Population Ecology and Structural Dynamics of Walleye Pollock
(Theragra chalcogramma)

Kevin M. Bailey
Alaska Fisheries Science Center, Seattle, Washington

Dennis M. Powers, Joseph M. Quattro, and Gary Villa
Hopkins Marine Station, Stanford University, Pacific Grove, California

Akira Nishimura
National Institute of Far Seas Fisheries, Orido, Shimizu, Japan

James J. Traynor and Gary Walters
Alaska Fisheries Science Center, Seattle, Washington

Abstract
In this paper, walleye pollock (Theragra chalcogramma) is characterized as a generalist species, occupying a broad niche and inhabiting a wide geographic range. Pollock's local abundance is usually high, dominating the fish biomass in many regional ecosystems. Thus, it appears to be an adaptable species capable of colonizing marginal habitats. The fields of macroecology, metapopulation dynamics, and genetic population structure are briefly reviewed and information on pollock is summarized within the framework of these concepts. Pollock show a pattern of apparent stock structure that has not always been indicated by genetic differences. Phenotypic differences between stocks, elemental composition of otoliths, and parasite studies indicate restricted mixing of adults. There are genetic differences between broad regions, but differences between adjacent stocks, especially within the eastern Bering Sea, are currently unresolved. The potential for gene flow mediated by larval drift is high between adjacent stocks. A generalized population structure for walleye pollock is proposed. The macro-population of walleye pollock is made of several major populations (such as the eastern Bering Sea and Sea of Okhotsk populations).
separated by large distances and geographic barriers with little gene flow between them, and numerous smaller populations with potential linkages among each other and the larger populations. Some populations may show local adaptations to their specific habitat, minimizing gene flow through reliance on larval retention features and natal homing. Application of high resolution genetic techniques, such as microsatellite polymorphisms, show promise for distinguishing adjacent pollock stocks. The architecture of stock structure, including metapopulation aspects of dispersal and colonization, are potentially important considerations in management of pollock fisheries.

Introduction

Walleye pollock (*Theragra chalcogramma*) is one of the world’s largest commercial fisheries. Annual harvests have ranged from 4 to 7 million t in the North Pacific Ocean over the past decade. In U.S. waters catches are on the order of 1.5 million t with a value exceeding hundreds of millions of dollars. A large portion of the resource is bound for the export market, contributing to reduction of the U.S. trade deficit. Without question, this natural resource is of critical importance to the health of domestic fisheries. Furthermore, pollock is the dominant groundfish species in many of the regional ecosystems across the North Pacific, including the eastern Bering Sea, and has been implicated in the dynamics of higher trophic levels (see National Research Council 1996). As a key element in the North Pacific ecosystem, pollock is the target species for numerous research programs, past and present, in the eastern Bering Sea as well as in other seas.

The stock structure of pollock across the North Pacific, and especially in the Bering Sea, has been a topic of investigation for many years. Many studies have been based on pollock phenotypic characteristics, such as meristics and morphometrics, while other studies have been based on genotypic characters, such as allozyme frequencies. A broad characterization of pollock stock structure has come from these approaches. In general, allozyme studies have weakly distinguished eastern Pacific populations from western Pacific populations, but phenotypic characters suggest a more detailed stock structure. Only recently, using high resolution molecular techniques (Powers, unpubl. data reported here) has there been strong resolution between populations on either side of the Bering Sea and between Gulf of Alaska populations and eastern Bering Sea populations.

Fisheries resource management is based on the concept of renewable stocks. For pollock the regional stocks are managed separately; for example, the Gulf of Alaska population is managed separately from the Bering Sea, and the eastern and western Bering Sea and Aleutian Basin populations are managed separately. However, there may be isolated populations on even finer scales; within the Gulf of Alaska there may be separate
spawning populations in Shelikof Strait, Prince William Sound, and the Shumagin Islands region. Furthermore, the degree of intermingling of stocks, recolonization of depleted areas from healthy stocks, and other ecological questions about resource mixing within the greater population framework are almost completely unknown.

Although the overall catch of pollock on the U.S. side of the North Pacific is relatively stable, some populations have experienced declines and fisheries closures in recent years, including stocks in Puget Sound, Shelikof Strait, Donut Hole, and Bogoslof Island. More recently, there are reports that the western Pacific stocks are in a state of decline. The eastern Bering Sea shelf populations have been at healthy levels in the past, but there is concern about the sustainability of present harvest levels. Pollock harvests were especially high during the 1980s and 1990s resulting from relatively strong recruitment, high abundance levels, and unrestricted high seas fisheries. Wespestad (1996) lists 12 geographically distinct stock (although not necessarily genetically distinct) groupings and their catch trends (Table 1). Biomass and catch trends for the major stock groupings indicate declining levels since the mid-1980s in the major fishing

Table 1. Geographic distribution of walleye pollock stocks according to Wespestad (1996).

<table>
<thead>
<tr>
<th>Stock</th>
<th>Stock characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>North American</td>
<td></td>
</tr>
<tr>
<td>Southeast Alaska-Canada</td>
<td>Small stock, minor fisheries</td>
</tr>
<tr>
<td>Western-Central Gulf of Alaska</td>
<td>Variable stock, 50-200 thousand t catch</td>
</tr>
<tr>
<td>Eastern Bering Sea</td>
<td>Large stock, 1-2 million t catch</td>
</tr>
<tr>
<td>Asian</td>
<td></td>
</tr>
<tr>
<td>Northwest Bering Sea</td>
<td>Mix of US and Russian fish, 0.5-1 million t catch</td>
</tr>
<tr>
<td>Western Bering Sea</td>
<td>Moderate stock, 0.5-1 million t catch</td>
</tr>
<tr>
<td>East Kamchatka</td>
<td>Small-medium stock, 100-300 thousand t catch</td>
</tr>
<tr>
<td>West Kamchatka</td>
<td>Large stock, near 1 million t catch</td>
</tr>
<tr>
<td>North Sea of Okhotsk</td>
<td>Moderate stock, 0.5-1 million t catch</td>
</tr>
<tr>
<td>Sakhalin</td>
<td>Small stock, 65 thousand t average catch</td>
</tr>
<tr>
<td>Kuril Islands</td>
<td>Small-moderate stock</td>
</tr>
<tr>
<td>Japan Sea</td>
<td>Heavily fished</td>
</tr>
<tr>
<td>Japan Pacific</td>
<td>Moderate catch to 0.5 million t</td>
</tr>
</tbody>
</table>
Figure 1. Trends in major stock groupings of walleye pollock: (top) Abundance trends for major stocks, (bottom) Catch trends for Asian and North American stocks (from Wespestad 1996).
grounds (Fig. 1a,b). The greatest declines in biomass and catches for pollock seem to be away from the center of pollock's biomass. For example, in the Gulf of Alaska, catches peaked at 307 thousand t in 1984 and declined to 55 thousand t in 1996. At the extreme southern end of its range in the eastern North Pacific, pollock in south Puget Sound may almost be extinct (Palsson et al. 1996). Likewise for the southern end of its range in the western North Pacific, catches around northern Japan are reduced by 3-4 times from their maximal values in the 1970s (H. Yoshida, Hokkaido Central Fisheries Expt. Station, Hamanaka 238, Yoichi-cho, Hokkaido 046, Japan, pers. comm., February 1994).

There are many complex and unresolved issues involving the structure of the pollock population, including recent stock declines, discoveries of heretofore unknown stocks, potential consequences of fishing on selected components of the population, possible relationships between subunits, and potential fishing pressure on the same subpopulation at different times from different geographic and quota regions. What is needed, but currently lacking, is an understanding of the macroscale population ecology of pollock that incorporates the relationship among different subpopulations of the greater population, the rate of gene flow between these subpopulations, the relationship between juvenile and adult distributions as linked together by ontogenetic migrations, and the magnitude of colonization processes. A theoretical framework about the geographical structure and population ecology of pollock needs to include ecological concepts that can help us better understand the dynamics of this species and consider new approaches to management. One such concept is macroecology, the study of patterns of distribution of organisms in relation to their environment (Brown 1995). Many of the macroecological questions regarding pollock are unanswered, such as the relationship between range size and population abundance, and the effect of environmental factors on distribution of pollock. Another concept is that of metapopulation dynamics, the study of conditions by which the processes of population turnover and establishment of new populations are maintained in balance (Hanski and Gilpin 1991). Viewing pollock in the context of a metapopulation is a potential framework to study the linkage of stock structure, dispersal, and colonization events.

In this synthesis, we review the concepts of macroecology, metapopulations, and stock structure and point out areas where they intersect. We then summarize historical and current information on pollock, including stock structure and we propose a “strawman” conceptual model of the population macroecology of pollock.

**Theoretical Framework: Structural Dynamics**

The size of fish populations is determined by three major elements: (1) available habitat determines the potential size, (2) dynamics within local populations as influenced by the environment, competition, and predation
determine the specific size of a subpopulation, and (3) movement and colonization determine the spread of a population, and modify local dynamics. In this model, distribution, dispersal and population structure are closely linked and interwoven characteristics of populations.

A population is a group of individuals of the same species living in a sufficiently restricted area such that any member can mate with any other; in large widespread populations it is recognized that individuals in the same locality are more likely to mate and share common ancestry. Local subpopulations may form intrabreeding units of geographically structured populations. Geographical structure in populations is the nonrandom pattern of spatial distribution that may be related to historical or current barriers between local populations, environmental patchiness, and/or environmental gradients. The term structural dynamics integrates change in population structure and aspects thereof, such as range, genetics, and dispersal patterns.

**Distribution and Macroecology**

Geographic range considerations are an important characteristic of populations. It is recognized that many species with broad niches become both widespread and locally abundant (Brown 1984), and that large ranges, abundance, and invasion ability are linked characteristics within a species (Lawton et al. 1994). Those species with extraordinary invasion abilities are generally those best adapted for marginal habitats (MacArthur and Wilson 1967). As described below, these concepts are especially relevant to pollock population biology. On the other hand, habitat specialization often limits colonization. For example specialized feeders such as benthic feeding flatfishes would appear to be tied to specific habitat types; thus they cannot move and colonize new habitats freely as adults or settled juveniles compared with species that have more generalized requirements. Furthermore, if the range of a species with specialized requirements is made of a mosaic of habitat patches, colonization by demersal stages may be impeded by regions of unfavorable habitat.

Some populations may expand their range as they become more abundant, although others do not show this trend but show increases in local density. As noted above, species with highly specialized niches may not expand their range readily, and indeed no range/abundance relationships have been found for some relatively specialized flatfish species such as rock sole (Lepidopsetta bilineata), Alaska plaice (Pleuronectes quadrituberculatus) (McConnaughey 1995), and American plaice (Hippoglossoides platessoides) (Swain and Morin 1996). Thus for these species, the range size/population size relationship due to density-dependent dispersal may not occur. More generalized species such as Atlantic cod (Gadus morhua) (Swain and Wade 1993) and arrowtooth flounder (Atheresthes stomias) (McConnaughey 1995) are observed to expand their range as abundance increases.

Physical impediments (i.e., temperature, salinity, and substrate availability) and biological factors (i.e., the presence of competitors and pred-
ators) may limit range expansions. There also may be historical structure in the environment, such as changes in the occupation of niches due to disease and environmental events. When competition or predation pressure is removed there can be an “ecological release” (MacArthur and Wilson 1967) resulting in an invasion event.

**Metapopulations and Geographical Structure**

Within the distributional range of animals, there may be considerable population structure. The realization that animal populations are composed of local populations has a rich history going back to Andrewartha and Birch (1954). In fisheries, knowledge of local populations goes back to the developments and ideas of Schmidt, Heincke, and Hjort in the early 1900s (Sinclair 1988). The concept of population structure was formalized as that of metapopulations by Levins (1970). In the metapopulation view, a local population is the spatial unit within which most interaction such as breeding occurs, and a metapopulation is an ensemble of local populations (Taylor 1991a) with some potential of interaction. Although many fish populations are not metapopulations in the strict sense, viewing them within a relaxed definition of metapopulations (i.e., populations with non-continuous distributions and some possibility of local extinction) (McCullough 1996) might be useful to applied fisheries science.

Harrison (1991) showed five potential types of metapopulations with examples of their degree of dependency and interaction (Fig. 2). These include: (A) the Levins metapopulation, where population sizes are nearly equal and all populations interact and habitats are patchy within the range area; (B) the core-satellite (Boorman and Levitt 1973) metapopulation, where habitats are patchy within the range, but one major population is the source of fringe populations; (C) the patchy population, where habitats are continuous throughout the species range, but local populations are aggregated; (D) a non-equilibrium metapopulation, which is like the Levins model except there is no movement between local populations, and (E) an intermediate model between B and C. According to Harrison (1991) the dominant metapopulation structure is that of a large local population in a large favorable habitat patch, surrounded by relatively unstable populations in smaller habitat patches.

In the metapopulation view, local subpopulations are connected by dispersal, which includes larval dispersal and colonizing movements of adults. Fish migrations, which are movements of individuals coordinated in space and time (Quinn and Brodeur 1991), can be ontogenetic, seasonal, or daily. These migrations are distinguished from dispersal or nomadic behavior, which is undirected and out of the natal or home range. Dispersal can occur due to environmental factors, such as El Niño events, and also due to density-dependent effects. As demonstrated for some fishes, fidelity to home range depends on habitat quality (Matthews 1990), which can depend on density. The advantages of dispersal are colonization of new habitats and avoidance of unfavorable local conditions (Quinn 1993). The
Figure 2. Different kinds of metapopulations: (A) Levins metapopulation; (B) core-satellite metapopulation; (C) patchy population; (D) non-equilibrium metapopulation; and (E) an intermediate case that combines B and C. Closed circles represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate the boundaries of populations. Arrows indicate migration (colonization) (from Harrison 1991.)
effectiveness of movement between populations depends on the extent of the movement and the mortality of the dispersing individuals.

One of the major issues of the subpopulation concept is the fidelity to a home range or natal site (natal philopatry). Through natal homing, animals that stray away from their natal site may return for reproduction. In many fishes where juveniles and adults make seasonal and ontogenetic migrations related to feeding or reproduction, they may utilize one of three mechanisms, or a combination thereof, to return to their natal site and maintain philopatry. The three mechanisms are: (1) imprinting on environmental cues; (2) learning from other fishes (social tradition); and (3) genetically based homing. The nature of the homing mechanism, when it occurs, has some interesting implications for management issues, as discussed below.

**Genetic Structure**

How populations are organized as metapopulations and their genetic structure are closely linked, genetic structure being influenced by the amount of gene flow between local populations. There are widely differing opinions on the degree of structure in marine fish populations, ranging from a lot of subpopulation structure to almost none. At one end is Sinclair's (1988) member/vagrant hypothesis, whereby there are many discrete populations, genetically distinct through larval retention and mortality of vagrants. This concept was founded on observations of specific spawning locations that seem to favor retention of larvae. At the other end of the spectrum is Smith et al. (1990) whose dynamic population concept has stocks with no discrete genetic status as homogeneous isolates, but as dynamic heterogeneous components of the species; some genetic differences may occur from isolation by geographical distance and gene selection. This concept arises from observations of high genetic variability within an area and low genetic differentiation between areas.

Genetic divergence among subpopulations is promoted by mutation, genetic drift, and natural selection favoring adaptation to local environments and hindered by the homogenizing process of gene flow from movements of gametes, individuals, or populations (Slatkin 1987). Genetic drift is also minimized by the huge sizes of many marine fish populations. Phenotypic and genotypic characteristics have been used to distinguish fish subpopulations. The use of phenotypic characters is still widely practiced, but when used alone is generally received with some skepticism. Biochemical and molecular genetic techniques are powerful tools for fisheries; there have been many studies of protein polymorphisms and more recently molecular genetics, looking for differences between nearby geographical populations, with the goal of finding genetically isolated management units. Many studies of marine fishes fail to distinguish populations (Pawson and Jennings 1996) due to the state of technology as applied to population genetics, due to high levels of gene flow, either historical or ongoing, or due to poor resolution power due to small sample sizes (Taylor
1991b). However, there have also been some great successes; for example, distinguishing smelt populations on opposite sides of the St. Lawrence River (Bernatchez and Martin 1996), distinguishing mosquito fish populations within several hundred meters of shoreline (Kennedy et al. 1986) and distinguishing Fundulus populations along coastal transects (Gonzalez-Villasenor and Powers 1990).

In marine fishes, the importance of larval dispersal on gene flow and population structure has been shown by several studies (Waples and Rosenblatt 1987, Avise 1994). For example, Doherty et al. (1995) used isozymes to show that a reef species, the damselfish (Acanthochromis polycanthus), whose offspring are reared in the parental territory and which lacks larval dispersal, demonstrates negligible gene flow over ca. 1,000 km. Doherty showed that other species with larval dispersal had genetically homogeneous subpopulations resulting from gene flow. However, high dispersal potential may not always translate into high gene flow and genetic homogeneity. There may be physical impediments to dispersal such as retention mechanisms, early life stages may not be passive drifters, and later stages may have natal homing behavior.

**Characterization of Pollock**

**Distribution and Population Ecology**

Walleye pollock is a species with a very broad niche. Although commonly associated with the outer shelf and slope regions of oceanic waters, as a species it is capable of utilizing a wide variety of habitats including near-shore eelgrass beds (J. Norris, School of Fisheries, University of Washington, Seattle, WA 98195, pers. comm.), large estuaries like Puget Sound, coastal embayments, and open ocean basins such as the Aleutian Basin of the Bering Sea. Although adults of the species are often described as semidemersal, in some areas they are strictly pelagic (Bakkala 1993). Pollock commonly feed on a wide assortment of prey from pelagic copepods to epibenthic organisms as well as pelagic and demersal fishes.

Pollock has a broad range from Puget Sound to the northern Bering Sea and on across the North Pacific (Fig. 3). It is most abundant in the eastern Bering Sea and the Sea of Okhotsk. Besides an extensive range, the local abundance of pollock is usually high, and it often dominates regional groundfish communities. Based on its ecological plasticity, broad range and high levels of abundance, pollock can be characterized as a classical generalist species capable of invading and adapting to marginal habitats.

