Biological and physical determinants of marine bird distribution in the Bering Sea

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Abstract

Most of the seabird species nesting in the Bering Sea are north-boreal in origin. Nonnesting migrants, primarily procellarids, move into the region in summer. The spatial distribution of seabirds depends on many factors, including the location and extent of ice; circulation patterns associated with the continental shelf; the location of the fishing fleet; and processes influenced by large-scale gyres. Seasonal movements of birds are associated with the retreat of ice in spring, and are guided also by topographic features such as the shelf break, island arcs, and the coastline. Pelagic seabirds are characterized by species that search large areas, feed only near the sea surface, and do not dive well. Seabird abundances match patterns of production in a general way, but several factors cloud the clarity of these relationships, especially annual variability in the timing of movements, and differences in prey availability. Fronts contribute to the variation in availability by collecting prey from larger areas. Foraging conditions depend on the fine structure of the ocean environment, as well as on general oceanic conditions and the ecological character of each species. Further progress in understanding seabird distribution depends on accumulation of information from small-scale surveys in relation to the ocean environment.

Résumé

La plupart des espèces d'oiseaux marins, qui nichent dans la mer de Béring, appartiennent à la région polaire boréale. Les espèces migratrices, qui nichent ailleurs, fréquentent la mer de Béring pendant l'été. Il s'agit surtout de procellariidés. De nombreux facteurs influent sur la distribution géographique des oiseaux marins, y compris l'emplacement et l'étendue des glaces, les schémas de circulation des courants procédant de la plate-forme continentale, la position des flottilles de pêche et les processus causés par les tourbillons de grande envergure. Les facteurs qui influent sur les déplacements saisonniers des oiseaux sont le retrait des glaces au printemps et les éléments du relief, comme la rupture de pente, les arcs insulaires et la ligne de côte. Les groupes pélagiques d'oiseaux marins sont représentés par des espèces qui prospectent de vastes régions, qui s'alimentent exclusivement près de la surface de la mer et qui sont de mauvais plongeurs. En règle générale, l'abondance des oiseaux marins correspond aux schémas de production. Cependant, plusieurs facteurs affectent la netteté de ces relations, surtout la variabilité annuelle du moment des déplacements et les écarts de disponibilité des proies. Les fronts océaniques accentuent les écarts de disponibilité, en élargissant le territoire de collecte des proies. Les conditions d'alimentation dépendent de la microstructure du milieu océanique, de l'état général de l'océan et du caractère écologique de chaque espèce. Pour mieux comprendre la répartition des oiseaux marins, il faut recueillir davantage de données dans des relevés de portée restreinte en fonction du milieu océanique.

1. Introduction

The largest volume of water within the Bering Sea originates in the Pacific Ocean. This water enters the Bering Sea primarily via the Attu Current, which flows between the Aleutian and the Commander islands. Hence the Bering Sea is essentially a bay of the Pacific Ocean.

Laysan Albatross *Diomedea immutabilis* and Mottled Petrel *Pterodroma inexpectata* regularly occur over the deep-water basins in summer and fall. Black-footed Albatross *D. nigripes* and Leach's Storm-Petrel *Oceanodroma leucorhoa* are most numerous in the southern part of the Bering Sea. Rare penetration of Flesh-footed Shearwater *Puffinus carneipes* and Pink-footed Shearwater *P. creatopus* into the Bering Sea is likely a consequence of the thermal preferences of those warm-temperate species.

Most of the seabird species nesting in the Bering Sea belong to the north-boreal complex. Generalizations from data accumulated during the 1960s concerning pelagic distribution (Shuntov 1972), as well as more recently published information, are described here.

2. The Bering Sea in winter

Although winter is the period of fewest birds in the Bering Sea, there are still several million individuals present during that time (Shuntov 1972). Recent work by Bogoslovskaya and Votrogov (1981), Kosygin (1985), and Trukhin and Kosygin (1987) has not only supplemented our knowledge of the winter distribution of birds, but has also contributed greatly to the understanding of migrations of certain arctic species such as Ross' *Rhodostethia rosea* and Ivory *Pagophila eburnea* gulls.

