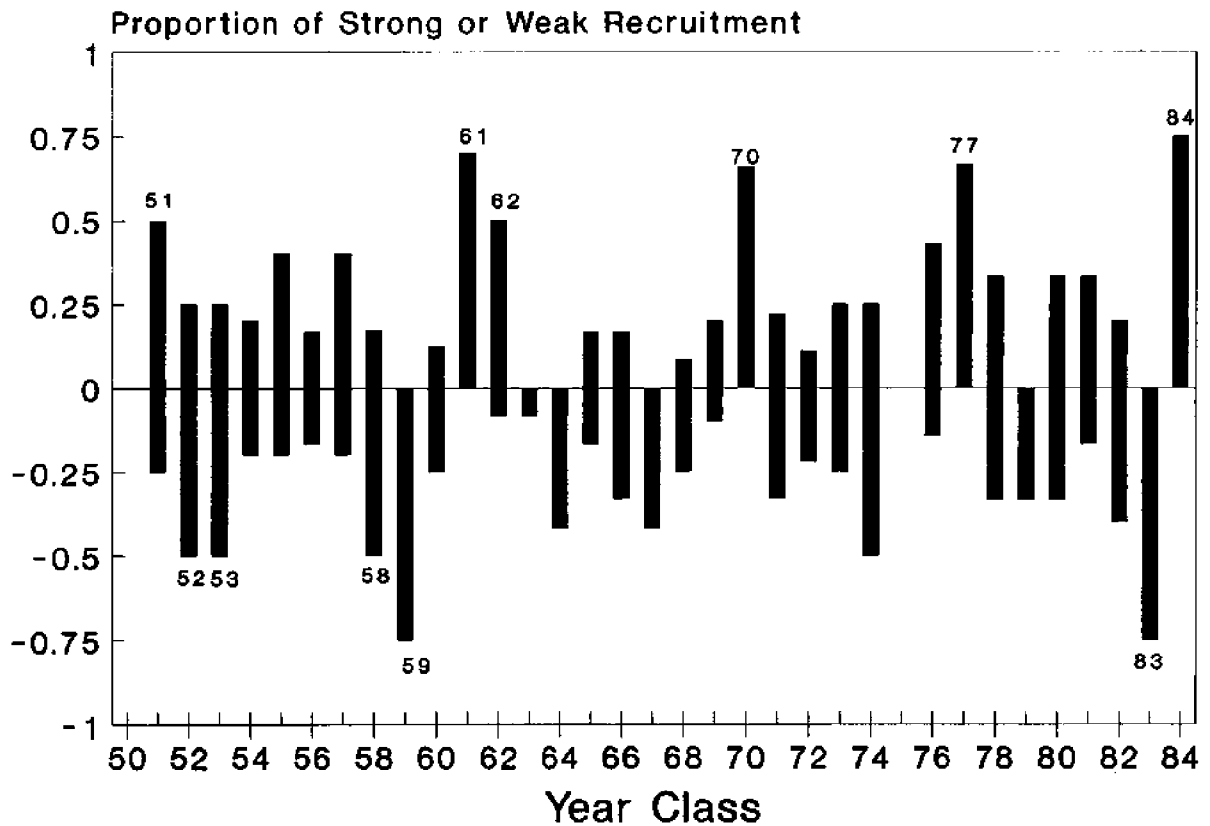
Figure 3. Summary of the percentage of northeast Pacific groundfish stocks that had extreme year classes. Years when 50% or more of the stocks were extreme are indicated (from Hollowed and Wooster 1992).

Table 1. Summary of quantitative data sources.

Stock	Scientific name	Spawning location	Source
Pacific hake	*Merluccius productus*	CA	Dorn et al. (1991)
Dover sole	*Microstomus pacificus*	WA-OR	Demory et al. (1984)
P O P (Vancouver)	*Sebastes alutus*	WA-OR	Ito et al. (1986)
P O P (Columbia)	*Sebastes alutus*	WA-OR	Ito et al. (1986)
Petrale sole	*Eopsetta jordani*	WA-OR	Demory (1984)
English sole	*Parophrys vetulus*	WA-OR	Golden et al. (1986)
Widow rockfish	*Sebastes entomelas*	CA-WA	Hightower and Lenarz (1989)
Pacific halibut	*Hippoglossus stenolepis*	CAN-GOA	I.N.P.H.C. (1991)
Rock sole	*Lepidopsetta bilineata*	CAN-HS	Fargo (1989)
English sole	*Parophrys vetulus*	CAN	Fargo (1990)
Petrale sole	*Eopsetta jordani*	CAN	Ketchen and Forrester (1966)
Pacific cod	*Gadus macrocephalus*	CAN-WVI	Tyler and Foucher (1990)
Pacific cod	*Gadus macrocephalus*	CAN-HS	Tyler and Foucher (1990)
P O P	*Sebastes alutus*	CAN-QC	Archibald et al. (1983)
Walleye pollock	*Theragra chalcogramma*	GOA	Hollowed and Megrey (In prep.)