The distribution of pollock is closely linked to temperature. The vertical distribution of juvenile pollock, and horizontal distribution of schools of adults and juveniles are influenced by fronts, temperature, and depth (Bailey 1989, Swartzman et al. 1994). The interaction of temperature with behavior of pollock has been well-studied (Olla et al. 1996, Sograd and Olla 1996). The horizontal distribution of pollock is limited by cold tem-
temperatures, from 0-2°C, as shown by distribution of commercial catches, and catches of juveniles and adults in research surveys (Francis and Bailey 1983). Detailed studies have not been conducted at high temperatures, but the range of pollock appears to be limited by temperatures of 10-12°C.

We tracked the distribution pattern of several year classes in the eastern Bering Sea to examine ontogenetic dynamics in distribution of different year classes. The 1982 year class was found predominately in the outer shelf region of the southeastern Bering Sea as larvae (Fig. 4A); as age-0 juveniles they had moved northward and inshore (Fig. 4B). As age-1 fish, they had distributed themselves farther northward and also a large portion of the population was found shoreward (Fig. 4C). As age-3 fish in summer, a portion of the 1982 year class returned to the southern outer shelf region, but a large number of fish remained in the northeastern outer shelf (Fig. 4D). The 1989 year class was not sampled as larvae, but as age-0 juveniles in summer it was broadly distributed across the middle shelf in the south and along the outer shelf region in the northwest (Fig. 5A). This pattern persisted for age-1, age-2, and age-3 fish (Figs. 5B-D). Portions of the year class distributed inshore tended to persist there through age-3. The 1993 year class was sampled as larvae along the outer shelf region of the south (Fig 6A). It was not sampled as age-0 juveniles, but as age-1's was found far northward in a band extending along the northern outer shelf (Fig. 6B,C). The distribution of age-3 fish appears similar to that of age-2, perhaps with a slight shift southward (Fig. 6D). Overall, these patterns indicate generally northward movements of age-0 and age-1 fish. However, there appears to be considerable interannual variability in distribution patterns; sometimes these two age classes move shoreward also. By age-3 it appears that pre-spawning fish shift their distribution southward again.

Figure 3. The distribution range of walleye pollock shown with cross-hatching. Major spawning locations are shown with closed circles.
Figure 4. Relative distribution patterns of the 1982 year class of walleye pollock in the eastern Bering Sea: (A) larvae in June from ichthyoplankton surveys; (B) age-0 juveniles in autumn from midwater trawl surveys; (C) age-1 in summer from bottom trawl surveys; and (D) age-3 in summer from bottom trawl surveys. Contour shows area of highest abundance. Dashed line shows approximate region surveyed.
Figure 5. Relative distribution patterns of the 1989 year class of wall-eye pollock in the eastern Bering Sea: (A) age-0 juveniles in summer from midwater trawl surveys; (B) age-1 in summer from bottom trawl surveys; (C) age-2 in summer from bottom trawl surveys; (D) age-2 in summer from midwater trawl surveys; and (E) age-3 in summer from bottom trawl surveys. Contour shows area of highest abundance. Dashed line shows approximate region surveyed.
Figure 6. Relative distribution patterns of the 1993 year class of walleye pollock in the eastern Bering Sea: (A) larvae in May from ichthyoplankton surveys; (B) age-1 in summer from bottom trawl surveys; (C) age-1 in summer from midwater trawl surveys; and (D) age-3 in summer from bottom trawl surveys (age estimated from length class). Contour shows area of highest abundance. Dashed line shows approximate region surveyed.
Characterization of pollock as a colonizing species, and knowing that physical and biological factors impede the invasion of colonizing species, lend support to historical suggestions that the rapid increase in pollock populations occurring in the late 1960s was due to an "ecological release" caused by removing competitive pressure of Pacific Ocean perch (*Sebastes alutus*) due to harvesting (Somerton 1978) and decreases in abundance of Pacific herring (*Clupea harengus*). Under this scenario, pollock were a classic $r$-selected species with rapid growth, early maturity, and high fecundity that were capable of rapidly taking over this niche opening; most likely, juvenile pollock were the stage capable of exploiting prey resources made available. The expanding population of juveniles could have made them the most available prey for pollock adults resulting in their cannibalistic nature in the eastern Bering Sea.

In the Gulf of Alaska, an increase of pollock in the mid-1980s coincided roughly with a regime shift occurring in 1977-78 (Hollowed and Wooster 1995) and possibly was associated with good conditions for juveniles of the 1976-78 year classes. Recently, however, pollock stocks in the Gulf of Alaska have declined markedly. Curiously, the age of maturity has increased (Megrey 1988) in spite of declining density. Furthermore, since the mid-1980s juvenile survival has been relatively poor; from 1980 to 1985, 5 of 6 year classes had relative age 0-2 mortality lower than the 1980-91 mean value. By contrast, from 1986 to 1991, 5 of 6 year classes had higher than the mean long term mortality (from data in Bailey et al. 1996). These data tend to indicate trends of increasing predation pressure on juveniles or eroding environmental conditions for juveniles and adults.

The relationship of distributional range and population abundance has not been formally examined for pollock because historical records over the whole range of pollock are not available. However, based on the historical declines of abundance in populations outside the major fishery area, while the central area of pollock biomass has remained relatively stable, pollock can be characterized as a species with a main central range and numerous fringe populations; the overall range of the population may not shrink with population decreases unless local fringe populations go extinct. Within local populations there may be a positive range and abundance association, similar to that found for Atlantic cod (Swain and Wade 1993). This is supported by Tsugi's (1989) assertion that during times of increasing commercial catch levels (and therefore abundance) pollock expand into adjacent waters.

Comparing the mean and variance of subpopulation abundances over time can characterize how populations are controlled in different areas of the species’ range. In the case of pollock, a plot of mean subpopulation abundance versus variability shows a slope less than unity, indicating that peripheral, less abundant pollock stocks vary more than central, more abundant stocks (Fig. 7). These results could either indicate more density dependence in the central stocks, including density-dependent colonization
of peripheral populations, or that environmental conditions are more variable and have a greater effect on peripheral populations.

**Year-Class Dynamics**

For all of the major pollock groupings, stock fluctuations are strongly influenced by intermittent recruitment of strong year classes. For example, Fig. 8 shows the impact of a series of strong year classes on stock abundance in the Gulf of Alaska, as well as the drop in abundance related to subsequent recruitment of relatively poor year classes. In the eastern Bering Sea, the 1978 year class comprised 67% of the pollock population in 1981 and 53% of the population in 1982. Many regions share the same strong year classes; for example, 1978 was a strong year class in the Gulf of Alaska, Aleutian Basin, eastern Bering Sea, western Bering Sea, and Sea of Okhotsk. Likewise 1982, 1984, and 1989 were strong across the Bering Sea, although not in the Gulf of Alaska. Strong year classes in the Gulf of Alaska including 1976, 1977, 1979, and 1988 did not appear strong in the Bering Sea. Therefore there is not a consistent association of strong year classes among the Bering Sea and Gulf of Alaska populations, indicating a lack of density-dependent dispersal between these geographic regions. However, within the Bering Sea, there appears to be an association of strong
year classes among the different regions. The occurrence of similar strong year classes in different regions of the Bering Sea has been cited as evidence of panmixia within the Bering Basin (Dawson 1994). At the extreme ends of the range of pollock (e.g., Puget Sound) the strong year classes (1972-75; Palsson et al. 1996) were quite different from those in the centers of abundance.

**Genetic and Metapopulation Structure**

Pollock show repeated, predictable, and discrete spawning at specific sites and times, which is a piece of evidence for natal philopatry. Some of these persistent spawning sites are shown in Fig. 3. Among the best studied spawning aggregations is that in Shelikof Strait which has been monitored since 1981. The Shelikof Strait spawning aggregation is the largest spawning biomass in the Gulf of Alaska, and mostly spawns within a limited area (40 × 80 km) during the first week in April (Kendall et al. 1996). The geographic and temporal consistency of spawning for this and other spawning aggregations argues against the notion that the timing and position of spawning is random, depending on suitable conditions. Mark-recapture studies where pollock were tagged during the spawning season (April) indicate dispersed feeding migrations but return homing to specific spawning locations (Tsuji 1989; Fig. 9). Thus, pollock show a relatively continuous
distribution during the feeding season, and a more patchy distribution during the spawning season. Over recent geologic times (i.e., the past 10,000 years), local pollock populations have presumably undergone local extinctions and recolonizations due to heavy glaciation of fjords and lower sea levels. As noted above, the local population in south Puget Sound has gone extinct for all practical purposes. Thus, some groups of pollock populations may be viewed as metapopulations under a relaxed definition of the term (McCullough 1996).

We have summarized studies on stock structure of pollock according to their phenotypic, acquired, or genetically based nature. Briefly, phenotypic characteristics of pollock both within small geographic regions and across much broader areas indicate considerable population structure (Table 2). For example, Koyachi and Hashimoto (1977) and Hashimoto and Koyachi (1977) used differences in vertebral counts and in growth
rates to distinguish 11 groups of pollock across its range. Within a small area (i.e., around the islands of Japan) there are also distinct groups (Iwata and Hamai 1972).

Naturally acquired tags such as elemental composition of otoliths and parasite characteristics indicate restricted mixing among pollock juveniles and adults of different subpopulations (Table 3). For example, the chemical “fingerprint” of otoliths near the nucleus (deposited during early larval life) could be utilized to assign fish to their capture location as juveniles with 70-85% accuracy over broad regions of the eastern Bering Sea (Mulligan et al. 1989), indicating limited movement and mixing of fish from different geographic regions. Using parasite frequencies, adult pollock caught on the south side of Vancouver Island can be distinguished from those on the west side with about 75% accuracy (Arthur 1983). In the Sea of Okhotsk, several different populations of pollock were distinguished based on parasite frequencies (Avdeev and Avdeev 1989). By contrast, mark-recapture studies where pollock were tagged in summer indicate broad movement of individuals across areas of the Bering Sea (Fig. 10). However, critical studies of marking spawning pollock have not been conducted. Tagging results to date in the Bering Sea do not give information on spawning migrations or spawning site fidelity, but do indicate potential for dispersal during the summer feeding period. Nor have these studies provided information indicating whether individuals are moving with large schools as migrating populations, whether individuals are vagrants and mixing with local populations, or whether dispersal patterns in the Bering Sea are part of ordered seasonal migrations. Tagging studies around Japan do support dispersed feeding migrations and homing migrations to specific spawning areas (Tsuji 1989).

Studies using biochemical and molecular methods on pollock show mixed results for distinguishing stock structure of pollock, varying somewhat by technique (Table 4). Using allozymes, Grant and Utter (1980) detected minor differences between the Gulf of Alaska and Bering Sea, but no differences within either region. Using mitochondrial (mt) DNA sequence data from a 76 base pair (bp) spacer from the control region, Shields and Gust (1995) reported slight genetic differences between eastern and western Bering Sea pollock. Mulligan et al. (1992) employed mtDNA restriction fragment length polymorphism (RFLP) on fish collected during the spawning season and using pairwise comparisons of haplotype frequencies distinguished among stocks in the Gulf of Alaska, Donut Hole/Bogoslof Islands, and Aleutian Islands.

More recently, using sequences of mtDNA cytochrome b and ATPase-8, Powers (1996) and his colleagues (J. Quattro and D. Powers, unpubl. data, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950) identified haplotype differences between Asian and North American pollock. The unique DNA sequences allowed them to develop an enzyme method to rapidly identify individuals by RFLP. An analysis of molecular variance (AMOVA) on the combined data identified sharp distinctions between Asian
### Table 2. Summary studies of pollock stock structure using phenotypic characteristics.

<table>
<thead>
<tr>
<th>Author</th>
<th>Method</th>
<th>Area</th>
<th>Results</th>
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<tbody>
<tr>
<td>Ogata (1959)</td>
<td>Meristics: vertebrae counts</td>
<td>Sea of Japan and Pacific Ocean side of Japan</td>
<td>Sea of Japan has 3 different stocks. Sea of Japan differs from the Pacific Ocean side.</td>
</tr>
</tbody>
</table>
| Iwata and Hamai (1972) | Meristics: vertebrae counts | Sea of Japan, Sea of Okhotsk, and Pacific Ocean near Hokkaido | 8 “local forms”:
- 2 groups in the Sea of Japan.
- 3 groups in the Okhotsk Sea.
- 3 groups in the Pacific Ocean. |
| Temnykh (1994)  | Morphometrics                           | Western Bering Sea and eastern Kamchatka | Western Bering and Eastern Kamchatka stocks distinguished.               |
| Ishida (1954)   | Morphometrics: otoliths                 | Northern Sea of Japan, Sea of Okhotsk, and northern Pacific Ocean coast of Japan | Otolith size is larger in Sea of Japan pollock than Okhotsk Sea. Otoliths are similar between Sea of Japan and Pacific Ocean pollock. |
| Shaw and McFarlane (1986) | Morphometrics: length-at-age          | British Columbia: Dixon Entrance, Strait of Georgia | 2 stocks discriminated: Strait of Georgia pollock are smaller. Little interaction between pollock north and south of Queen Charlotte Sound. |
| Thompson (1981) | Morphometrics: length-at-age            | British Columbia: Dixon Entrance, Strait of Georgia, Queen Charlotte Sound | 3 separate stocks: each area contains its own distinct stock. Little mixing occurred between them. |
| Saunders et al. (1989) | Morphometrics: life history | British Columbia | Separate stocks in Strait of Georgia, Hecate Strait/Dixon Entrance, Queen Charlotte Sound, and Western Vancouver Island. |
| Lynde et al. (1986) | Morphometrics: length-at-age          | Eastern Bering Sea and Bering Sea basin | Northeastern shelf and slope and Aleutian Basin represent one stock distinct from other regions of the eastern Bering Sea. |
| Hinckley (1987) | Spawning time and location, morphometrics: length-at-age, fecundity | Aleutian Basin and eastern Bering Sea shelf and slope | 3 spawning stocks in the eastern Bering Sea: basin, northeastern slope, and eastern shelf and slope. |
| Mulligan et al. (1989) | Spawning time and location | Eastern Bering Sea and Aleutian Basin | 3 spawning areas separated in space and time: eastern Bering Sea southeastern shelf, eastern Bering Sea northwestern shelf, and Aleutian Basin. |
| Serobaba (1977) | Meristics and morphometrics             | Northern, western, eastern, and southern Bering Sea | Different stocks occupy each region. |
| Janusz et al. (1989) | Meristics and morphometrics          | Donut hole and eastern Bering sea shelf | 2 stocks distinguished in Donut Hole and eastern Bering Sea. |
Table 2. (Continued.) Summary studies of pollock stock structure using phenotypic characteristics.

<table>
<thead>
<tr>
<th>Author</th>
<th>Method</th>
<th>Area</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitta and Sasaki</td>
<td>Morphometrics</td>
<td>Donut hole, eastern Bering Sea, near Japan</td>
<td>Characteristics distinguish 3 stocks, with about 90% classification accuracy.</td>
</tr>
<tr>
<td>Gong et al. (1990)</td>
<td>Meristics</td>
<td>Asian and Bering Sea</td>
<td>Asian stock and Bering Sea stocks distinguished but stocks within these regions not distinguished.</td>
</tr>
<tr>
<td>Koyachi and Hasimoto (1977)</td>
<td>Meristics: fin ray, gill raker, and vertebrae counts</td>
<td>Entire Pacific Ocean</td>
<td>12 subpopulations, including the Bering Sea and Gulf of Alaska.</td>
</tr>
</tbody>
</table>

Table 3. Summary studies of pollock stock structure using acquired characteristics.

<table>
<thead>
<tr>
<th>Author</th>
<th>Method</th>
<th>Area</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nakano et al. (1991)</td>
<td>Otolith chemistry: adults, whole otolith homogenates</td>
<td>Eastern Bering Sea, western Bering Sea, Donut hole</td>
<td>Differences in 3 areas, little mixing.</td>
</tr>
<tr>
<td>Severin et al. (1995)</td>
<td>Otolith chemistry: juveniles, outer otolith increments</td>
<td>Eastern Bering Sea: Bristol Bay; and Gulf of Alaska</td>
<td>Distinguish 5 areas, some mixing.</td>
</tr>
<tr>
<td>Arthur (1983)</td>
<td>Parasites</td>
<td>British Columbia: Strait of Georgia, west side of Vancouver Island, Queen Charlotte Sound, and Dixon Entrance</td>
<td>3 stocks in this area: Strait of Georgia, Vancouver Island, and Queen Charlotte Sound/ Dixon Entrance.</td>
</tr>
<tr>
<td>Misc. authors, see Figs. 9, 10</td>
<td>Tagging studies</td>
<td>Western and eastern Bering Sea, Japan</td>
<td>Broad movements, homing migrations to spawning site.</td>
</tr>
</tbody>
</table>
and North American pollock and considerable substructure within the American and Asian clusters (Fig. 11).

Powers and Gary Villa (unpubl. data, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950) screened populations for DNA microsatellite loci that allowed the discrimination between populations on a finer scale than was possible by mtDNA analysis. Based on pairwise comparisons for the two microsatellite loci examined (Gmo-145 and Gmo-2; Brooker et al. 1994) significant differences between Asian and American stocks were confirmed and, furthermore, differences between Gulf of Alaska and Bering Sea stocks were resolved (Fig. 12). One microsatellite primer scored for a null allele in the western Bering Sea samples that was responsible for the major east-west differences, which warrants examination with more primers. Even though the statistical results are tentative, they are generally supportive of data from life history characteristics and phenotypic patterns that indicate considerable population heterogeneity in pollock. Avise (1994, 1995) cautions, however, that solid conclusions on

Figure 10. Movement of walleye pollock tagged by Japanese scientists in the Bering Sea (from Dawson 1994). Note: Most tagging and recoveries occurred during the summer/autumn feeding season. Note cluster of April recoveries near Unimak Pass in the spawning season.
Table 4. Summary of stock structure studies on walleye pollock using biochemical genetics characteristics.