Many birds leave the Bering Sea entirely or almost entirely in the winter. The winter assemblage is dominated by diving species (alcids, sea ducks, cormorants), by large gulls, and by light-phase Northern Fulmars *Fulmarus glacialis*. Thermophilic species, particularly those obtaining food in the upper layers of the water (e.g., storm-petrels, kittiwakes, terns, puffins, phalaropes, planktivorous small alcids, and dark-phase fulmars), are generally absent from the Bering Sea in the winter (Shuntov 1972).

Large differences in climatic and oceanographic conditions between the cold near-Asian and warmer southeastern sectors of the Bering Sea greatly influence the distribution of bird species that overwinter in the Bering Sea. The shelf and contiguous sections of the western Bering Sea (i.e., the best feeding grounds) are covered with ice at that time: this likely is the principal cause of the reduced abundance of birds. Within the ice, the most common gull species are Ross', Ivory, Glaucous *Larus hyperboreus*, Glaucous-winged *L. glaucescens*, and Slaty-backed *L. schistisagus* gulls. Although Slaty-backed Gulls do not penetrate north of the Navarin area, Ivory Gulls are found far into the solid ice areas. Less abundant species that overwinter at the ice edge and in open water in the western Bering Sea are fulmars and murres (Trukhin and Kosygin 1987).

In more northern areas, covered with solid ice, some birds are found throughout the winter only at polynyas and leads. For example, there are important wintering areas near St. Lawrence Island and the southern and the eastern coasts of the Chukotskii Peninsula (Fay and Cade 1959; Portenko 1972, 1973; Bogoslovskaya and Votrogov 1981). In general, the position of the ice edge, as well as the distribution and size of the leads, changes with ice motion and drift. However, there are a few comparatively stable areas of thin ice, such as the large Sirenikovskaya polynya in the vicinity of the southern coast of the Chukotskii Peninsula. Oldsquaws *Clangula hyemalis* and King Eiders *Somateria spectabilis* are the most numerous species in leads beyond the ice edge, although Common Eiders *S. mollissima*, Pigeon Guillemots *Cepphus columba*, Black Guillemots *C. grylle*, Glaucous Gulls, Ivory Gulls, Ross' Gulls, and murres also occur. Although it has been reported that Sabine's Gulls *Xema sabini* are found in leads and polynyas in winter (Bogoslovskaya and Votrogov 1981; Trukhin and Kosygin 1987), it is suggested that these reports are erroneous: these gulls winter at tropical latitudes.