Abbreviations: P O P: Pacific ocean perch; CA: California; WA-OR: Washington-Oregon; CAN: Canada; CAN-HS: Hecate Strait; CAN-WVI: West coast of Vancouver Island, Canada; CAN-QC: Queen Charlotte; GOA: Gulf of Alaska; I.N.P.H.C. International North Pacific Halibut Commission, Seattle, Washington.

indicated on atmospheric pressure maps (Hamilton 1984). Strong Aleutian Lows were defined as years when the area less than 100 kPa was greater than 250,000 square nautical miles during the winter (December-February).

Although pollock stocks in the Bering Sea and Gulf of Alaska exhibited strong year classes in 1977, the 1978 year class was the strongest year class on record for both stocks. In the Bering Sea, the 1978 year class was roughly twice as large as any other observed year class (Wespestad and Dawson 1991). Strong year classes of walleye pollock are particularly important because juvenile pollock are an important prey item for several marine mammals and birds in the Bering Sea and Gulf of Alaska ecosystems (Kajimura and Loughlin 1988, Smith 1981).

The shift in ocean conditions in the North Pacific Ocean and Bering Sea appears to have influenced the abundance of several marine species. The recent period of ocean warming (1977-1984) in the Bering Sea and Gulf of Alaska coincided with a period of high production of groundfish (Fritz et al., this proceedings). Survival of pink salmon increased dramatically in Alaskan waters after 1977 and remained high throughout the 1980s (Francis and Sibley 1991). Pandalid shrimp populations in Pavlov Bay (in the Gulf of Alaska) declined after 1977 (Albers and Anderson 1985).

LINKS BETWEEN OCEAN CONDITIONS AND RECRUITMENT SUCCESS

The information presented in this paper indicates that the period of transition from cool to warm ocean conditions was associated with strong recruitment of groundfish stocks. In this section, we develop several explanations for this recruitment response.

Table 2. Summary of winter ocean temperature conditions in the Gulf of Alaska and the intensity of the Aleutian Low pressure index (McFarlane and Beamish 1992).

Recruitment Event	Coastal Surface Temperature	Dec.-Feb. Aleutian Low[a]
1961	Warm	Strong
1970	Warm	Strong
1977	Warm	Strong
1984	Warm	-

[a] Aleutian Low pressure index from McFarlane and Beamish (1992) representing the area of the North Pacific Ocean less than 100 kPa atmospheric pressure at sea surface as indicated on atmospheric pressure maps (Hamilton 1984). Strong years represented by values greater than 250,000 square nautical miles.

The strong recruitment observed in several northeast Pacific fish stocks in 1977 and 1978 may be a response to the strong gradient in ocean conditions observed in the winter of 1976-1977. This explanation was proposed by Saetersdal and Loeng (1987) who observed marked change in recruitment of several marine fish stocks in the North Atlantic Ocean at the beginning of periods of warm ocean conditions.

An alternative explanation of the results is that recruitment of several groundfish species is favored by warm ocean conditions and intense Aleutian Lows. These ocean conditions could influence recruitment of marine fish by (a) changing the abundance and distribution of prey, (b) favoring transport of larvae to suitable nursery grounds, or (c) by altering the rate of predation of fish during the early life stages.

As noted in the first section of this paper, warm SSTs and intense Aleutian Lows are associated with below normal ice cover in the Bering Sea. If fish respond to ice cover, the retreat of the ice edge during warm ocean conditions may broaden the geographical opportunity of fish to encounter suitable prey concentrations in the Bering Sea. Shifts in the areal extent of suitable habitat can play an important role in recruitment success (MacCall 1990, Iles and Sinclair 1982).

Intensification of the Aleutian Low may alter the speed and flow trajectories of the Alaska gyre. Ingraham et al. (1991) noted that large-scale circulation in the Alaska gyre could influence bottom water properties which may influence the spawning location or transport of pollock eggs in Shelikof Strait. Parker (1989) found that strong winter-averaged wind conditions favored the production of large year classes of Pacific halibut.

Increased survival could occur if accelerated growth rates resulting from warmer temperatures (Pepin 1991) were coupled with prey densities sufficient to satisfy the increased metabolic demands. The importance of matching peak periods of larval abundance with the availability of suitable prey have been shown by Cushing (1969) and Lasker (1975, 1978).

Warm conditions in the north may foster development of suitable prey for larval and juvenile fish (MacCall 1990, Iles and Sinclair 1982). In the North Pacific, McFarlane and Beamish (1992) noted that the mean number of copepods per cubic meter at Ocean Station P during March, April, and May showed a marked increase in the most recent warm period 1976-1980. Brodeur and Ware (1992) found a positive correlation between the intensity of winter winds and subsequent summer zooplankton biomass in the subarctic gyre.