<table>
<thead>
<tr>
<th>Author</th>
<th>Method</th>
<th>Area</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mulligan et al. (1992)</td>
<td>mtDNA RFLP</td>
<td>Eastern Bering Sea basin, Aleutian Islands, and Gulf of Alaska</td>
<td>2 distinct stocks in Aleutian Islands and Donut Hole/Bogoslof; Gulf of Alaska and Donut Hole/Bogoslof have informative differences.</td>
</tr>
<tr>
<td>Grant and Utter (1980)</td>
<td>Allozyme</td>
<td>Southeastern Bering Sea and Gulf of Alaska</td>
<td>Minor genetic differences between the two areas. No differences within the areas.</td>
</tr>
<tr>
<td>Johnson (1977)</td>
<td>Allozyme</td>
<td>Eastern Bering Sea and Gulf of Alaska</td>
<td>No significant differences found.</td>
</tr>
<tr>
<td>Iwata (1973)</td>
<td>Allozyme</td>
<td>Northern Sea of Japan and North Pacific coast of Japan</td>
<td>No differences found.</td>
</tr>
<tr>
<td>Iwata (1975a,b)</td>
<td>Allozyme</td>
<td>Northern Sea of Japan and eastern Bering Sea</td>
<td>Highly significant differences found between the two areas.</td>
</tr>
<tr>
<td>Efremov et al. (1989)</td>
<td>Allozyme</td>
<td>Northern Sea of Okhotsk</td>
<td>Allozyme variability suggesting that aconitase could be genetic marker.</td>
</tr>
<tr>
<td>Powers (1996)</td>
<td>mtDNA RFLP and DNA microsatellite</td>
<td>Bering Sea and Gulf of Alaska</td>
<td>Eastern and western Bering Sea distinguished using mtDNA; Gulf of Alaska and eastern Bering Sea stocks have informative differences using microsatellite DNA.</td>
</tr>
</tbody>
</table>

Population structure need to be based on multiple loci, setting up this future study as an important research priority.

There is a pattern of apparent stock structure in walleye pollock, that has not always been indicated by genetic differences. Phenotypic differences between stocks, elemental composition of otoliths and parasite studies indicate restricted mixing of adults. In addition, otolith elemental composition data indicate restricted mixing of juveniles between adjacent stocks (eastern Bering Sea shelf and basin). There are genetic differences between broad regions, but differences between adjacent stocks, especially within the eastern Bering Sea, is currently unresolved. The potential for gene flow mediated by larval drift is high between adjacent stocks. However, since there appears to be an unresolved degree of structuring within the Bering Sea, reduced gene flow due to larval retention mechanisms or strong natal homing and philopatry is also possible.

The standard metapopulation models of Harrison (1991; Fig. 2) do not fit the apparent population structure of pollock as known to date. We propose a generalized metapopulation structure that represents an intermediate model. The overall population of pollock is made of several large and major populations separated by large distances and geographic barriers (such as the eastern Bering Sea and Sea of Okhotsk populations) with little gene flow between them, and numerous smaller populations with potential linkages amongst each other and the larger populations (Fig.
13). Some populations may show local adaptations to their specific habitat, minimizing gene flow through reliance on larval retention features and natal homing.

**Management Implications**

When fisheries fluctuate, are local populations waxing and waning independently or are they connected in some way? This has been a central issue in fisheries since the time of Hjort (1914). Since that time, however, fisheries science has often been based on the concept of populations as closed and homogeneous systems. For example, prior to the collapse of the northern Atlantic cod (*Gadus morhua*) population in the Northwest Atlantic Ocean it was believed that there was no genetically based population structure due to extensive egg and larval drift, followed by opportunistic and nonphilopatric recruitment of juveniles to adult assemblages (deYoung and Rose 1993). Isozymes and mtDNA studies had little success in differentiating Northwest Atlantic cod stocks. Bentzen et al. (1996) used the relatively new technique of DNA microsatellite analysis which has, in this case at least, higher resolution and found that the northern cod pop-
Figure 12. UPGMA clustering of genetic distances among walleye pollock stocks from allele frequencies determined with microsatellite primers Gmo-2 and Gmo-145. Pairwise ANOVA comparisons showed significant differences between the eastern and western Bering Sea and Gulf of Alaska (from Powers 1996). Scale bars represent genetic distance.

ulation does not comprise a single panmictic assemblage, but rather there are genetically distinguishable subunits, each of which is affiliated with a distinct spawning area. The development of technology that enables a higher level of resolution of stock structure will also need to be accompanied by new management strategies.

There are several issues in lumping genetically or geographically discrete subpopulations as single management units. The major issue is the depletion of unidentified local subpopulations and their possible extinction (Ovenden 1990). If genetically distinct subpopulations by definition have little movement among them, specific stock adaptations to local habitat conditions can impede recovery from extrinsic sources. The rate of recovery of geographically discrete populations will depend on the level of gene flow between subpopulations. Furthermore, Daan (1991) indicates that if Virtual Population Analysis is applied to a heterogeneous unit stock (a metapopulation), then fishing effort is underestimated and fishing mortality deviates from the recent true trend. This leads to the possibility of overfishing. Pawson and Jennings (1996) also indicate that lumping stocks leads to reductions in short-term yields.

In the case of pollock, whether broad-scale migrations can result in seasonal mixing of subpopulations is also a central issue. For example, if eastern or western Bering Sea fish migrate across or around the basin (as believed by Dawson 1994), they may be harvested on either side of the
Figure 13. Hypothetical nonspecific pictograph representing the population structure of walleye pollock. Closed circles represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate boundaries of populations. Arrows indicate relative gene flow through migration or larval transport. Probable main populations for pollock are Sea of Okhotsk and eastern Bering Sea shelf.
Bering Sea basin each of which has its own harvest quota. Therefore, a migratory population would experience two independent sources of fishing mortality.

The mechanism of natal-site fidelity has broad implications to fisheries management and sustainable harvesting of these populations. For example, if fish learn their migration routes from older fish, currently thought to be important for cod (Rose 1993) and herring (Corten 1993), then removing older fish from the population can lead to increased straying of younger fish due to loss of social tradition. Furthermore, this mechanism implies that larvae dispersed from the range of adults can adopt new local populations. The mechanism of a "genetic memory" is that there are environmental clues which direct fish to return to an ancestral spawning location, and recognition of clues is inherent. If fish have this inherited sense, then colonization processes depend on natural selection and adaptation to local conditions. Vagrants from other populations are unlikely to spawn with local populations in the same region. Imprinting is a mechanism by which fish learn the clues of their spawning location by their own experience. Under this scenario, depleted populations can be restocked. In fact, marine fish species probably use a combination of all of these mechanisms for natal fidelity, and the response to any one stimulus is graded against others. It is not known which homing mechanisms are utilized by pollock during spawning migrations; however, based on the complex range of behaviors pollock are capable of exhibiting (Olla et al. 1996) it should not be surprising that they show considerable flexibility in their homing behavior.

Recently, new local populations of pollock have been discovered, and whether they can be maintained as self-sustaining populations or whether they are ephemeral stocks is a question that depends upon the mechanism of natal spawning and local adaptation for reproductive success. For example, in recent years a spawning population of 300,000 tons has been found around the Shumagin Islands in the western Gulf of Alaska (C. Wilson, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, pers. comm., October 1996). This population is largely composed of the 1989 year class, which was strong in the Bering Sea, but weak in the rest of the Gulf of Alaska. It is unknown whether this population originated from density-dependent dispersal from the Bering Sea, or whether it represents an increase in a local subpopulation. Alternatively, vagrants from the Bering Sea could have joined a small local spawning population. In any case, for this population to sustain itself, there has to be local adaptation to the time and location of spawning to ensure reproductive success; or, larvae originating from the population can be dispersed vagrants, and maintenance of the population depends on a combination of recruitment from an upstream source and learning where to spawn from current inhabitants.

Given the high potential for gene flow in marine species, genetic approaches alone may not completely resolve stock structure issues. Low
levels of diversity in marine fish populations have also been attributed to historical bottlenecks or recent founding of the population relative to the rate of mutation and genetic drift detectable in the particular genetic structure (mtDNA, microsatellite, etc.) analyzed. Tagging studies offer another way to study linkages between fish populations, providing information on stock separation and migration (Pawson and Jennings 1996). Carefully planned tagging experiments, or experiments utilizing naturally acquired tags are needed to establish relationships between fishes in different regions. Although not necessarily showing levels of gene flow between areas, tagging and/or transplant experiments offer a powerful approach to studying migration mechanisms. These studies of dispersal, in coordination with modern genetic studies, should contribute significantly to understanding links between population dynamics and structure of pollock populations.

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Use of a Surface-Current Model and Satellite Telemetry to Assess Marine Mammal Movements in the Bering Sea

Thomas R. Loughlin and W. James Ingraham Jr.
Alaska Fisheries Science Center, Seattle, Washington

Norihisa Baba
National Research Institute of Far Seas Research, Shizuoka, Japan

Bruce W. Robson
Alaska Fisheries Science Center, Seattle, Washington

Abstract

We used satellite-linked time-depth recorders (SLTDRs) to monitor movements of eight free-ranging adult male northern fur seals (Callorhinus ursinus) in the Bering Sea and North Pacific Ocean during October through January 1993. We investigated whether the movements of adult male northern fur seals at sea during migration are independent of ocean surface currents by comparing fur seal movements obtained from SLTDRs to the movement of surface currents derived by the numerical model Ocean Surface Current Simulations (OSCURS). Results from this study suggest that movements of fur seals are independent of surface currents but that the seals likely cue on currents during migration and as an aid in finding prey. The eight male northern fur seals generally swam in the same direction as surface current trajectories calculated by the OSCURS model. Seals that left the Bering Sea toward the west, and all seals while in the Pacific or Gulf of Alaska, had movements similar to water surface current trajectories calculated by OSCURS. However, four seals that left the Bering Sea through passes in the eastern end of the Aleutian Islands chain swam opposite to the weak northerly water flow in the southeastern Bering Sea. Once in the North Pacific and Gulf of Alaska, their movements were similar to calculated surface water trajectories.
Introduction

There are 116 species of marine mammals in the world oceans of which 25 are known to inhabit the Bering Sea (Lowry et al. 1982, Kajimura and Loughlin 1988). Little is known about the ecology and life history of most of these mammals with the exception of a few species that received scientific study or that had been exploited by commercial whalers or sealers. Information on prey for most marine mammal species is based on small sample sizes and even less is known about their movement patterns and foraging behavior. Current information on marine mammals at sea is based primarily on opportunistichic sightings; few directed studies of movements of marine mammals in the Bering Sea have occurred. One exception is the northern fur seal (*Callorhinus ursinus*). Identification of its prey and feeding habits around the Pribilof Islands is well documented (Kajimura 1984, Sinclair et al. 1994) and information on foraging ecology (e.g., feeding locations and depths) has been studied (Loughlin et al. 1987, Goebel et al. 1991). However, identification of the oceanographic factors that influence movements of fur seals while at sea during migration remains largely undetermined. A major reason for this lack of information has been the difficulty of obtaining data on movements, foraging locations, and diving of free-ranging marine animals. Instruments which record diving depths over time (time-depth recorder or TDR) have existed since the 1970s and have allowed researchers to track some pinniped movements vertically in the water column during foraging trips (e.g., Gentry and Kooyman 1986). Subsequent studies coupled the TDR with a VHF radio transmitter and a ship or aircraft was used to track northern fur seals to obtain a partial picture of their pelagic movements (Loughlin et al. 1987, Antonelis et al. 1990, Goebel et al. 1991). Application of this technique has received limited use due in part to the high costs of aircraft and ship time, and the need to recapture the animal to recover the TDR data.

Recent developments in satellite telemetry allow tracking of marine animals using satellite-linked transmitters (e.g., Hill et al. 1987, Hills 1987, Stewart et al. 1989). Through the Service-Argos system on board NOAA Tiros-series satellites, it is possible to track and retrieve data from free-ranging animals using uplink communications between satellite transmitters attached to animals and receivers on board satellites. Locations at sea are determined from the Doppler shift of a series of signals received by the satellite (Fancy et al. 1988, Stewart et al. 1989).

By combining a satellite transmitter and TDR it is possible to determine locations and collect diving information while the animal is at sea. The TDR collects dive data which can be transmitted while the animal is at sea or saved for later transmission while the animal is on land. This is particularly important for animals like male northern fur seals which inhabit relatively inaccessible areas and return to their tagging site on an infrequent basis.
We used a satellite-linked time-depth recorder (SLTDR) developed for pinnipeds (Merrick et al. 1994) to provide information gained on free-ranging adult male northern fur seals in the Bering Sea and North Pacific Ocean. We describe their movements during October 1992 through January 1993. We report on the relationship between adult male northern fur seal movements at sea during migration and ocean surface currents (Fig. 1; Ohtani 1973). We compared fur seal movements derived from SLTDR locations to the movement of daily surface currents at the fur seal’s location derived by the numerical model Ocean Surface Current Simulations (OSCURS) (Ingraham and Miyahara 1988).

### Methods

#### SLTDR Protocol

We deployed Type 3 (½ watt) SLTDRs from Wildlife Computers, Redmond, WA, USA, during October 1992 on eight adult male northern fur seals at St. Paul Island, Alaska (Table 1). All eight were estimated to be between 7 and 11 years of age, based on physical size, coloration, and form of the head and neck. Each showed indications of having fasted for a long period (breeding period) and were likely holders of territories before being instrumented. The male fur seals were immobilized with Telazol injected remotely with a 5 cc dart fired from a pneumatic dart gun (Loughlin and Spraker 1989, Kiyota et al. 1992b). The SLTDR was then attached directly to the

<table>
<thead>
<tr>
<th>SLTDR</th>
<th>Date deployed</th>
<th>Final transmission</th>
<th>No. days</th>
<th>Date left Bering Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>14100</td>
<td>10/22/92</td>
<td>01/06/93</td>
<td>76</td>
<td>a</td>
</tr>
<tr>
<td>14101</td>
<td>10/24/92</td>
<td>01/31/93</td>
<td>&gt;99</td>
<td>11/14/92</td>
</tr>
<tr>
<td>14102</td>
<td>10/24/92</td>
<td>12/23/92</td>
<td>60</td>
<td>11/07/92</td>
</tr>
<tr>
<td>14103</td>
<td>10/26/92</td>
<td>01/31/93</td>
<td>&gt;97</td>
<td>12/07/92</td>
</tr>
<tr>
<td>14104</td>
<td>10/27/92</td>
<td>12/13/92</td>
<td>47</td>
<td>12/07/92</td>
</tr>
<tr>
<td>14105</td>
<td>10/27/92</td>
<td>11/26/92</td>
<td>30</td>
<td>11/16/92</td>
</tr>
<tr>
<td>14106</td>
<td>10/27/92</td>
<td>01/31/93</td>
<td>&gt;96</td>
<td>12/15/92</td>
</tr>
<tr>
<td>14107</td>
<td>10/28/92</td>
<td>01/21/93</td>
<td>85</td>
<td>11/30/92</td>
</tr>
</tbody>
</table>

* a Seal 14100 did not leave the Bering Sea.
animal's back using 5-minute epoxy glue (Loughlin et al. 1987). Duration of SLTDR operation varied from 30 to more than 98 days (Table 1).

Software built into the SLTDR controlled three functions—data collection, summarization, and transmission. Once the animal had gone to sea the unit collected data on location and depth readings at 10 s intervals throughout the trip. This report contains only information on locations at sea; the foraging (dive depth and dive duration) data will be reported elsewhere. While the animal was at sea, a 32-bit data message was transmitted at 45 s intervals whenever the animal surfaced (as determined by a conductivity sensor, "saltwater switch"). These messages included summarized dive data and were used to calculate animal locations.

Service-Argos classifies the accuracy of locations as class 3 (accurate to 150 m), class 2 (accurate to 350 m), class 1 (accurate to 1 km), and class 0 (no accuracy assigned) (Service-Argos 1984). Most locations we received were class 1 and 0. Data were received from Service-Argos on floppy diskettes and formatted using software developed by Wildlife Computers. At-sea information is presented as track lines over time representing numerous locations at sea.

**OSCURS**

We used the computer program known as the Ocean Surface Current Simulations (OSCURS) numerical model to hind cast oceanic surface water drift in relation to fur seal movements during migration determined by SLTDR location data. OSCURS is an empirical ocean-wide surface current model that covers the Subtropic and Subarctic Pacific Region and Bering Sea from 10° to 66°N with a 90 km grid. Surface currents are calculated daily from a gridded-daily sea level atmospheric pressure database which extends back to 1946. By choosing any starting date and location within the grid (i.e., a fur seal sighting), surface water displacement trajectories may be calculated for any desired time interval (i.e., to compare the water movement with the fur seal movements).

Daily current fields are computed in three steps from empirical formulae (Ingraham and Miyahara 1988). First, wind speed and direction fields are computed from pressure gradients within the daily (0000 GMT) U.S. Fleet Numerical Meteorology and Oceanography Center (FNMOC) sea level atmospheric pressure fields after Larson (1975). Second, the wind-induced currents in the surface mixed layer (generally the upper 30-50 m) are calculated from empirical functions summarized by Huang (1979); speed is proportional to the square root of the wind speed (Witting 1909) and the angle (between 20° and 30°) to the right of the wind vector is a function of wind speed (Weber 1983). Third, the long-term mean geostrophic current (0/2,000 dbar) is added vectorially to the wind current to form the total current field. The total current velocity at the start location acting for 24 hours would then move the surface water to a new location which is the start location for the next day's calculations. Trajectories are thus formed
by repeating this procedure day by day for the desired time interval (i.e.,
the number of days the fur seal was tracked). Speed coefficients were
tuned (Ingraham and Miyahara 1989) so that the model trajectories matched
the trajectories of satellite-tracked drifters (drogued at 20 m) from the
Gulf of Alaska (Reed 1980).