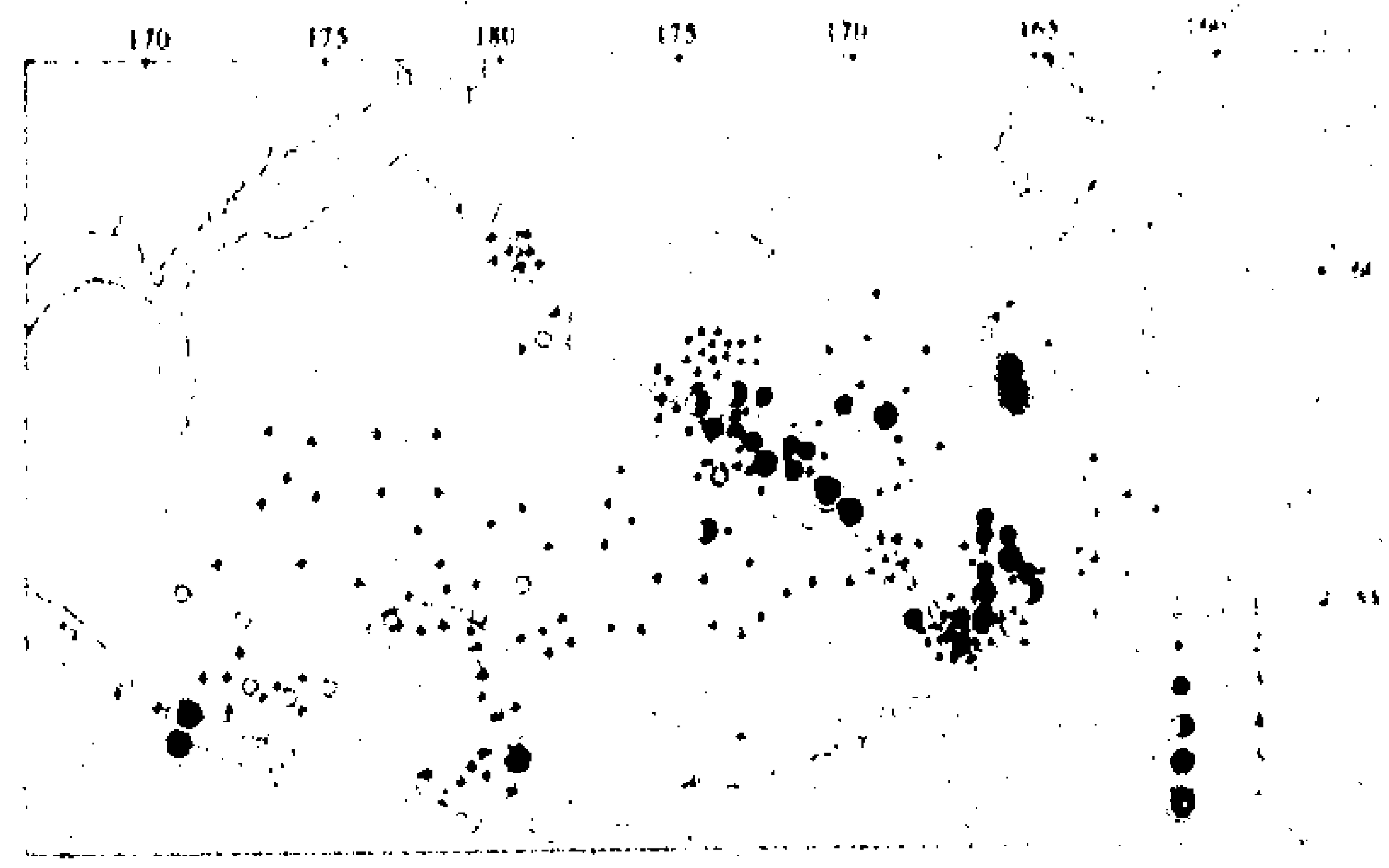
The overwintering of large numbers of Oldsquaws and eiders in the extreme northern areas of the Bering Sea is quite remarkable considering that these species feed primarily on benthic and nectobenthic molluscs, mysids, amphipods, echinoderms, and a few species of fish (Ainley and Sanger 1979; Krasnow and Sanger 1982; Sanger and Robert 1984).

Although low numbers of Ross' Gulls have been observed in the Northern Atlantic during winter (Zubakin et al. 1988), the majority of individuals overwinter on pack ice in the western Bering Sea, and the Sea of Okhotsk. Most Ross' Gulls reach the Bering Sea through the Bering Strait, starting at the end of autumn, while at the same time some gulls reach Anadyr Bay across land (Ostapenko et al. 1983). The spring migration of Ross' Gulls differs considerably from the winter dispersal. According to Portenko (1973), Firsova and Levada (1982), Tomkovich and Sorokin (1983), Gerasimov (1985), Kosygin (1985), Trukhin and Kosygin (1987), and Kischinskii (1988), many Ross' Gulls fly northwest across land from the Bering Sea to the tundra of Kolyma, Yana, and Indigirka from May to June. In contrast, few gulls migrate during spring across the Bering Strait and the Chukchi Sea.

Ivory Gulls are found over ice throughout the entire Bering Sea. They remain in the northwestern part of the Bering Sea and near the Bering Strait throughout June (Kosygin 1985; Trukhin and Kosygin 1987).