This analysis has identified a suite of environmental conditions that may represent some of the pre-conditions necessary for strong recruitment of marine fish. Support for the importance of these ocean conditions is found in the large number of stocks that exhibited strong year classes simultaneously. The next step will be to investigate whether stocks exhibit decadal scale variations in the probability of recruitment. If linkages between decadal scale climate conditions and recruitment exist, then the abundance of pelagic fish populations in the Gulf of Alaska and Bering Sea may not be stable.

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MODELING THE TROPHIC RELATIONSHIPS BETWEEN FISH AND MARINE MAMMAL POPULATIONS IN ALASKAN WATERS

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One hypothesis to explain the decline of some birds and marine mammals in the Gulf of Alaska and Bering Sea is that the abundance of forage fish has declined. This decline could be due to natural causes or fishing. One way to test this hypothesis is to construct an energetics model relating the abundance of forage fish to food consumption to subsequent survival and growth of mammals and birds. Our work consisted of constructing a *simple* model of the interaction between marine mammal populations and their food supply, and our goal was to test the hypothesis that the observed decline could have been produced by changes in size and structure of fish populations.

Model simplicity was sought by reducing to a minimum the number of processes and interactions explicitly included in the model and, therefore, reducing the number of parameters we dealt with. The emphasis on low model complexity was strengthened because experi-ence with community models has shown that their explanatory power drops dramatically when the model gets too big and complex. A model complex enough will, in general, be able to reproduce the behavior of a natural system, but it will be very difficult to understand the effect that different components of the model have on the results. In this case the amount of insight gained from the modeling exercises will be small.

Our major simplification was to avoid modeling the dynamics of fish, but instead we used observed time series of fish species abundances in Alaskan waters. NMFS survey data provided estimates of total abundance for each year for the major species. Commercial CPUE data were used to estimate the spatial distribution of the stock. Thus our data base was the number of fish of each species and age class available in different sections of the Bering Sea and Gulf of Alaska.

The first component of the model consists of a foraging model, represented by a Holling multi-prey disk-equation. This equation represents the amount of composition of the food consumed as a function of the prey species densities. This model considers that there is a maximum amount of prey that an individual can eat per time interval, and that prey choice is governed by relative prey preference and prey abundance.

The second component of the model relates the amount of energy consumed to the expected fecundity and survival. The rationale underlying this is that there are some levels of energy intake above which reproduction and survival are optimum, and below which reproduction and survival are, in some degree, compromised. We used logistic functions to model the relationship between reproduction or survival and daily energy intake. The third and last component is a full age structured model which represents the dynamics or change in numbers of the bird or mammal population as affected by survival and reproductive rates.

This model was used in two different general modes. In the first one, the time series of fish abundance estimates were used, together with values extracted from the literature for the different parameters in the model; then, an "expected" time series bird or mammal abundance was produced. This trajectory was then checked against the observed abundances for consistency.

In the second mode, the model was imbedded within an estimation framework. Values for parameters for which estimates were not available were estimated in order to produce the time series of abundances that best fit the observed abundances. Apart from considering how well the time series of abundances could be reproduced, the plausibility of the parameter values obtained by this procedure was evaluated by either comparing with those available for related species or contrasting against current knowledge or plain common sense.

The application of the model to particular populations was done in different ways according to the amount and type of information available. In some cases, such as Gulf of Alaska sea lion populations, we did not have information on important prey species abundance over time. In this case we estimated the trajectory of food supply required to explain the observed abundances of sea lions (Pascual and Adkison, Ecological Applications, in press). We could say that if the food supply had changed in this way, we could explain the observed demographic changes.

For the bird populations, the time series of abundances display a high degree of variability, although the trajectories are seldom declining. The analysis of bird information was intended as a way to indirectly approach the mammal problem. The rationale was that given that birds and mammals have many prey species in common, the ability to explain the variability observed in bird populations could shed some light on the mammal problem. One of the problems found when working with bird data was that the counts at the colonies give a very distorted measure of population abundances, because the attendance to the colony varies widely among years. The procedure used in this case was to apply only the two first components of the model to the data. The energetics model component was modified to use the amount of energy consumed as a predictor for the productivity in the colony, measured as the number of chicks fledged per nest initiated, instead of fecundity and survival as in the mammal case. In this application of our model the last component (consisting of the population dynamics) was dropped and the whole fitting procedure became a "non-linear regression" between the food abundance and the birds' productivity.

During the workshop few participants expressed any interest in using the models. The working groups in general did not have enough time to get down to any form of data analysis. It was also clear that the underlying fisheries data base had quite incomplete coverage of

many of the important forage species, such as sand lance and squid. The fisheries data base was most complete for key commercial species, which were often not the primary food items of the age classes of mammals or birds that were of concern.

Thus modeling did not make any major contribution to the workshop, but did serve to force the synthesis of the existing fisheries data, and help to identify how this data base could be improved in the future. In addition, the model itself is of considerable potential utility, particularly when used in its "estimation" mode, in which we ask what change in food supply would have been required to explain the observed demographic changes.

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