We did not use generalized current patterns known for the study area
because the OSCURS model previously indicated that near-surface winter
circulation in the northern Gulf of Alaska varied considerably from year to
year (Ingraham et al. 1991; Ebbesmeyer and Ingraham 1992, 1994). In-
stead we used current estimates derived from the model for October 1992
through January 1993.

Large scale movements through the course of each seal’s migration
were examined in relation to monthly summaries of OSCURS current vec-
tors throughout the Bering Sea and North Pacific. To examine finer scale
(short-term) seal movements in relation to daily surface current vectors,
we chose one location per day for each of 5-15 consecutive days for se-
lected seals using location quality and proximity to 0000 GMT as selection
criteria. Daily fixes were used as starting locations for calculating surface
current (surface water displacement) trajectories in OSCURS for each 24
hour period. We examined each seal’s movements in relation to the daily
current trajectory and the direction of surrounding current vectors.

Results

Generalized Locations and Movements

The male fur seals traversed most oceanic areas and the outer domain of
the continental shelf of the Bering Sea from about 80 km north of St. Mat-
thew Island south, and from about the 100 m isobath on the continental
shelf west to Shirshov Ridge in the western Bering Sea (Fig. 1). None en-
tered the shallow waters of the eastern Bering Sea shelf east of the Pribilof
Islands although one animal (14102) was active southwest of St. Paul Island
in the middle shelf domain in water about 70 m deep. Some animals moved
erratically while others moved in direct lines to locations where diving
occurred. Eventually all (but one) male fur seals left the Bering Sea for
either the Gulf of Alaska or west toward the Kuril Islands and Japan (Fig.
2).

While in the Bering Sea, male fur seals had diving bouts, which we
assumed were related to feeding, in areas associated with the outer do-
main of the continental slope and underwater ridges and sea mounts.
Typical locations included Bowers Ridge, a large, crescent shaped ridge
extending north and west from Semisopochnoi Island in the central Aleu-
tian Island chain, and northwest of the Pribilof Islands on the continental
shelf in water from 100 to 250 m deep. Relatively little time was spent
over deepwater masses (>1,000 m) of the Bering Sea. Four animals spent
time diving west of St. Matthew Island over the shelf and shelf break div-
ing in water <100 m (number 14100—30 days, number 14103—20 days, number 14106—22 days, and number 14107—17 days).

One seal remained in the Bering Sea for the duration of the study period; the other seven entered the North Pacific from the Bering Sea through Aleutian Island passes from Unimak Pass west to the Commander Islands. Three used Unimak Pass (eastern Aleutian Islands); one used Samalga Pass (central Aleutian Islands); one passed through near Kiska Island (near the end of the chain); and two passed through near the Commander Islands. None had re-entered the Bering Sea by the end of the study period.

Movement of the four fur seals that migrated into the Gulf of Alaska did not follow surface current trajectories produced by OSCURS, but traveled south or southeast primarily in waters over the continental shelf where the northward current is very weak and dominated by tidal currents (Fig. 3; Stabeno and Reed 1994). Once they entered the Gulf of Alaska, the seals swam offshore and traveled in the same easterly direction as the surface water trajectories calculated by the model; such movement is consistent with the flow of the Subarctic Current into the Gulf of Alaska Gyre. Two of the seals (numbers 14101 and 14102) then moved northeast, similar to the direction of surface water movement calculated by OSCURS and into the westerly flowing Alaskan Stream during December 1992, diving and

Figure 1. Map depicting the Bering Sea and North Pacific Ocean subarctic water circulation and transition zones (modified from Ohtani 1991).
Figure 2. Movements of male northern fur seals equipped with SLTDRs in 1992. A represents three fur seals in the eastern Bering Sea and Gulf of Alaska; B represents three seals in the western Bering Sea and western Pacific Ocean (modified from Loughlin 1993).
Figure 3. Plot showing the movements of male fur seal number 14101 in the Gulf of Alaska and the movement of surface water during December 1992 as predicted by the OSCURS model in the Bering Sea and North Pacific Ocean. The thick, solid line represents the movements of fur seal number 14101 over the entire study period; locations on the first day of each month are noted for comparison to OSCURS water movement. The small solid circles represent a particle of water at the start of the month and the lines and arrows emanating from the circles show the predicted movement of the particle. Large arrows equal fast moving water and small arrows slow. The arrowhead at the end of each trajectory indicates the average direction and speed for the last ten days of the month. The figure suggests that fur seal movements at sea are similar to surface water movements as predicted by OSCURS in the area shown.

probably foraging, north of the gyre or downstream in the Alaskan Stream southwest of Kodiak Island. Location data for fur seal number 14107 ended prior to its movement into the Alaskan Stream but it did follow the same water flow as the other seals in the offshore Subarctic Current into the Gulf of Alaska Gyre. Seal number 14105 appeared to briefly follow the Subarctic Current into the western portion of the Gulf of Alaska Gyre. The last locations for seal number 14105 were received downstream of the Alaskan Stream near the Shumagin Islands.

Three male fur seals that went west (numbers 14103, 14104, and 14106) tended to follow the water flow pattern calculated by OSCURS (Fig. 4). Two of the three (numbers 14103 and 14104) left the Pribilof Islands then meandered in a northwest (number 14103—St. Matthew I.) and southwest (number 14104—Bowers Ridge) direction until offshore the Kamchatka Peninsula; they then entered the East Kamchatka Current and followed
the general flow south and west out of the Bering Sea and south offshore of the Kuril Islands to northern Japan. The surface currents calculated by OSCURS show westward water movements across the Bering Sea along the northern part of the Bering Sea Gyre then south by the East Kamchatka Current. Seals entered the Western Subarctic Gyre as they left the Bering Sea where they likely fed in these productive waters. Fur seal number 14103 meandered south into the Oyashio Current and Oyashio Gyre off the Kuril Islands and remained there until the end of the study period.

Fur seal number 14106 made one trip northwest of the Pribilof Islands but then returned to the Pribilof Islands before heading southwest through the Aleutian Islands then toward the Kuril Islands. Its movements were

Figure 4. Plot showing the movements of male fur seal number 14103 in the western Bering Sea and western North Pacific and the movement of surface water during December 1992 as predicted by the OSCURS model in the Bering Sea and North Pacific Ocean. The thick, solid line represents the movements of fur seal number 14103 over the entire study period; locations at the first day of each month are noted for comparison to OSCURS water movement. The small solid circles represent a particle of water at the start of the month and the lines and arrows emanating from the circle show the predicted movement of the particle. Large arrows equal fast moving water and small arrows slow. The arrowheads at the end of the trajectory indicate the average direction and speed for the last ten days of the month. The figure suggests that fur seal movements at sea are similar to surface water movements as predicted by OSCURS in the area shown.
Figure 5. Figure depicting a fine-scale comparison between fur seal daily movements and surface water movement in the Gulf of Alaska as predicted by OSCURS. The solid line with numbers associated is the movement of fur seal number 14101 from November 26, 1992 (921126), to December 10, 1992 (921210), in the Gulf of Alaska. The vectors and arrows (larger arrow represents faster speed) on this line suggest the direction and speed of a particle of water at that location as predicted by OSCURS. The other solid lines with overlaying arrows are the fine-scale surface water movements predicted by OSCURS. The figure shows the association of the fur seal with the general movement pattern of surface water and the location of the seal with the nearby transition zone of opposite-flowing water. The transition zone is where high concentrations of prey are assumed to occur.
not as well matched to the surface water movements while in the Bering Sea as were the other two male seals that went west.

**Fine-Scale Comparisons**

Surface current trajectories calculated at daily locations of individual seals indicated that the movements of fur seals were influenced, but not dictated by, location and direction of surface currents. Movements of three seals that migrated into the Gulf of Alaska (numbers 14101, 14102, 14107) were consistent with daily OSCURS vectors as they followed the eastward flow in the northern portion of the Subarctic Current into the Gulf of Alaska Gyre (Fig. 5). The three seals that migrated westward showed similar move-
ments in respect to daily OSCURS current vectors once they left the Bering Sea (Fig. 6).

Fur seals numbers 14103 and 14104 swam southward in the East Kamchatka Current then into the Western Subarctic Gyre, while fur seal number 14106 followed the direction of the Alaskan Stream extension for 2-3 days before entering the Western Subarctic Gyre from the east. While in the East Kamchatka Current or Alaskan Stream daily OSCURS vectors were consistent with fur seal movements; however, fur seals often traveled in the zone of weaker flow and eddies at the margin of these fast moving boundary currents where surface current flow, and consequently the relationship between daily directional vectors and seal movements, were less consistent.

Of the seven seals that left the Bering Sea, six arrived at similar times and remained for extended periods in one of the large cyclonic gyre systems of the North Pacific. Three of the eastward migrating seals (numbers 14101, 14102, 14107) entered the area north of 48°00′N and east of 149°00′W in the Gulf of Alaska between 30 November and 14 December 1992, remaining (presumably foraging) at the southern margin of the Alaska Gyre in the productive waters where the cold water mass from the Subarctic Current is deflected northward into the Alaska Current (Stabeno and Reed 1994). The three seals which migrated west (numbers 14103, 14104, 14106) passed south of 50°N between 11-21 December 1992 and remained in the Western Subarctic Gyre until the end of the study period. In these regions daily OSCURS vectors and fur seal locations showed more variation due to the variable current trajectories within the gyres and the localized movements of fur seals.

Discussion

Based on results from this study, we conclude that adult male northern fur seal movements at sea during migration are independent of ocean surface currents, but they likely cue on currents to facilitate migration and foraging. Our results show that seven of eight male northern fur seals that we followed swam in the same direction, or in close association with surface current trajectories calculated by the OSCURS model. Male seals that left the Bering Sea toward the west, and all seals while in the Pacific Ocean or Gulf of Alaska, had movements similar to water surface current trajectories. However, four seals that left the Bering Sea through passes in the eastern end of the Aleutian chain swam opposite to the weak northerly water flow in the southeastern Bering Sea (Overland et al. 1994, Stabeno and Reed 1994). Once in the North Pacific and Gulf of Alaska, though, their movements were similar to OSCURS' surface water trajectories.

In our fine-scale comparison, vector results showed that movements were consistent with calculated surface water trajectories in areas where these hydrographic features are associated with areas of high productivi-
Four northern fur seals followed in our study went into the Gulf of Alaska along the northern margin of the Subarctic Current leading into the Alaska Gyre. This area is characterized by large aggregations of zooplankton during summer months (Brodeur et al. 1996). We postulate that the zooplankton (or similar prey) are also there in winter and provide forage to fish consumed by northern fur seals. In a similar fashion, males which migrated westward appeared to forage in association with the East Kamchatka Current while traveling along the confluence of the fast moving boundary current and the Western Subarctic Gyre.

We weren’t surprised to find that migration of adult male northern fur seals coincided with surface currents. Fur seal movements are not passive or dependent on surface currents but currents could provide a mechanism for orientation and moving in the open ocean. Traveling with surface currents can result in reduced energy expenditures by seals. Probably most important is that currents and the edges of fronts and gyres are where biological productivity is concentrated and food availability for fur seals is optimal (Sinclair et al. 1994).

Studies on the fall movements of pups migrating from the Pribilof Islands showed that they moved through a number of different eastern Aleutian Island passes as they swim into the eastern and central Pacific Ocean (Ragen et al. 1995). These pups left the rookeries in November and spent, on average, about ten days swimming to the Aleutian Islands, entering the North Pacific in early November to mid-December (Ragen et al. 1995). Four males that we monitored also used these passes; however, the pups had likely migrated beyond the Aleutian Islands before arrival of the males we monitored. Adult males and pups probably feed on different size prey, dive to different depths to feed, and are probably not competing for similar prey resources.

Information collected during this study on adult male fur seals, and in earlier studies on adult females and pups (Kiyota et al. 1992a, Ragen et al. 1995) suggests that all ages and both sexes of fur seals leave the Bering Sea during winter (February-March; Bigg 1990). However, unpublished reports suggest that some male fur seals haul out onto ice in the Bering Sea during late March and April. One seal that we monitored (number 14100) remained in the Bering Sea during the time we were able to monitor its movements (through January 1993). The proportion of the male population that remains in the Bering Sea is unknown. In our study all males except the one (for which the SLTDR transmitted long enough to provide the data) left the Bering Sea before January and had not returned by the end of February.

Male fur seals that migrated into the Gulf of Alaska arrived there at about the same time (December/January) as postmolt female northern elephant seals (*Mirounga angustirostris*) and near the end of the time (February) when postbreeding elephant seals arrived there (Stewart and De-Long 1995). Male northern fur seals were in the Gulf of Alaska during
December and January, and probably into February. Elephant seals dive deeper than fur seals and feed on different prey, but it is interesting that they both utilize this area during winter months.

Acknowledgments

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References


Marine Bird Populations and Carrying Capacity of the Eastern Bering Sea

George L. Hunt Jr.
University of California, Irvine, California

G. Vernon Byrd Jr.
Alaska Maritime National Wildlife Refuge, Homer, Alaska

Abstract
Marine bird populations in the Bering Sea have been monitored at selected colonies since the mid-1970s. At the Pribilof Islands, declines of black-legged (Rissa tridactyla) and red-legged (R. brevirostris) kittiwake populations occurred between the mid-1970s and the mid-1980s. Thick-billed murre (Uria lomvia) populations also declined at the Pribilof Islands during this period, as did common murres (U. aalge) at Bluff in Norton Sound. At the same time elsewhere in the Bering Sea, populations of most piscivorous seabirds remained stable, fluctuated without discernible trend, or increased. Food web dependencies differed between decreasing populations of piscivores and those that remained stable or increased. We hypothesize that between 1976 and 1985, one or more die-offs of adult kittiwakes and thick-billed murres occurred near the Pribilof Islands. In subsequent years, the remaining populations failed to increase their reproductive performance, despite markedly smaller resident populations. Therefore we hypothesize that, for kittiwakes and thick-billed murres, the carrying capacity of the waters near the Pribilof Islands has been significantly reduced. Lowered reproductive performances were associated with a decrease in the consumption of forage fish, in particular species with high fat content. Warming of surface waters, decreases in the size of the cold pool, and changes in the advective regime of the shelf-slope current could have influenced the vertical and horizontal distributions of forage fish, but data are lacking to test these hypotheses.
**Introduction**

Recently there has been considerable interest in using marine birds as indicators of changes in various marine ecosystems (e.g., Furness and Nettleship 1991, Montevecchi 1993). Studies that attempt to use seabirds as indicators of prey stocks (Berruti 1985, Croxall 1989, Klageges et al. 1992, Montevecchi and Myers 1992) are predicated on the assumption that variations in population size or reproductive performance of marine birds are closely linked to variations in prey populations (Cairns 1987, Hunt et al. 1991). This assumption is supported by several studies of seabird populations (e.g., Duffy 1980, Hamer et al. 1991, Ankar-Nielsen 1992) and reproductive performance (e.g., Anderson et al. 1982, Springer et al. 1986, Monaghan et al. 1989). Similar studies indicate that marine bird populations also vary with respect to regional changes in climate, but the linkages to changes in preferred prey populations have not always been evident (e.g., Aebischer et al. 1990; Ainley et al. 1996; Veit et al. 1996, 1997). Nevertheless, links between climate- or weather-driven changes in ocean conditions and marine bird foraging and reproductive ecology have been described (Dunn 1973, Birkhead 1976, Braun and Hunt 1983, Hunt et al. 1991).

In the eastern Bering Sea, results of programs to monitor breeding populations of marine birds (e.g., Byrd and Dragoo 1997) provide the basis for describing population trends and patterns in productivity over the past 20 years. Furthermore, research indicates that seabird communities in colonies and at sea vary with oceanographic regions (Hunt et al. 1981b, Springer and Roseneau 1985, Schneider et al. 1986). These data and others have been used to test hypotheses about links between variations in marine birds and various aspects of the physical (e.g., climate) and biological environment (e.g., changes in competition for prey with predatory fish and the effects of commercial fishing) (Murphy et al. 1986, 1991; Springer et al. 1986, 1996; Springer and Byrd 1989; Springer 1992, 1993; Decker et al. 1995; Hunt et al. 1996, 1997).

In this paper, we use monitoring data for black-legged (Rissa tridactyla) and red-legged kittiwakes (R. brevirostris), and thick-billed (Uria lomvia) and common murres (U. aalge), the species for which the most complete information on populations is available, to examine geographic patterns of population changes in relationship to food webs on which these piscivorous, cliff-nesting seabirds depend, or on physical processes which may influence the availability of prey.

**Methods**

**Amount and Geographic Distribution of Data**

Population data on kittiwakes and murres have been collected regularly since the mid-1970s at six colonies in the Bering Sea (Fig. 1), but the frequency and intensity of surveys has varied among sites and species (Table
1). Monitoring has continued at six sites primarily because they are on the Alaska Maritime and Togiak National Wildlife Refuges. In the first few years at most sites, single counts were made of birds either in the entire colony or on a series of index plots (Sowls et al. 1978). Later, due to daily fluctuations in attendance of birds at colonies, multiple counts, usually on index plots, were made at the least variable times of day and season to improve estimates (e.g., Birkhead and Nettleship 1980, Byrd 1989, Hatch and Hatch 1988). Pelagic distribution and foraging ecology also were studied initially in the Bering Sea in the 1970s and early 1980s (e.g., Hunt et al. 1981a,c,d; Gould et al. 1982).

**Geographic Settings of the Colonies**

Foraging habitats for kittiwakes and murres differ among the six nesting colonies addressed herein, most likely as a function of food web structure and carbon pathways (Iverson et al. 1979; Hunt et al. 1981a; Schneider et al. 1986; Springer 1991, 1992; Springer et al. 1987, 1996) related to physical phenomena in shelf waters (Coachman 1986, Schumacher and Stabeno 1998). For example, in the western Aleutian Islands, the marine environment of Agattu and Buldir Islands is dominated by the westward flowing Alaskan Stream. This current forms the northern edge of the North Pacific gyre and enters the Bering Sea through passes between the Aleutian Islands (Stabeno et al., chapter 1, this volume). Both Agattu and Buldir support a diverse marine avifauna, but the dominant prey used by kittiwakes and murres and the marine habitats around the two islands differ

![Figure 1. Locations of seabird colonies discussed in this paper.](image-url)
### Table 1. Population trends for kittiwakes and murres at selected breeding colonies in the Bering Sea.