The winter conditions are relatively more favourable in the southeastern Bering Sea (Fig. 1). During the second half of winter, the vast eastern Bering Sea shelf is covered with ice, whereas in the southeastern sections, a large area of shallow water either remains free of ice or is covered with only a thin layer of ice.

Figure 1
Average densities of seabirds in the Bering Sea during winter (1960s average data). The dotted line indicates the 200-m isobath; the solid line indicates the 1000-m isobath. Density indices are as follows: 1 = none, 2 = less than 5/km², 3 = 5–10/km², 4 = 10–20/km², 5 = 20–100/km², 6 = more than 100/km².



Almost all of the waters bounded by the Aleutian ridge do not freeze at all, providing diving birds with access to the shallow benthos. The lack of ice and the milder climatic and oceanographic regime of the southeastern Bering Sea provide a favourable overwintering place for millions of birds (Shuntov 1972). When describing the winter conditions for birds, it is imperative to mention the abundant schools of fish, notably walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and Pacific sand lance *Ammodytes hexapterus*, living in the eastern Bering Sea. Several million tonnes of walleye pollock alone reproduce during the winter–spring period (Bakkala and Alton 1986; Nishiyama et al. 1986; Bulatov 1987). Young fish of these and other species are abundant throughout the year.

Although Thick-billed Murres *Uria lomvia* are most numerous in the southeastern and southern Bering Sea in winter, other species including Northern Fulmars, Glaucous-winged Gulls, and Black-legged Kittiwakes *Rissa tridactyla* are also abundant. Sea ducks, auklets, and cormorants are numerous in the vicinity of the Aleutian and Commander islands (Shuntov 1972; Marakov 1977; Gould et al. 1982).

At times large concentrations of the fishing fleet greatly influence the distribution of gulls and fulmars. Fishing fleets have operated recently not only in the southeastern Bering Sea, in the Navarin and in the Olutorski–Karaginskii areas, but also in the deep-water Aleutian basins. Hundreds of thousands of gulls and fulmars have been observed feeding on offal near fishing boats. Such trends have been noted elsewhere (e.g., Wahl and Heinemann 1979; Vermeer et al. 1989).

According to average data from the 1950s and 1960s (Shuntov 1972), the winter density of birds over the deepest parts of the sea (0.8 birds/km²) is at least one-twelfth of the density observed over shelf and continental slope waters (10 birds/km²). The estimate for the shelf is possibly low because some large flocks of birds were not included in the calculations and because surveys were not conducted in the coastal zone where a large number of sea ducks overwinter. Earlier work (Shuntov 1966) indicated an average density of 45 birds/km² in the southeastern Bering Sea and 27 birds/km² in Aleutian waters. Based upon occasional aerial surveys conducted in the 1970s, Gould et al. (1982) estimated densities of 27.7 birds/km^2 over the shelf and 9.1 birds/km^2 at the continental slope, in the southeastern Bering Sea.