<table>
<thead>
<tr>
<th>Location</th>
<th>Species</th>
<th>Number</th>
<th>Range</th>
<th>Overall trend</th>
<th>Subset trends</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agattu</td>
<td>BLKI</td>
<td>8</td>
<td>75-94</td>
<td>Increase ($r^2 = 0.63, P &lt; 0.02$)</td>
<td>75-79 &lt; 88-94 ($t = 2.746, P &lt; 0.03$), no trend 88-94 ($r^2 = 0.03$)</td>
</tr>
<tr>
<td></td>
<td>UNMU</td>
<td>7</td>
<td>74-94</td>
<td>Increase ($r^2 = 0.55, P &lt; 0.06$)</td>
<td>74-79 &lt; 85-94 ($t = 5.086, P &lt; 0.01$), no trend 85-94 ($r^2 = 0.07$)</td>
</tr>
<tr>
<td>Buldir</td>
<td>BLKI</td>
<td>10</td>
<td>74-96</td>
<td>Increase ($r^2 = 0.87, P &lt; 0.01$)</td>
<td>74-76 &lt; 88-96 ($t = 12.109, P &lt; 0.01$), no trend 88-96 ($r^2 = 0.14$)</td>
</tr>
<tr>
<td></td>
<td>RLKI</td>
<td>10</td>
<td>74-96</td>
<td>Increase ($r^2 = 0.84, P &lt; 0.01$)</td>
<td>74-76 &lt; 88-96 ($t = 9.96, P &lt; 0.01$), no trend 88-96 ($r^2 = 0.15$)</td>
</tr>
<tr>
<td></td>
<td>TBMU</td>
<td>10</td>
<td>74-96</td>
<td>Increase ($r^2 = 0.86, P &lt; 0.01$)</td>
<td>74-76 &lt; 88-92 &lt; 94-96 ($F = 155.529, P &lt; 0.001$)</td>
</tr>
<tr>
<td>C. Peirce</td>
<td>BLKI</td>
<td>13</td>
<td>76-96</td>
<td>No trend ($r^2 = 0.01$)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>COMU</td>
<td>13</td>
<td>76-96</td>
<td>No trend ($r^2 = 0.10$)</td>
<td></td>
</tr>
<tr>
<td>Bluff</td>
<td>BLKI</td>
<td>14</td>
<td>79-95</td>
<td>Increase ($r^2 = 0.51, P &lt; 0.01$)</td>
<td>No trend 87-95 ($r^2 = 0.07$)</td>
</tr>
<tr>
<td></td>
<td>COMU</td>
<td>8</td>
<td>75-82</td>
<td>Decline ($r^2 = 0.75, P &lt; 0.01$)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>12</td>
<td>79-95</td>
<td>No trend ($r^2 = 0.01$)</td>
<td></td>
</tr>
<tr>
<td>St. Paul</td>
<td>BLKI</td>
<td>10</td>
<td>76-96</td>
<td>Decline ($r^2 = 0.63, P &lt; 0.01$)</td>
<td>No trend 87-96 ($r^2 = 0.31$)</td>
</tr>
<tr>
<td></td>
<td>RLKI</td>
<td>10</td>
<td>76-96</td>
<td>Decline ($r^2 = 0.75, P &lt; 0.01$)</td>
<td>No trend 88-96 ($r^2 = 0.78, P &gt; 0.10$)</td>
</tr>
<tr>
<td></td>
<td>COMU</td>
<td>10</td>
<td>76-96</td>
<td>Decline ($r^2 = 0.53, P &lt; 0.02$)</td>
<td>No trend 86-96 ($r^2 = 0.11$)</td>
</tr>
<tr>
<td></td>
<td>TBMU</td>
<td>10</td>
<td>76-96</td>
<td>No trend ($r^2 = 0.12$)</td>
<td>76 &gt; 82-96 ($t = 10.051, P &lt; 0.01$)</td>
</tr>
<tr>
<td>St. George</td>
<td>BLKI</td>
<td>10</td>
<td>76-96</td>
<td>No trend ($r^2 = 0.24$)</td>
<td>Decline 76-86 ($r^2 = 0.89, P &lt; 0.02$), no trend 87-96 ($r^2 = 0.64, P = 0.11$)</td>
</tr>
<tr>
<td></td>
<td>RLKI</td>
<td>10</td>
<td>76-96</td>
<td>Decline ($r^2 = 0.64, P &lt; 0.01$)</td>
<td>76-86 &lt; 87-96 ($t = 2.086, P &lt; 0.10$), no trend 87-96 ($r^2 = 0.01$)</td>
</tr>
<tr>
<td></td>
<td>COMU</td>
<td>10</td>
<td>76-96</td>
<td>Increase ($r^2 = 0.48, P &lt; 0.03$)</td>
<td>No trend 76-92 ($r^2 = 0.18$), increase based on 96 count</td>
</tr>
<tr>
<td></td>
<td>TBMU</td>
<td>10</td>
<td>76-96</td>
<td>No trend ($r^2 = 0.23$)</td>
<td>Decline 76-88 ($r^2 = 0.94, P &lt; 0.01$), apparent increase 89-96</td>
</tr>
</tbody>
</table>

---

**a** Codes: BLKI (black-legged kittiwake), RLKI (red-legged kittiwake), COMU (common murre), TBMU (thick-billed murre), UNMU (unidentified murre, includes both species).

**b** Number of years and earliest and latest year for which data are available.

**c** Trends indicated if simple linear models fit and slopes differed from zero at the 0.1 level.

**d** Trends suggested on graphs for subsets at least 4 years long were tested with regressions, and subsets were compared with t-tests or ANOVA to identify differences.

**e** Separate sets of data were analyzed for whole-colony counts (1975-1982) and plot counts (79-95).
Agattu is surrounded by a broad shelf where typical prey species include sand lance (*Ammodytes hexapterus*). In contrast, Buldir Island is oceanic, and birds there depend more on prey species of oceanic origin (e.g., lanternfish [Myctophidae]). Cape Peirce and Bluff are along the mainland coast adjacent to the shallow, well-mixed water of the coastal regime. These colonies support fewer seabird species than colonies near oceanic water, and are most strongly influenced by the northward flowing Alaska Coastal Current. Prey of importance here include sand lance and saffron cod (*Eleginus gracilis*). Near the edge of the shelf in the southeastern Bering Sea, the Pribilof Islands are close to three different oceanic regimes: (1) the well-mixed waters of the coastal shelf immediately around the islands; (2) the two layer system of the middle shelf in water 50-100 m deep; and (3) the outer edge of the shelf and the shelf slope regime. For the piscivorous birds of the Pribilofs, the dominant prey is juvenile walleye pollock (*Theragra chalcogramma*) and, to a lesser extent, sand lance and lanternfish (Hunt et al. 1981a,b, 1996; Schneider and Hunt 1984; Decker et al. 1995).

**Analytical Procedures**

We plotted single counts or annual means with 90% confidence bounds (for years in which multiple counts were made) for each species at each site. We used quadratic regressions to fit lines to the points to illustrate how trends have changed over the past 20 years. In addition, we tested for significant changes in population size over the entire sampling period using simple linear regression. We applied these models when correlation coefficients were significant at $P = 0.10$ and subsequently tested for increasing or decreasing slopes. Subsets within the overall time-series were examined with regression, $t$-test, or ANOVA as appropriate.

**Results**

Population trajectories for kittiwakes and for murres have varied among colonies in the Bering Sea (Figs. 2-4). In the western Aleutians at Agattu and Buldir islands, populations of kittiwakes and murres have increased since the mid-1970s (Fig. 2). Thick-billed murres at Buldir continued to increase throughout the period, but for other species at both islands, by 1988, populations were no longer increasing (Table 1). At Cape Peirce, one of the Alaska mainland colonies, no overall trends were evident for kittiwake or murre populations over the past 20 years (Fig. 3, Table 1). In contrast, farther north at Bluff, black-legged kittiwake populations increased between 1979 to 1995 (Fig. 3). However, within that overall increase, numbers showed no trend between 1987 and 1995 (Table 1). The only decline noted at either the western Aleutian colonies or those on the Alaska mainland was the decline in common murres at Bluff between 1975 and 1982, and numbers of this species at Bluff appear to have stabilized since the late 1970s or early 1980s (Fig. 3, Table 1).
Figure 2. Changes between 1974 and 1996 in the numbers of seabirds occurring at two colonies in the western Aleutian Islands. Error bars around points represent 90% confidence limits. Curves are quadratic regressions.
In 7 of 8 cases (4 species on each of 2 islands) at the Pribilof Islands, populations of kittiwakes and murres either declined over the study period as a whole, or over some portion of it (Table 1). At St. Paul Island, black-legged and red-legged kittiwake numbers have declined over the past 20 years, although populations have remained stable at reduced levels since the mid- to late 1980s (Fig. 4, Table 1). Thick-billed murre numbers were significantly higher in 1976 than they have been since, and common murres also declined (Table 1). At St. George Island, black-legged kittiwakes declined between 1976 and 1986, but numbers have stabilized or increased slightly since then, with the result that there is no overall trend in this population (Fig. 4, Table 1). Red-legged kittiwakes at St. George Island have declined over the past 20 years, with numbers between 1987 and 1996 lower than those between 1976 and 1986 (Table 1). Since 1987, red-legged kittiwake numbers on St. George Island have been stable. At St. George Island, thick-billed murre numbers showed a pattern similar to
that of black-legged kittiwakes, an initial decline between 1976 and 1988, with a stable or slightly increasing population since then that has resulted in no overall population trend (Fig. 4, Table 1). The only example of a population that has increased at the Pribilof Islands over the past 20 years is the common murre at St. George Island, although prior to 1996 there was no significant trend for this population (Table 1).

**Discussion**

Over the past 20 years, declines in breeding populations of piscivorous seabirds at colonies in the eastern Bering Sea have occurred primarily at Bluff (common murres) and at the Pribilof Islands (kittiwakes and murres). Most of the declines occurred between the mid-1970s and the mid-1980s. Murphy et al. (1986) modeled the decline of the common murre population at Bluff and concluded that such a rapid population decline could not be accounted for by low productivity alone. They proposed that winter
mortality must have played a significant role in the decline, and assumed that this mortality probably took place in the southeastern Bering sea near the ice edge where high numbers of murres spend the winter (Divoky 1978). The cause of the mortality remains unknown, although a reduction of pollock stocks by the fishery was suggested as a possible source of increased mortality of murres (Murphy et al. 1986) because the murres take juvenile pollock in winter (Divoky 1978). Another possibly critical time for murres at Bluff is spring, when water temperatures and ice cover can affect the availability of forage fish near the breeding colony.

The exact timing of declines in seabird populations at the Pribilof Islands will never be known because surveys were not conducted annually, particularly in the period of the declines. Nevertheless, by examining the population trajectories depicted by the graphs (Figs. 3, 4), it seems clear that most of the declines had ameliorated by 1985 or 1986. Whatever caused the declines must have occurred in the decade prior to the mid-1980s. For example, declines of kittiwakes at St. George may have been particularly steep between 1982 and 1984. On St. Paul Island, declines of
red-legged kittiwakes were also steep during this period, although black-legged kittiwakes had their steepest decline between 1976 and 1982. Declines in both species of murres were steepest between 1976 and 1982 on St. Paul Island and between 1976 and 1987 for thick-billed murres on St. George Island. The declines of seabirds at the Pribilof Islands may have occurred after, and were of longer duration, than those at Bluff. The declines in kittiwake populations on the Pribilofs, particularly on St. George Island, almost certainly occurred after the 1970s regime shift in the North Pacific Ocean and Bering Sea (National Research Council 1996).

Population declines of kittiwakes and murres at the Pribilof Islands must have resulted from one or more of three causes: a decline in the output of young resulting in reduced recruitment, emigration to other colonies, or an increase in adult mortality. Any presumptive cause must account for these factors: a sharp decline in populations between 1976 and 1987, with the steepest portion of the drop most likely in the early 1980s; a more severe effect on kittiwakes than on murres, particularly kittiwakes on St. Paul Island; a possible difference in the timing of declines on St. Paul and St. George Islands, and an apparent lack of population declines at most other colonies in the eastern and southern Bering Sea during the same time frame.

It seems unlikely that failure to produce sufficient young was the cause of the precipitous declines of kittiwakes and murres at the Pribilof Islands. In the 1970s, production of young at the Pribilof Islands was consistently "moderate," albeit lower than has been recorded elsewhere in the Bering Sea in "good" years (Hunt et al. 1981c, 1986; Byrd and Dragoo 1997). Young fledged from 1975 to 1979 would have recruited to nesting populations in 1978 to 1984, three to five years after they fledged. These new recruits should have been sufficiently numerous to maintain stable populations in the colonies of the Pribilof Islands. However, by 1984, most of the major declines in the numbers of birds on the census plots had taken place. Thus for that period, disappearance of birds from their cliff-face nesting plots greatly exceeded recruitment. Furthermore, although murre and especially kittiwake reproductive output was very low subsequent to 1984 (Decker et al. 1995, Byrd and Dragoo 1997), these failures to produce chicks were not reflected by further dramatic declines in the populations of these species at the cliffs on St. Paul and St. George islands. Although there is a need for modeling to determine the extent to which recruitment failure might account for the seabird population declines at the Pribilof Islands, given the information available, it seems unlikely that reproductive failure alone could have been responsible for the declines in black- and red-legged kittiwakes and thick-billed murres in the late 1970s or early 1980s.

Emigration of established breeding pairs from the Pribilof Islands to other colonies is also unlikely. However, detection of emigration by black-legged kittiwakes or thick-billed murres would be difficult because there
are many colonies to which they could have moved, and none has been sufficiently well monitored that immigration would have been certain to be detected. In contrast, red-legged kittiwakes are known to nest in only five or six colonies in the eastern Bering Sea, including St. George and St. Paul and Otter islands in the Pribilofs and Bogoslof and Buldir in the Aleutian Islands (Byrd 1978). The increased numbers of red-legged kittiwakes in these latter two colonies have been too low to account for the high numbers of birds that are no longer at the Pribilofs (Byrd et al. 1997). It is possible that adult birds that did not return to the colonies remained at sea and forewent breeding for several years (Hamer et al. 1991), but at least in the case of the red-legged kittiwake, it is highly unlikely that they emigrated to another colony.

A third possibility is that the mortality rate for adult kittiwakes and murres breeding at the Pribilof Islands was higher than normal between 1976 and 1984. Because declines apparently were concentrated in populations nesting in the Pribilof Islands, it would seem unlikely that excess mortality, if it indeed occurred, happened during the winter when birds from a number of colonies would be expected to be mingled. More likely, mortality events would have occurred in spring when murres and kittiwakes would have been gathering around their colonies prior to breeding, or in late September or October when birds were still in the vicinity of their colonies but were no longer being monitored. The most likely cause of this at-sea mortality would be lack of prey. Several seabird die-offs have been recorded in the Bering Sea in the 1970s and 1980s. DeGange and Rosapepe (1984) reported large numbers of dead murres in the eastern Bering Sea north of the Pribilofs in 1979, and a subsequent die-off of kittiwakes was reported in 1983 (Nysewander and Trapp 1984). These die-offs may have contributed to the population declines in the Pribilof Islands.

Several lines of evidence support the hypothesis that birds nesting at the Pribilof Islands could have experienced a shortage of food while attending their breeding colonies. Foremost is the marked reduction in the production of chicks shown by both species of kittiwakes and by thick-billed murres on the Pribilof Islands since the early 1980s (Decker et al. 1995). During the 1970s, both age-1 pollock and capelin (Mallotus villosus) were important components of the diets of kittiwakes and murres at the Pribilof Islands (Hunt et al. 1981a,b), and a decrease in their availability near the islands, particularly early in the season before age-0 pollock were available, could have caused increased adult mortality and/or reproductive failure. In the vicinity of the Pribilof Islands, there was a marked decline between 1979 and 1982 in the numbers of age-1 pollock taken in trawl surveys by the National Marine Fisheries Service (Hunt et al. 1997). Likewise, in the vicinity of the Pribilof Islands, the numbers of capelin declined at the same time (Hunt et al. 1996). Elsewhere, in the Gulf of Alaska, declines in the proportion of capelin in the diets of seabirds were accompanied by seabird population declines (Piatt and Anderson 1995).
Changes in the capacity of the Bering Sea to support seabird populations on the Pribilof Islands affected surface-foraging kittiwakes more severely than subsurface-foraging murres (Decker et al. 1995, Hunt et al. 1997), which can pursue prey to depths of 210 m (Croll et al. 1992). It therefore seems likely that, in addition to a decrease in the abundance of age-1 pollock within the foraging range of seabirds nesting at the Pribilof Islands, there also must have been a change in the vertical distribution of the remaining forage fish such that fewer fish were available in the upper few meters of the water column. Because red-legged kittiwakes, a species that specializes on myctophids, experienced a particularly severe decline, it is likely that the vertical distributions of fish other than pollock were also affected.

Sea surface warming that marked the Bering Sea regime shift in the late 1970s may have influenced the distribution of juvenile pollock near the Pribilof Islands (Decker et al. 1995; Hunt et al. 1996, 1997). In warm years with reduced winter ice cover, shrinking of the pool of cold water at the bottom in the middle domain may have resulted in juvenile pollock moving onto the shelf rather than being concentrated along the shelf edge, seaward of the cold bottom water (Ohtani and Azumaya 1995, Wyllie-Echeverria 1995). This shift would reduce the number of pollock close to the Pribilos. In warm years, more of the primary production in the middle domain is captured by copepods (Walsh and McRoy 1986), which would enhance foraging prospects for juvenile pollock there. In addition, a weaker pycnocline and warmer bottom waters near the Pribilos may have permitted juvenile pollock to move deeper in the water column at an earlier date (Olla and Davis 1990, Sogard and Olla 1993), thus reducing their availability to surface-foraging seabirds.

The possibility that predation by adult pollock depleted forage fish stocks near the Pribilof Islands cannot be rejected. However, Decker et al. (1995) argued that the limited data available on the timing of changes in forage fish stocks near the Pribilof Islands failed to reflect changes in the biomass of adult pollock there, and Hunt et al. (1997) failed to find a significant relationship between the number of age-1 pollock and the number of age-2 and older pollock in the vicinity of the Pribilof Islands or along the edge of the southeastern Bering Sea shelf.

Variations in ocean circulation affect the availability of prey in the vicinity of the Pribilof Islands. The causes of variability in the Green Belt, which occurs along the Bering Sea shelf break (Springer et al. 1996), are not well known, but must be related to the Bering Slope Current. The characteristics of the Bering Slope Current vary on time scales of months to perhaps years (Stabeno et al., chapter 1, this volume). At times it appears as a well defined, smooth flow with few eddies or meanders evident; at other times it is highly variable with numerous eddies and meanders (J. Schumacher, PMEL, 7600 Sand Point Way, N.E., Seattle, WA, Nov. 1997, pers. comm.). Transport is also variable, ranging from about 3 to 6-7 million m³/s (Stabeno et al., chapter 1, this volume). Increased shelf-slope ex-
change likely occurs when the Bering Slope Current contains numerous eddies and meanders (Schumacher and Stabeno 1994; van Meurs and Stabeno, in press). Continuous flow along the 100 m isobath from the vicinity of Unimak Pass to the Pribilof Islands has been revealed in satellite tracked drifter trajectories. The strength and persistence of the flow varies significantly from year to year.

The origin of the Bering Slope Current is threefold: flow through Unimak Pass, flow up Bering Canyon, and on-shelf fluxes along the shelf break (Stabeno et al., chapter 1, this volume). The latter two sources consist of Bering Slope Current water and have high concentrations of nutrients. Flow from the vicinity of Unimak Pass would advect zooplankton and larval fish originating in that region to the Pribilof Islands. Water originating in Pribilof Canyon is often entrained in the strong current (30 cm/s) south of St. George Island (Schumacher and Stabeno 1998). Satellite-tracked drifters originating in this region often end up circling St. Paul Island (Stabeno et al., chapter 9, this volume). These on-shelf transports could affect the concentrations of zooplankton in shelf waters around the Pribilos. Changes in zooplankton concentrations could affect the foraging opportunities, and thus the vertical distributions, of forage fish.

It is also possible that storms made foraging at the water's surface more difficult during the 1980s, compounding stress resulting from decreased abundance of prey in the water column. Surface-foraging seabirds are known to be adversely affected by stormy weather, which is alleged to have caused mass mortality of seabirds (Kazama 1968, Salt and Willard 1971, Dunn 1973) and depression of reproductive success (Braun and Hunt 1983). Likewise, subsurface-foragers also have greater difficulty foraging in rough weather (Birkhead 1976). It has been hypothesized that warming may lead to an increased storm frequency in the Bering Sea (Table 2 in U.S. GLOBEC 1996). The effects of storm frequency and the seasonal timing of storm events at the Pribilof Islands have not been investigated, but they could have considerable importance for seabird foraging and survival.

Declines in kittiwake and murre populations at the Pribilof Islands can be compared to declines in populations of Atlantic puffins (*Fratercula arctica*) and common murres on the west coast of Norway that occurred in response to collapses in prey stocks. Atlantic puffins nesting on Røst depend on migrating juvenile herring (*Clupea harengus*) for food during the summer (Myrberget 1962, Ankar-Nilssen 1992). After this stock of herring collapsed between 1957 and 1971, the more than one million puffins breeding on Røst continued to return to their colonies, but failed to breed successfully during the period when age-1 herring were absent from coastal waters (Ankar-Nilssen 1992, Wright et al. 1996). As the puffin population aged, between 1979 and 1989 the numbers of puffins returning to Røst declined at the rate of about 14% per annum, presumably from the attrition of aging individuals and the failure to produce young (Ankar-Nilssen and Røstad 1993, Wright et al. 1996). No large die-offs or beachings of dead puffins were reported. In contrast, in the north of Norway along the
Barents Sea coast, common murres depend on capelin as their major food, which are taken when the murres are at their colonies in summer, and also in winter and spring when the murres are migrating to their colonies prior to breeding (Furness and Barrett 1985, Erikstad and Vader 1989, Barrett and Furness 1990). Barents Sea capelin stocks decreased between 1975 and 1986-1987 from about 7 million t to 20,000 t (Wright et al. 1996). During the early years of the capelin decline, seabird populations appeared healthy and breeding success was high (Furness and Barrett 1985, Wright et al. 1996). However, during the winter of 1986-87, thousands of emaciated murres washed ashore along the coast of northern Norway. Counts made at the colonies in 1987 showed that between 1985-86 and 1987 the numbers of common murres at colonies had decreased by about 80% and the number of thick-billed murres by 33 to 63% (Vader et al. 1987, Wright et al. 1996).

The steep declines in the murre and kitiwake populations of the Pribilof Islands have similarities to both the crash in the common murre population in the north of Norway, and to the long-term gradual elimination of aging puffins at Røst. We favor the hypothesis that the declines in both species of kitiwakes and thick-billed murres at St. Paul and St. George Islands were caused by large die-offs of adults from these populations. The ongoing lack of reproductive output by kitiwakes and to a lesser extent by murres on the Pribilofs is similar to the situation at Røst prior to the decline in the puffins due to old age. If kitiwakes at the Pribilofs continue to have low levels of reproductive success, we can expect a further decline in their numbers as adults now attending the colonies die.

Summary

In the past two decades, kitiwake and murre populations have increased at some colonies and decreased at others. Particularly strong increases have occurred at Buldir Island, where kitiwakes and murres depend on a mesopelagic oceanic food web. In contrast, decreases in common murre populations have occurred at Bluff, an Alaska Coastal Current food web, and kitiwakes and thick-billed murres have declined on the Pribilof Islands where walleye pollock constitute a significant portion of the diets of these seabirds. At the Pribilof Islands, evidence for changes in both prey abundance and prey availability between the late 1970s and the mid-1980s supports the hypothesis that an inability to obtain sufficient food may have resulted in higher than usual mortality of adult kitiwakes and thick-billed murres in the breeding populations between 1976 and 1984. A simultaneous die-off of pre-recruits would have prevented a rebound of these seabird populations. The failure of the seabird populations on the Pribilof Islands to show enhanced reproductive performance subsequent to the reduction of breeding populations suggests that the carrying capacity of the southeastern Bering Sea declined for seabirds in the early 1980s and was reset at a new, lower, level than had existed in the mid-
1970s. Because kittiwake populations were apparently only affected at the Pribilof Islands, we suggest that the mortality must have occurred when birds would have been near their colonies.

Acknowledgments

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Seabirds of the Western Bering Sea

Vyacheslav P. Shuntov
Pacific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, Russia

Abstract

I examined the distribution, species composition, and foraging ecology of seabirds in the western Bering Sea over the past two decades. There is large variability in estimates of number of nesting seabirds in the western Bering Sea, because of differences in assessment methods. Over 4.1 million individuals were estimated to nest in the western Bering Sea in the 1960s to 1980s but more recent, precise methods provide an estimate of nearly 11 million individuals. The most abundant species include alcids, followed by gulls and tube-nosed seabirds. An estimated 2-3 million semiaquatic birds that nest in the interior basins migrate through the Bering Sea. The number of seabirds in both the eastern and western sections of the Bering Sea appears to have increased slightly in recent years. I classified the abundance and distribution of seabirds based on their food capture method. Those species that capture prey by diving were most abundant (63% of the total) followed by those that feed on or near the surface (37%). I also examined the seasonal distribution of seabirds in the western Bering Sea. During winter, sea ice and low air temperatures limit the abundance and number of species. Species that occur there in winter include light-colored fulmars, various gull species, and some auks. Many of these species feed at the ice edge or in polynyas. As spring approaches and the ice begins to melt, the abundance and number of species entering the western Bering Sea increases dramatically. The migration route into the area varies by species and includes the shore, over the shelf in contiguous zones of deep water, and along the deep water as ice retreats. Shearwaters begin forming enormous feeding aggregations and by May increase in numbers into the millions, probably feeding on abundant krill resources developing along the retreating ice edge. A considerable number of local birds, including some immature individuals, occur at nesting sites during summer and early autumn, a period of high productivity in the western Bering Sea. Diving birds make up two-thirds of the total number of breeding birds. In autumn the dispersal of birds begins away from the coast.
resulting in an increase in the number of diving birds appearing off the shelf and continental slope. The long-term dynamics in the ecology and number of seabirds likely are related to ecosystem cycles on the order of 40-60 years. Associated with these cycles are changes in habitat, pulsations of faunistic complexes, and long-term tendencies for changes in the number of species.

Introduction

The Bering Sea is one of the regions of the World Ocean where large numbers of seabirds are observed throughout the year. Because they represent a large group in terms of both species and individuals, they undoubtedly play a significant role in the ecosystem, particularly where they occur in large numbers. We must, however, be cautious about attributing the influence of seabirds at certain colonies to a particular ecosystem. For example, remember that no less than half of the seabirds of the Commander Islands do not extract food in the Bering Sea but in oceanic Pacific waters (a similar situation occurs for birds of the Aleutian Islands).

In recent years, ecosystem investigations have increased particularly in regard to biological resources and the relationship and role of seabirds. Significant progress has been made in studies during seabird nesting periods, especially in the American section of the Bering Sea. Few studies on seabird ecology have occurred in the western Bering Sea, but recent studies there have provided new information on seabird distribution, nesting behavior, and the number of colonies.

Many recent publications have addressed the relationship between bird distribution and oceanographic characteristics in the Bering Sea (Schneider 1982; Kinder et al. 1983; Schneider et al. 1987; Shuntov 1993; Springer et al. 1993, 1996; Decker and Hunt 1996; Hunt et al. 1996a). These publications suggest that the continental slope is important. In the 1960s, the first large-scale complex study of the Bering Sea by TINRO and VNIRO was restricted to areas between the shelf and deepwater basin (which was then termed a life zone). It was noted that this zone was the site of constant, increased concentrations of seabirds (Shuntov 1972). Springer et al. (1996) called this zone the “Green Belt” due to the high level of primary productivity there.

The unusual role of various life zones on the continental slope in the lives of Bering Sea biota was linked to the complex dynamics of water (Kotenev 1995, Sapozhnikov 1995). Dynamic processes over the continental slope consisted of an exchange between organic matter and energy at varying depths, including enrichment of the euphotic layer by mineral biological producers. Also, the cooling of currents along the continental slope causes a series of meanders and diversely directed vortices which are characteristic of areas with complex bottom reliefs (canyons, steep slopes, or bending isobaths); these areas are important foraging areas for birds. All this complexity contributes to the accumulation of macroplank-
ton and early life stages of nekton in localized areas. A similar situation is applicable to islands and straits where the complexity of the hydrodynamic process strengthens the ebb and flow phenomena.

It is important to emphasize that the horizontal spottiness and the vertical stratification of zooplankton and fine nekton distribution is characteristic for shelf regions. The true character of this distribution can differ at wide and narrow shelves. For example, in the wide eastern Bering Sea shallow waters of the coastal, middle, and exterior secondary fronts, which are located at the 50, 100, and 170 m isobaths, have a great effect on the distribution of birds. In the interior regions of the shelf, diving murres and shearwaters predominate, but in the exterior sections of the shelf, surface-feeders occur (i.e., fulmars, kitiwakes, and storm-petrels) (Schneider and Hunt 1982, Schneider et al. 1986). The Gulf of Anadyr is similar (Shuntov 1993); however, the warm Navarin Current there “disrupts” the cool spot in the middle of the shelf and affects the location and configuration of secondary fronts. This current has a similar effect in the Bering Strait where it meets cold, northern water and creates gradient zones where large numbers of alcids (Alcidae), especially auklets, forage. In other regions of the western Bering Sea the shelf is narrower and the water is under the influence of currents along the slope. It appears that the middle of the shelf’s front is displaced toward the exterior edge of the shallow water, and along the vertical sections it is often connected with external surface fronts (Verkhunov 1995). For this reason distinct ecological groupings here are not always spatially separated.

Composition and Number of Seabirds in the Western Bering Sea

Studies during the 1960s to 1980s suggested that the number of nesting seabirds in the western Bering Sea was 4.1 million individuals (Schneider and Shuntov 1993, Shuntov and Dulepova 1995, Vyatkin 1986, Smirnov and Velizhanin 1986). Subsequent observations, particularly in the northwestern Bering Sea, indicated that the population was >7 million individuals (Table 1). Schneider and Shuntov (1993) summarized data on the number of nesting birds in the southwestern Bering Sea. Between Dezhnev Bay and Cape Olyutorsk, approximately 364,000 individual birds nested (Vyatkin 1986). Of the 7 million estimated seabirds, more than half were concentrated in the northwestern section of the Bering Sea. Alcidae were in highest abundance (61.8%), followed by gulls (Laridae, 24.8%), and tubenosed seabirds (tubinares, 11.1%). Less than 3% were cormorants (Phalacrocoracidae), terns (Sternidae), jaegers (Stercorariidae), and phalaropes (Phalaropodidae). Six species exceeded 0.5 million individuals each, including black-legged kitiwakes (Rissa tridactyla), least auklets (Aethia pusilla), thick-billed murres (Uria lomvia), northern fulmars (Fulmarus glacialis), crested auklets (Aethia cristatella), and common murres (Uria aalge).
Table 1. Composition and number (thousands of individuals) of seabirds nesting in the western Bering Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>NW Bering Sea</th>
<th>SW Bering Sea</th>
<th>Commander Islands</th>
<th>Total</th>
</tr>
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<td>110.0</td>
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<tr>
<td>Xema sabini</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>NW Bering Sea&lt;sup&gt;a&lt;/sup&gt;</td>
<td>SW Bering Sea&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Commander Islands</td>
<td>Total</td>
</tr>
<tr>
<td>-------------------------</td>
<td>---------------------------</td>
<td>--------------------------</td>
<td>--------------------</td>
<td>---------</td>
</tr>
<tr>
<td>Common tern</td>
<td>1.0</td>
<td>20.0</td>
<td>–</td>
<td>21.0</td>
</tr>
<tr>
<td><em>Sterna hirundo</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic tern</td>
<td>1.0</td>
<td>1.0</td>
<td>–</td>
<td>2.0</td>
</tr>
<tr>
<td><em>Sterna paradisaea</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aleutian tern</td>
<td>1.0</td>
<td>2.0</td>
<td>–</td>
<td>3.0</td>
</tr>
<tr>
<td><em>Sterna camtschatica</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pigeon guillemot</td>
<td>21.0</td>
<td>2.0</td>
<td>3.2</td>
<td>26.2</td>
</tr>
<tr>
<td><em>Cepphus columba</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common murre</td>
<td>443.0</td>
<td>147.0</td>
<td>60.0</td>
<td>650.0</td>
</tr>
<tr>
<td><em>Uria aalge</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Thick-billed murre</td>
<td>982.0</td>
<td>310.4</td>
<td>190.0</td>
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</tr>
<tr>
<td><em>Uria lomvia</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parakeet auklet</td>
<td>25.0</td>
<td>5.0</td>
<td>10.0</td>
<td>40.0</td>
</tr>
<tr>
<td><em>Cyclorrhynchus psittacula</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crested auklet</td>
<td>750.0</td>
<td>12.0</td>
<td>0.1</td>
<td>762.1</td>
</tr>
<tr>
<td><em>Aethia cristatella</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whiskered auklet</td>
<td>–</td>
<td>–</td>
<td>5.0</td>
<td>5.0</td>
</tr>
<tr>
<td><em>Aethia pygmaea</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Least auklet</td>
<td>1,500.0</td>
<td>0.2</td>
<td>0.1</td>
<td>1,500.3</td>
</tr>
<tr>
<td><em>Aethia pusilla</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marbled murrelet</td>
<td>–</td>
<td>0.5</td>
<td>–</td>
<td>0.5</td>
</tr>
<tr>
<td><em>Brachyramphus marmoratus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kittlitz's murrelet</td>
<td>5</td>
<td>1</td>
<td>–</td>
<td>6.0</td>
</tr>
<tr>
<td><em>Brachyramphus brevirostris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ancient murrelet</td>
<td>–</td>
<td>–</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td><em>Synthliboramphus antiquus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tufted puffin</td>
<td>55.0</td>
<td>12.5</td>
<td>200.0</td>
<td>267.5</td>
</tr>
<tr>
<td><em>Fratercula cirrhata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Horned puffin</td>
<td>40.0</td>
<td>1.0</td>
<td>5.0</td>
<td>46.0</td>
</tr>
<tr>
<td><em>Fratercula corniculata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>5,143.8</td>
<td>1,348.1</td>
<td>1,259.7</td>
<td>7,751.6</td>
</tr>
</tbody>
</table>

<sup>a</sup>Northwestern section of sea, north of Cape Olyutorsk.

<sup>b</sup>Southwestern section of sea, south of Cape Olyutorsk.

Note: This table was compiled using data from Vyatkin 1986, 1992; Artyukhin 1991; Kondrat’ev 1991, Kondrat’ev 1993; Vyatkin and Artyukhin 1994; and Shuntov 1998).
Note that these values are only estimates. For example, at one time I estimated the number of least auklets in the western Bering Sea at 1.5 million individuals. In recent “gray” literature (e.g., Konyukhov 1990, Kondrat’ev 1991), the number of least auklets ranged from 100,000 to 250,000 individuals, but in my opinion the assessment methods used often resulted in underestimates. A recent recounting of several colonies in the Okhotsk Sea and Bering Strait resulted in higher counts (Kondrat’ev et al. 1992, Zubakin et al. 1992, Springer et al. 1993, Faris et al. 1996). Thus, for Ratmanov Island (Big Diomede), different methods produced numbers from 0.7 to 4.4 million individual least auklets and from 0.3 to 2.2 million crested auklets.