3. Spring migration

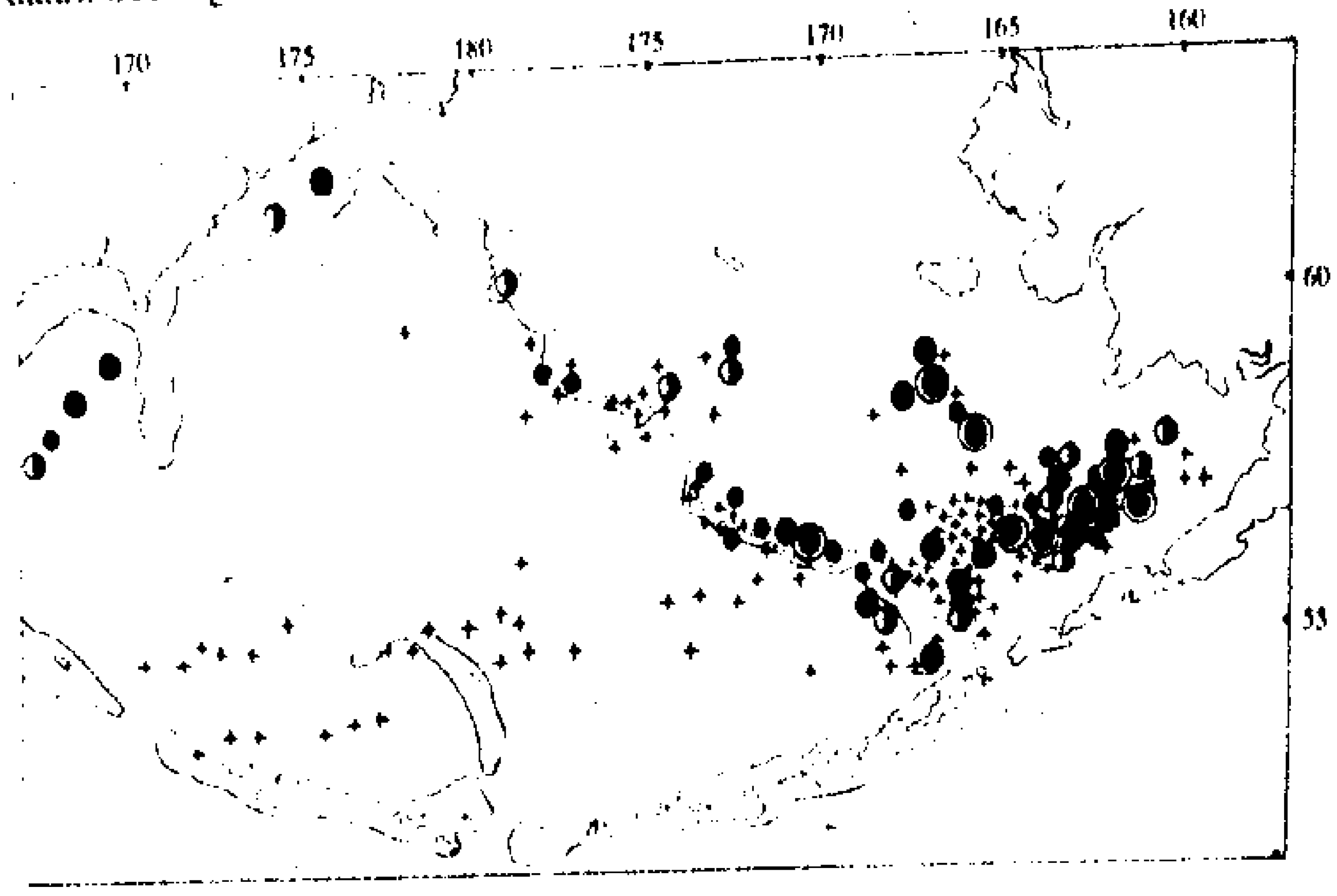
The spring movement of birds begins at the end of March, but the major changes in numbers and species composition occur in April and May. Although the timing of the spring migration is a function of the breeding chronology, distance between nesting and overwintering places, and the particular ecological features of each species, the major spring passage generally occurs much earlier than the most favourable feeding time (Shuntov 1972). Despite the rapidity of processes in the spring, ice retreats slowly from the northern shelf. During this period polynyas and leads beyond the edge of ice are especially important as stopovers for early migrants (Bogoslovskaya and Votrogov 1981).

In spring, the numbers of birds increase severalfold both on the shelf and in the deep-water area of the Bering Sea. There is considerable variation in the estimates of total number of birds present during this period (e.g., Shuntov 1972; Hunt et al. 1981a; Gould et al. 1982). However, common to all of these papers is the observation that the density of birds over the shelf is approximately five times that found over deeper water, implying that the main migration routes take place over the shelf and in coastal areas. Spring migrations have been best observed in the eastern Bering Sea (Shuntov 1972; Hunt et al. 1981a; Gould et al. 1982). The directions of migratory passage are determined in part by the fact that a large number of birds overwinter in the northeastern Pacific, by the configuration of the coastline and shelf, and by the location of islands. Birds enter the Bering Sea through passes in the eastern Aleutians, then travel northeast to interior parts of Bristol Bay or directly north. At the beginning of spring, when ice still occupies a significant part of Bristol Bay, migratory passage can be observed along the ice edge in a contrary direction (i.e., to the southwest) by birds (especially murres) that apparently overwintered in southern Bristol Bay. However, there is in general a shift of birds to the northwest as they return to the huge colonies on the Pribilof, St. Matthew, St. Lawrence, and Diomede islands.