The high biological productivity and optimal feeding conditions of the Bering Sea attract a large number of birds from other regions. The most numerous of these are short-tailed shearwaters (*Puffinus tenuirostris*) and sooty shearwaters (*P. griseus*) from the Southern Hemisphere. The geographic position of the Bering Sea, particularly its contact with the Arctic Ocean through Bering Strait, provides an important transit area through which the migration of northern birds is facilitated; it also provides an important wintering area for many of them. Accurately determining the number of these birds is complex considering their population dynamics, migration patterns, and redistribution between the western and eastern Bering Sea. It is particularly difficult to estimate numbers for species whose nesting ranges include the Bering Sea and contiguous regions. For example, the number of non-nesting seabirds in the western section of the Bering Sea has been conservatively (and tentatively) estimated at 3 million individuals (Table 2). In sum, the overall number of seabirds in the western Bering Sea is nearly 11 million individuals (Tables 1 and 2).

A large number of birds that nest in the interior basins migrate through the Bering Sea. Some of them (e.g., jaegers, phalaropes, and gulls) are included in Tables 1 and 2. Some loons (*Gavia* spp.) and a large number of diving ducks (*Anatidae*) migrate to the Bering Sea after the nesting period. A significant portion of the diving ducks (e.g., oldsquaw, *Clangula hyemalis*; king eiders, *Somateria spectabilis*; and common eiders, *S. mollissima*) remain in the Bering Sea to winter in polynyas. The number of these semi-aquatic birds which migrate through the western Bering Sea has been estimated at 2-3 million individuals.

Despite the fact that the number of seabirds in the western Bering Sea seems to be higher than recently reported, it does not change the relationship in their numbers between Russian and American waters. In American waters, the number of nesting birds has also gradually increased (Sowls et al. 1978, Lensink 1984, Schneider and Shuntov 1993, Faris et al. 1996). A recent estimate of 36 million seabirds in the eastern Bering Sea and Aleutian Islands was proposed (i.e., approximately three times more than in the western section). The number of southern shearwaters alone was estimated at approximately 12 million individuals with extreme counts from 9 to 502 million individuals (Gould et al. 1982).
Table 2. Composition and number of non-nesting seabirds in the western Bering Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Numbers, thousands of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-tailed albatross, <em>Diomedea albatrus</em></td>
<td>+</td>
</tr>
<tr>
<td>Laysan albatross, <em>D. immutabilis</em></td>
<td>50.0</td>
</tr>
<tr>
<td>Black-footed albatross, <em>D. nigripes</em></td>
<td>+</td>
</tr>
<tr>
<td>Northern fulmar, <em>Fulmarus glacialis</em></td>
<td>200.0</td>
</tr>
<tr>
<td>Mottled petrel, <em>Pterodroma inexpectata</em></td>
<td>10.0</td>
</tr>
<tr>
<td>Sooty shearwater, <em>Puffinus griseus</em></td>
<td>200.0</td>
</tr>
<tr>
<td>Short-tailed shearwater, <em>P. tenuirostris</em></td>
<td>1,500.0</td>
</tr>
<tr>
<td>Fork-tailed storm-petrel, <em>Oceanodroma furcata</em></td>
<td>200.0</td>
</tr>
<tr>
<td>Leach's petrel, <em>O. leucorhoa</em></td>
<td>+</td>
</tr>
<tr>
<td>Pelagic cormorant, <em>Phalacrocorax pelagicus</em></td>
<td>4.0</td>
</tr>
<tr>
<td>Red phalarope, <em>Phalaropus fulicarius</em></td>
<td>70.0</td>
</tr>
<tr>
<td>Red-necked phalarope, <em>P. lobatus</em></td>
<td>150.0</td>
</tr>
<tr>
<td>Pomarine jaeger, <em>Stercorarius pomarinus</em></td>
<td>20.0</td>
</tr>
<tr>
<td>Parasitic jaeger, <em>S. parasiticus</em></td>
<td>40.0</td>
</tr>
<tr>
<td>Long-tailed jaeger, <em>S. longicaudus</em></td>
<td>45.0</td>
</tr>
<tr>
<td>Ivory gull, <em>Pagophila eburnea</em></td>
<td>5.0</td>
</tr>
<tr>
<td>Ross's gull, <em>Rhodostethia rosea</em></td>
<td>25.0</td>
</tr>
<tr>
<td>Herring gull, <em>Larus argentatus</em></td>
<td>25.0</td>
</tr>
<tr>
<td>Glaucous-winged gull, <em>L. glaucescens</em></td>
<td>10.0</td>
</tr>
<tr>
<td>Glaucous gull, <em>L. hyperboreus</em></td>
<td>5.0</td>
</tr>
<tr>
<td>Mew gull, <em>L. canus</em></td>
<td>10.0</td>
</tr>
<tr>
<td>Black-legged kittiwake, <em>Rissa tridactyla</em></td>
<td>200.0</td>
</tr>
<tr>
<td>Sabine's gull, <em>Xema sabini</em></td>
<td>5.0</td>
</tr>
<tr>
<td>Arctic tern, <em>Sterna paradisaea</em></td>
<td>50.0</td>
</tr>
<tr>
<td>Aleutian tern, <em>S. camtchatica</em></td>
<td>5.0</td>
</tr>
<tr>
<td>Common tern, <em>S. hirundo</em></td>
<td>5.0</td>
</tr>
<tr>
<td>Dovekie, <em>Alle alle</em></td>
<td>+</td>
</tr>
<tr>
<td>Common murre, <em>Uria aalge</em></td>
<td>20.0</td>
</tr>
<tr>
<td>Thick-billed murre, <em>U. lomvia</em></td>
<td>350.0</td>
</tr>
<tr>
<td>Black guillemot, <em>Cepphus grylle</em></td>
<td>15.0</td>
</tr>
<tr>
<td>Kittlitz's murrelet, <em>Brachyramphus brevirostris</em></td>
<td>1.0</td>
</tr>
<tr>
<td>Horned puffin, <em>Fratercula corniculata</em></td>
<td>2.0</td>
</tr>
<tr>
<td>Tufted puffin, <em>Fratercula cirrhata</em></td>
<td>1.0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>3,223.0</td>
</tr>
</tbody>
</table>

+ Very low quantity.
To all appearances the eastern Bering Sea is a more favorable habitat for seabirds. The eastern Bering Sea has a milder climate, optimal hydrological regime, and most important, nesting on island cliffs is easier. These points optimize feeding conditions for seabirds, although according to the general level of biological productivity, the western and eastern sections are difficult to contrast. Zooplankton concentrations are approximately the same (Shuntov et al. 1993); however, Markina and Khen (1990) speculate that zooplankton biomass in the western section is 1.5 times greater than in the east. Benthic biomasses in the eastern Bering Sea are somewhat lower (Neyman 1963) but nekton and nekton-benthos there are considerably higher. In the 1980s, fish biomass in the Bering Sea was at 50-60 million t, but only one-fourth of it was in the western section (Shuntov et al. 1993, Shuntov and Dulepova 1995). But when analyzing bird feeding ecology, it is not only important to consider overall abundance of fish as prey; it is also important to consider the concentration of prey at depths accessible to the birds. These types of comparisons between the western and eastern sections of the Bering Sea are not possible at present.

**Ecological Groups of Birds**

The composition of birds in any region of the World Ocean depends on the structure, abundance, relative concentration, and distribution of the prey base, with the exception of biogeographical and climatic-oceanographic characteristics. Seabirds can be roughly divided into two groups: those that capture food in the surface layer (surface-feeders) and those that capture food by diving.

The predominate species (63%) which nest in the western Bering Sea capture food by diving and include cormorants and alcids. Those that capture food from the surface or in the uppermost 0.5-1.0 m (including coastal areas) comprise the remaining and include gulls, tube-nosed birds, jaegers, and phalaropes. Similar proportions of diving (67%) and non-diving (33%) nonbreeding species were observed (Table 2); among these southern shearwaters were predominant.

Non-diving birds constitute approximately 65% of the total in the western Bering Sea (around 11 million individuals). This increases to approximately 70% if one also considers birds breeding in fresh water (ducks and loons). The very large percent of diving species (number of individuals) is indirectly confirmed through high biological productivity and fish production in the Bering Sea, and by the high concentrations of macroplankton, benthos, nekton, and nekto-benthos accessible to birds.

Shuntov (1972) examined the distribution of seabirds and suggested that they fall into categories of historically neritic (coastal), neritic-oceanic (offshore), and oceanic groupings. The neritic-oceanic group also includes very specialized ice-neritic species (Shuntov 1972).

The western Bering Sea, and other water masses in the Russian Far East, is open to currents from the Pacific Ocean. Consequently, there are
more oceanic bird species here, such as albatrosses (*Diomedea* spp., Fig. 1), mottled petrels (*Pterodroma inexpectata*), Leach’s storm-petrels (*Oceanodroma leucorhos*), and some red-legged kittiwakes (*Rissa brevirostris*). Their distribution is restricted by deepwater basins and the continental slope where the effect of oceanic water circulating in cyclonic, large scale vortices is quite noticeable. The number of oceanic species is relatively small, particularly in the western Bering Sea which is influenced by runoff of the Kamchatka Current. Oceanic species represent approximately 1% of the total number of seabirds in the western Bering Sea.

The distribution of fork-tailed storm-petrels is similar to the oceanic type (Fig. 2). In contrast to the typical oceanic Leach’s storm-petrel, the fork-tailed storm-petrel is also encountered in shallow water.

The more numerous species in the Bering Sea are the neritic or coastal groups (e.g., cormorants, *Phalacrocorax* spp.; murrelets, *Brachyramphus* spp.; pigeon guillemots, *Cepphus columba*; mew gulls, *Larus canus*; and black-headed gulls, *L. ridibundus*). These birds are no farther than several kilometers away from the coast. This group, however, is small in terms of the number of individuals in the western Bering Sea. The proportion of these neritic species to all seabirds is 1-2%, excluding semiaquatic ducks and divers.

Birds with neritic-oceanic and interzonal types of distribution predominate in the Bering Sea in terms of species and individuals. Neritic-oceanic species are more numerous at the shelf but rare in the continental slope, the deepwater basins, and within 16 km and even hundreds of kilometers from the coast. Examples of the quantitative distribution of remote-neritic types is given in Figs. 3-5. In many respects they have a similar distribution and the same number of species as slaty-backed gulls (*L. schistisagus*) and crested auklets.

In summer, when similarly large masses of birds are attracted to shelf waters, some interzonal species occur there, such as kittiwakes, tufted puffins (*Fratercula cirrhata*), and horned puffins (*Fratercula corniculata*). However, during migration and during the winter, interzonal species occur in large numbers in oceanic regions. Northern fulmars are important among the nesting birds in the Bering Sea (Fig. 6) as are sooty shearwaters among the migrants.

**Quantitative Distribution of Birds: Regional and Seasonal Aspects**

**Winter Period**

In the western Bering Sea the ecology of seabirds in winter and spring periods is nearly unstudied. At the height of winter, ice covers essentially all of the shelf making survival difficult for those birds which do not migrate south in winter. For this reason there are no prominent wintering birds there, although to a lesser extent large aggregations of birds occur in the
Figure 1. The distribution of Laysan albatrosses (Diomedea immutabilis) in the western Bering Sea and contiguous ocean waters in September-November 1986. (1) none; (2) less than 0.3; (3) 0.3-1.0; (4) 1.0-2.0 individuals/km². Arrows = the generalized scheme of the currents.
Figure 2. The distribution of fork-tailed storm-petrels (Oceanodroma furcata) in the western Bering Sea and contiguous ocean waters in September-November 1986. (1) none; (2) less than 0.5; (3) 0.5-1.0; (4) 1.0-5.0; (5) 5.0-10.0 individuals/km². Isolines = surface isotherms; numbers in squares = month of observation.
Figure 3. The distribution of least auklets (Aethia pusilla) in the western Bering Sea and contiguous ocean waters in September-November 1986. (1) none; (2) less than 0.5; (3) 0.5-1.0; (4) 1.0-5.0; (5) 5.0-10.0; (6) more than 10 individuals/km². Isolines = surface isotherms; numbers in squares = month of observation.
Figure 4. The distribution of herring gulls (Larus argentatus) in the western Bering Sea and contiguous ocean waters in September-November 1986. (1) none; (2) less than 3; (3) 3-10; (4) 10-20; (5) 20-50; (6) more than 50 individuals/count (including birds near the ship). Isolines = surface isotherms; numbers in squares = month of observation.
Figure 5. The distribution of murres (Uria spp.) in the western Bering Sea and contiguous ocean waters in July to the first half of September 1960. (1) none; (2) less than 0.5; (3) 0.5-1.0; (4) 1.0-10.0; (5) more than 10 individuals/km².
Figure 6. The distribution of light (left illustration) and dark (right illustration) morphs of northern fulmars (Fulmarus glacialis) in the western Bering Sea and contiguous ocean waters in September-November 1986. (1) none; (2) less than 0.5; (3) 0.5-1.0; (4) 1.0-5.0; (5) 5.0-10.0; (6) more than 10 individuals/km². Isolines = surface isotherms; numbers in squares = month of observation.
southeastern section of the Bering Sea near the Aleutian Islands. Very low winter air temperatures have a great effect on thermophilous and relatively thermophilous species. The magnitude of seasonal migrations of nesting birds at the Asiatic shores is greater in comparison with those birds observed in the American region. A large segment of the birds from the western region migrate to the waters of western subarctic circulation and to all appearances, to the eastern Bering Sea with the contiguous oceanic waters. In particular, counts by experts of the number of birds in winter in the western Bering Sea (including Commander Island waters) was approximately one-tenth that in other seasons.

Judging from spotty observations (Shuntov 1972, Kosygin 1985, Lobkov 1986, Trukhin and Kosygin 1987, Shuntov 1993) kittiwakes, fork-tailed petrels, Leach’s storm-petrels, tufted puffin, horned puffin, all species of jaegers, phalaropes, and other species completely migrate from the western section of the Bering Sea. Seabirds that overwinter were composed of light morph fulmars, large gulls, slaty-backed and glaucous-winged gulls (L. glaucescens), herring gulls (L. argentatus), glaucous gulls (L. hyperboreus), ivory gulls (Pagophila eburnea), Ross’s gulls (Rhodostethia rosea), and some alcids. Among the latter group are both species of murres, black guillemots (Cepphus grylle), and Kittlitz’s murrelets (Brachyramphus brevirostris). Some auklets, especially least auklets, winter in the western section. Due to the sparseness of observations, there are no data regarding bird aggregations in the western section. However, concentrations of gulls and fulmars do occur near commercial fishing operations that catch walleye pollock (Theragra chalcogramma) in the Navarin region and the deep continental slope off Olyutorsk and Karagin bays.

All or nearly all species of seabirds avoid ice or are displaced by it. However, in polynyas and near the ice edge more favorable conditions exist for seabirds to capture prey. For ice-neritic species this habitat is preferable. There are three species of birds that overwinter in the Bering Sea: black guillemots (Cepphus grylle), ivory gulls, and Ross’s gulls. These gulls and a number of black guillemots descend to the ice fields and settle at the southern terminus of Kamchatka and penetrate to the Okhotsk Sea.

Polynyas sheared off by extensive ice are distinctive localities that influence winter distribution of some birds. These polynyas form even in the highest latitudes and offer a preferable habitat for some birds in winter. In the Bering Sea, such polynyas include Sireniki Polynya, near the south coast of Chukotka (Konyukhov 1990), and numerous polynyas next to St. Lawrence Island (Fay and Cade 1959). Ten bird species were noted on the Sireniki Polynya: oldsquaw (C. hyemalis), common eiders (Somateria mollissima), king eiders (S. spectabilis), spectacled eiders (S. fischeri), glaucous gulls, black guillemots, thick-billed murres, pelagic cormorants, Kittlitz’s murrelets, and ivory gulls. The first two species occur in high numbers (Konyukhov 1990). The latter species and Ross’s gull do not avoid the ice; however, the greatest number winter near the ice edge but not in the interior polynyas. Some birds descend into the Kuril Islands and the Okhotsk
Sea while moving along the pools of open water in the ice near the east coast of Kamchatka.

**Spring Period**

Ice plays an important role in the distribution of birds during spring migration which begins at the end of March and extends into April and May. In April, ice conditions are still only slightly different from winter; in Kara-gin Bay ice can occur into June and off Chukotka ice can be seen in May. Once spring begins, the birds cross over the ice fields and use open pools and polynyas as reference points to move in a northerly direction, toward their nesting sites.

The basic spring run of birds in the western Bering Sea occurs along the coast and over the shelf with contiguous zones of deepwater drop-offs that have a basic orientation toward the ice edge. The migration goes toward the Asiatic coasts in the northwestern Bering sea and from the southeastern Bering Sea where the ice edge forms along the contours of the shelf. The quantity of birds increases in open water of the Commander and Aleutian basins. Here, while bypassing the waters of the Aleutian-Commander Island region, the birds migrate within the wide marine range of the North Pacific.

In the western Bering Sea, migration may be later since it is related to the severity of winter conditions and the corresponding delay in the development of hydrobiological processes. Differences in the phenology of biological phenomena in the western and eastern sections of the Bering Sea are reflected in the timing and numbers of southern shearwaters (i.e., *Puffinus tenuirostris*), which fly north to molt and forage. By mid-May they are encountered in small numbers in the northwestern Bering Sea (Trukhin and Kosygin 1987). Their numbers, however, remain low even in the southwestern section at the beginning of summer (Shuntov 1972, 1998) when they form large aggregations in Asiatic regions, in oceanic waters, and in the southern half of the Okhotsk Sea. There is an earlier warming of the southeastern Bering Sea and by May shearwaters form enormous molting and foraging aggregations; they may number into the millions. Evidently, the relative stability of the feeding areas has a definite effect which must be important for the molting birds. Recent observations by me and by Hunt et al. (1996b) suggest that these shearwater feeding aggregations are focusing on krill. By spring the biomass of macroplankton in surface layers of the western Bering Sea is insignificant, resulting in no visible stable, large foraging areas. In the northwestern Bering Sea the situation is reminiscent of early summer in the southeastern section, consistent with the summer-autumn period. At the northwestern shelf and over deepwater drop-offs maximal zooplankton biomass was observed (Shuntov et al. 1993, Volkov 1996). Large masses of short-tailed shearwaters migrate here particularly in the second half of summer.

One of the important features of the spring migration in the western Bering Sea, as in other regions, is its duration during the closing stages.
The first and most powerful waves of flight consisted of mature individuals for whom breeding was imminent. In the second half of spring and in June there was a gradual gathering of immature birds toward the breeding regions. However, those less abundant species (e.g., large puffins, jaegers, and others) remained beyond the range of the Bering Sea for the entire summer.

**Periods of Productivity: Summer and Early Autumn**

During summer a considerable portion of the local birds, including some immature individuals, are concentrated at nest sites. Typically, in nesting locations where the continental shelf is narrow, bird colonies have a weak influence on the density of bird species 32-48 km from the colonies, and in some instances 16-24 km. In areas with a wide shelf, for example north of the Bering Sea, birds are more widely disseminated during the nesting period. This can be seen in Fig. 5 which shows the distribution of murres (*Uria* spp.). This distributional information is further supported by the information in Tables 3 and 4 and Figs. 7 and 8. These data were obtained on two expeditions in the Bering Sea from September to October 1986 and June 1991. In both instances, bird, plankton, and nekton data were collected 16-24 km beyond the coastal zone. Diving birds were the dominant (two-thirds of the total number) breeding birds in the western Bering Sea. In the southwest, surface-feeding birds (tube-nosed birds and gulls) were nearly everywhere beyond the coastal zone. There was a high proportion (but <50%) of diving birds in the Karagin region (Fig. 9).

In regions 1-8 (Fig. 10) September weather is similar to that in summer. The most numerous birds were capturing food at the surface, with the exception of the upper sections of the Gulf of Anadyr and the waters off Chukotka. Southern shearwaters, mainly short-tailed shearwater (*P. tenuirostris*), were the dominant diving birds in Chukotka-Anadyr-Navarin waters.

In autumn with the dispersal of birds from the coast, the number and percentage of diving birds (mainly auklets, Alcidae) increased off the shelf and the continental slope. In the southwestern section, the density of birds increased 3-6 times (Table 4, Fig. 8). In deepwater regions there was a predominance of non-diving birds (tube-nosed birds) which commonly fly hundreds of kilometers from the nesting colonies.

Areas of the Bering Sea with increasing plankton biomass merge in the second half of summer and at the beginning of autumn to the north of the Bering Sea. The concentration of macroplankton there is several times higher than in the southwestern section (Table 4). This concentration gradient is the main reason for the redistribution of close-flying tube-nosed birds (particularly massive numbers of shearwaters and fork-tailed storm-petrels, *O. furcata*) from the southern regions.

Despite the high concentration of plankton in the north, the biological resources there are less than in deepwater basins, perhaps because of
Table 3. Ratio of the density of concentration of seabirds, zooplankton, and nekton in the southwestern Bering Sea in June 1991.

<table>
<thead>
<tr>
<th>Animal group</th>
<th>Regions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Birds, individuals/km²</td>
<td>1.5</td>
</tr>
<tr>
<td>Macroplankton, mg/m³</td>
<td>670</td>
</tr>
<tr>
<td>Macroplankton without Sagitta spp., mg/m³</td>
<td>222</td>
</tr>
<tr>
<td>Nekton, t/km² (0-50 m)</td>
<td>0.9</td>
</tr>
<tr>
<td>Squids, t/km² (0-50 m)</td>
<td>0.1</td>
</tr>
</tbody>
</table>

Note: Areas as in Figs. 9 and 10.
+ Very low quantity.

Table 4. Ratio of the density of concentration of seabirds, zooplankton, and nekton in September-October 1986 in the western Bering Sea.

<table>
<thead>
<tr>
<th>Animal group</th>
<th>Regions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Birds, individuals/km²</td>
<td>26.4</td>
</tr>
<tr>
<td>Macroplankton, mg/m³</td>
<td>2,073</td>
</tr>
<tr>
<td>Macroplankton without Sagitta spp., mg/m³</td>
<td>2,222</td>
</tr>
<tr>
<td>Nekton, t/km² (0-50 m)</td>
<td>1.93</td>
</tr>
<tr>
<td>Squids, t/km² (0-50 m)</td>
<td>−</td>
</tr>
</tbody>
</table>

Note: Areas as in Figures 9 and 10.
+ Very low quantity.
shallow water in the north. In deepwater areas, surface and interzonal plankton, together with mesopelagic fishes and squids, rise to the surface in dark warm periods and constitute an unlimited food source for those seabirds that have the ability to hunt in loose concentrations (e.g., albatrosses, fulmars, storm-petrels, and gadfly petrels [Procellaridae]).

As can be seen in a whole series of cases in Table 4, high densities of birds occur precisely in areas where, on average, greater concentrations of macroplankton and nekton are observed. But there are inconsistencies here also in that abundant plankton and nekton may not always be accessible to birds. On the other hand, where food resources are low, local accumulations of food may form in certain discrete areas and layers, which are accessible to foraging birds.

Figure 8 provides a quantitative distribution of birds for the western Bering Sea. In other seasons their density on the shelf and continental slope is higher than in open, deepwater basins. These high densities are likely associated with higher overall biological productivity at shallow slope areas and the presence of large secondary fronts, high gradient zones,
Figure 8. The distribution of the general density of seabirds in the western Bering Sea (September-November 1986) and contiguous ocean waters (November 1986). Designations are the same as in Fig. 7.
and meso-micro-circulation where there is a passive build up of plankton, larvae, and small nekton.

**Late Autumn Period**

The autumn migration period is drawn out. It is curious that at the end of summer (August) one can also see birds move in a counterclockwise direction and many birds begin to fly south (e.g., phalaropes, jaegers, terns, and mature shearwaters). Simultaneously in the north, the redistribution of immature shearwaters and other birds (i.e., fork-tailed storm-petrels and several gull species) continues.

The autumn migration of birds in the Bering Sea is primarily in the second half of September to the first half of November. However, in the first half of winter, with expanding ice, there is still a noticeable, gradual migration of birds in a southern direction. In waters of the western Subarctic circulation, where many birds from the Bering and Okhotsk seas winter, there is still an accumulation of birds into December.
Figure 10. The relationship of bird groups according to the method of food capture in the western Bering Sea in September-October 1986. Designations the same as in Fig. 9.
Along the edges of the western Bering Sea the migration routes are apparent in that many birds move south by following the coastline and shelf (e.g., least auklets and herring gulls; Figs. 3, 4). Some birds migrate from the northwestern section to southeastern and pre-Aleutian waters. At deepwater basins they do not follow any routes; the oceanic species migrate along the wide fronts to the south of oceanic and other waters. Tufted puffins and horned puffins from the western Bering Sea migrate south along the shelf in deepwater basins.

### Long-Term Dynamics of the Ecology and Number of Birds

Although many birds are basically long-lived species, their number and distribution reflect changes in climatic, oceanographic, and biological phenomena. Examples of climatological events include alternating warm and cold epochs and periods. Within the limits of these cycles are large spans separated into cycles varying from 2 to ~10 years. Much recent attention has been given to average cycles, including those associated with the El Niño phenomenon. In my opinion the effect of this variation in climatic and oceanographic factors on the number of birds should not be exaggerated. Its effect usually is local and is related to temporal and regional parameters. More recent observation suggests that for seabirds of the North Pacific, and perhaps the entire ecosystem, a cycle of some 40-60 years should be considered (Klyashtorin and Sidorenkov 1966, Shuntov et al. 1997).

### Table 5. Biomass and proportion (thousands t/%) of the basic species of fishes in the epipelagial of the Bering Sea in the 1980s and 1990s (Shuntov et al. 1997).

<table>
<thead>
<tr>
<th>Species and group</th>
<th>1980s</th>
<th>1990s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Walleye pollock, <em>Theragra chalcogramma</em></td>
<td>20,000/87.9</td>
<td>8,000/66.4</td>
</tr>
<tr>
<td>Pacific herring, <em>Clupea pallasi</em></td>
<td>700/3.1</td>
<td>1,500/12.4</td>
</tr>
<tr>
<td>Deepsea smelt, <em>Leuroglossus schmidtii</em></td>
<td>125/0.5</td>
<td>1,401/1.2</td>
</tr>
<tr>
<td>Northern lampfish, <em>Stenobrachius leucopsarus</em></td>
<td>790/3.5</td>
<td>900/7.5</td>
</tr>
<tr>
<td>Salmon, <em>Oncorhynchus</em> spp.</td>
<td>315/1.4</td>
<td>470/3.9</td>
</tr>
<tr>
<td>Capelin, <em>Mallotus villosus</em></td>
<td>360/1.6</td>
<td>500/4.1</td>
</tr>
<tr>
<td>Other fishes</td>
<td>465/2.0</td>
<td>540/4.5</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>22,755/100</strong></td>
<td><strong>12,050/100</strong></td>
</tr>
<tr>
<td><strong>T/km²</strong></td>
<td><strong>9.9</strong></td>
<td><strong>5.2</strong></td>
</tr>
</tbody>
</table>
al. 1997). Associated with these cycles are changes in habitat, pulsations of faunistic complexes, and long-term tendencies for changes in the number of fluctuating species.

The second half of a warm period in this century occurred from the early 1970s to the early 1990s, similar to periods in the 1920s and 1930s. In the middle of the 1990s the base temperature in the Far Eastern seas remained elevated; however, at the beginning of the 1990s a change began in the biota which was reminiscent of circumstances for the 1940s-1960s. For instance, a decrease in the number of pollock resulted in a decrease of fishery productivity of the Bering Sea (Table 5), but the portion of predatory chaetognaths (*Sagitta* spp.), which have little value as prey to other zooplankton (Shuntov 1986a, 1994), increased.

In my opinion this is all associated with the warm epochs of the 1970s-1980s, at least with the subsequent changes in the distribution and number of birds. A significant rise in the number of auklets in the northern Bering Sea has been reported (Konyukhov 1991, Springer et al. 1993). In the 1980s there were noticeably more common murrels north of the Bering Sea which began to breed on Wrangel and Herald islands. Tufted puffins began to nest on Wrangel Island at the same time (Stishov et al. 1991, Kondrat'ev 1991). The range for some species of terns expanded to include northeast Asia in the 1970s-1980s. In the 1960s I recorded only light-colored fulmars in the Gulf of Anadyr (Shuntov 1972). In September 1980 there were approximately 5% more light-colored and more oceanographic dark-colored morphs there (Shuntov 1998).

Conversely, significant climatic, oceanographic, and ecosystem restructuring in the North Pacific will have negative consequences for seabirds. The reduction in breeding of kittiwakes (Kondrat'ev 1993, 1995; Hatch et al. 1993) was probably a consequence of such restructuring; this change originally started in American waters and extended to the Asiatic region by the 1990s. In the 1990s, a random reduction in breeding of other birds in Far Eastern seas was reported. Whether this is an expression of the long-term cycles or only the result of interannual variability must be shown by subsequent observations.

One of the effects of climatic and oceanographic epochs on bird diversity over time is the redistribution of some species of birds between the Bering Sea and the North Pacific. In the summer of the 1960s, fork-tailed storm-petrels were numerous in the Okhotsk and Bering seas (Shuntov 1972). By the 1980s their numbers in the Okhotsk Sea were several times lower. In the 1990s they became numerous again during summer in the Okhotsk Sea (Shuntov 1997). In comparing Figs. 2 and 11 one can see somewhat similar localities in the western section of the Bering Sea; during the 1980s, when the greatest concentration was observed in the same places as in the 1960s, however, the numbers were much lower. It is not known if there has been a recovery of fork-tailed storm-petrels here in the 1990s to the level of the 1960s.
Figure 11. The distribution of fork-tailed storm-petrels (Oceanodroma furcata) in August-October 1960. (Shuntov 1998). (1) none; (2) less than 0.5; (3) 0.5-1.0; (4) 1.0-5.0; (5) 5.0-10.0; (6) more than 10.0 individuals/km².
Questions about the Role of Birds in the Bering Sea Ecosystem

When evaluating the role of birds in the marine ecosystem, consideration must be given to the complexity of their food web and the amount and diversity of prey consumed. Seabirds of the western Bering Sea were not systematically studied in this respect. However, judging from fragmentary information scattered in many publications (e.g., Ogi and Hamanaka 1982, Ogi et al. 1985), seabird feeding in the Russian section of the Bering Sea does not reflect what has been seen in the more thoroughly studied eastern section. The principal prey consists of nekton such as pollock, Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasi*), Atka mackerel (*Pleurogrammus monopterygius*), daubed shanny (*Lumpenus maculatus*), macroplankton (krill, copepods, amphipods), and small mesopelagic fishes and squids in deep-water regions.

Recent studies that plotted the biological balance of Bering Sea seabirds included the flow of matter and energy in the diagram (Shuntov and Dulepova 1995). The calculations, however, were done with insufficient data on the abundance of birds. One must also recognize that estimates of seabird prey consumption are complicated not only by the scarcity of data on annual rations, but also on the population dynamics of birds by season and taxonomic group. Therefore, at this stage it is only possible to make rough estimates of the composition and magnitude of the annual ration. One such version is given in Table 6. The portion of nekton in the diet is assumed to be the following: For fulmars and short-tailed shearwater nekton represented 30%, storm-petrels and ducks = 10%, medium-sized alcids, kittiwakes, large gulls and albatross = 90%, cormorants = 95%, small alcids = 20%, and murres = 70%.

Using a method for estimating prey consumption by birds by season in the western Bering Sea produced an estimate of 337,000 t of which nearly half was nekton (mainly fish; Table 6). An extrapolation of these data to the eastern Bering Sea (based on the entire Bering Sea) results in approximately 2 million t (of this 0.8-1.0 million t is nekton). These figures are impressive considering the annual commercial catch from 1970 to 1990 in the Bering Sea usually fell within a range of 2.5-4.5 million t. The approximate scale of the biological resources and the production at different trophic levels are now known for the Bering Sea (Shuntov et al. 1993, Shuntov and Dulepova 1995). The mean biomass of plankton for spring was estimated at 453 million t, for summer 601 million t, for autumn 459 million t, and for annual production it was 3,810 million t. Biomass and fish production for the 1980s was estimated at 50-60 million t, of which 80% was pelagic (biomass and production are roughly 20% lower now); the biomass and production of squids was 4 and 12 million t, respectively. In the 1980s, walleye pollock consumed 189-252 million t of
Table 6. **Number of birds and their fish and invertebrate consumption in the western Bering Sea. Based on methods of Shuntov (1986b).**

<table>
<thead>
<tr>
<th>Species and group</th>
<th>Species (10^3) individuals</th>
<th>Daily ration</th>
<th>Food consumption, (10^3/t)</th>
<th>Nekton consumption (10^3/t)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Summer (000)</td>
<td>Winter (00)</td>
<td>Summer (00)</td>
<td>Winter (00)</td>
</tr>
<tr>
<td>Fulmar</td>
<td>600</td>
<td>200</td>
<td>150</td>
<td>18.0</td>
</tr>
<tr>
<td>Shearwaters and gadfly petrels</td>
<td>1,700</td>
<td>+</td>
<td>130</td>
<td>33.0</td>
</tr>
<tr>
<td>Storm-petrels</td>
<td>250</td>
<td>+</td>
<td>15</td>
<td>0.75</td>
</tr>
<tr>
<td>Albatrosses</td>
<td>50</td>
<td>+</td>
<td>500</td>
<td>5.0</td>
</tr>
<tr>
<td>Murres</td>
<td>2,000</td>
<td>200</td>
<td>250</td>
<td>100.0</td>
</tr>
<tr>
<td>Small guillemots</td>
<td>2,300</td>
<td>200</td>
<td>50</td>
<td>23.0</td>
</tr>
<tr>
<td>Average size guillemots</td>
<td>200</td>
<td>20</td>
<td>100</td>
<td>4.0</td>
</tr>
<tr>
<td>Kittiwake</td>
<td>1,700</td>
<td>20</td>
<td>100</td>
<td>34.0</td>
</tr>
<tr>
<td>Large gulls and jaegers</td>
<td>150</td>
<td>30</td>
<td>350</td>
<td>10.5</td>
</tr>
<tr>
<td>Phalaropes</td>
<td>90</td>
<td>5</td>
<td>400</td>
<td>7.2</td>
</tr>
<tr>
<td>Ducks</td>
<td>300</td>
<td>1,000</td>
<td>300</td>
<td>10.8</td>
</tr>
<tr>
<td>All birds</td>
<td>9,340</td>
<td>1,675</td>
<td>246.25</td>
<td>90.9</td>
</tr>
</tbody>
</table>

Note: In the calculations for the summer level of numbers we accepted 150 days for shearwaters, 120 for ducks, 200 for the remaining birds; for winter: 245 days for ducks, 165 days for the remaining birds.

+ Very low quantity.

Macroplankton and small nekton which is now half that amount; pollock predators consumed 7 million t during the year. When one reflects on these values, the volume of biomass consumed by birds appears to be insignificant when considering the ecosystem as a whole (i.e., the overall role of seabirds in its biological balance is small). There is evidently a completely different picture at sites of mass aggregations of birds, particularly in shallow water regions. The Bering Strait-Navarin region, and the waters adjacent to the Commander Islands and Karagin Island, is a region of stable and long-term aggregations of large numbers of birds. In these regions many birds are concentrated both during breeding season and in other seasons. However, for concrete judgments about the role of birds in the functional biota of these regions, further specialized and complex investigations are needed.
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