In the western Bering Sea the main migratory route in spring is towards the northeast, following the configuration of the coast and the shelf (Trukhin and Kosygin 1987). The ratio of eastern to western population size may be indicative of the numbers of birds that migrate through the western and eastern parts of the Bering Sea. The number of breeding birds in the eastern Bering Sea, with the exception of the Aleutian Islands, may be as high as 20.5 million (Sowls et al. 1978; Hunt et al. 1981b). No more than three million birds have been tallied in the western Bering Sea with the exception of the Commander Islands (Velizhanin 1978; Vyatkin 1986; Smirnov and Velizhanin 1986).

Intensive observations conducted at sea during spring in the first half of the 1960s and in the 1970s covered most of the southeastern Bering Sea. Results from both survey periods indicate that dense concentrations of birds occur along the outer part of the shelf and the continental slope, and also along the 50-m isobath in the interior part of Bristol Bay (Fig. 2). More shearwaters were observed in spring during the early 1960s than during the 1970s, when mass aggregations did not settle in until June. In the early 1960s shearwaters were found in the eastern Bering Sea as early as the end of April, and by mid-May

Figure 2
Average densities of seabirds in the Bering Sea during spring (1960s average data). See Figure 1 for density codes.



aggregations of thousands of shearwaters were found in Bristol Bay (Shuntov 1961). The climate during this period was notably colder than normal for the eastern Bering Sea (Khen 1989).

The arrival of large numbers of shearwaters in the Bering Sea compensates for the decline in local nesting birds in open-water regions. Shearwaters do not occur in large concentrations in the western Bering Sea, where the ice retreats more slowly, although they do penetrate to Anadyr Bay during May.

During spring migration the shelf and deep-water regions retain their differences in species. In the deep-water regions, in addition to the species characteristic of these waters (primarily dark-phase fulmars, storm-petrels, and Black-legged and Red-legged *R. brevirostris* kittiwakes), a spring increase occurs in some species (especially auklets) that usually remain on the shelf or even near the coast. These species cross the deep-water area, migrating directly from their wintering area in the vicinity of the Commander and Aleutian islands.

4. Summer and fall

Patterns of the spatial distribution of birds in the Bering Sea have resulted mostly from observations conducted during summer and fall. The best coverage (in the 1960s) occurred in waters over the northern shelf and the continental slope of the central Bering Sea (Fig. 3). During the 1970s, most efforts concentrated over the shelf and shelf break in the eastern Bering Sea (Hunt et al. 1981a; Gould et al. 1982). During the 1960s few fall observations were made east of the longitude of the Pribilof Islands (Fig. 4), whereas many observations were made there in the 1970s (Hunt et al. 1981a; Gould et al. 1982). Thus a comparatively complete picture of seabird distribution in the southeastern Bering Sea is available for summer and fall.

In comparing data between years one cannot fail to notice stable areas of high and low concentrations of birds, especially considering the annual variations in seabird numbers. The configuration of these areas apparently corresponds with patterns of water circulation, the locations of water masses of different structure, oceanic fronts, and the distribution of productive zones.

The circulatory scheme of the Bering Sea consists of a system of large, rotating formations (Khen 1989; Markina and Khen 1990). Three distinct cyclonic macro-gyres are located in the deep-water part of the sea, and a smaller-scale anti-cyclonic eddy is found to the south of Cape Navarin. A large anti-cyclonic gyre occupies most of the shelf between St. Lawrence Island and

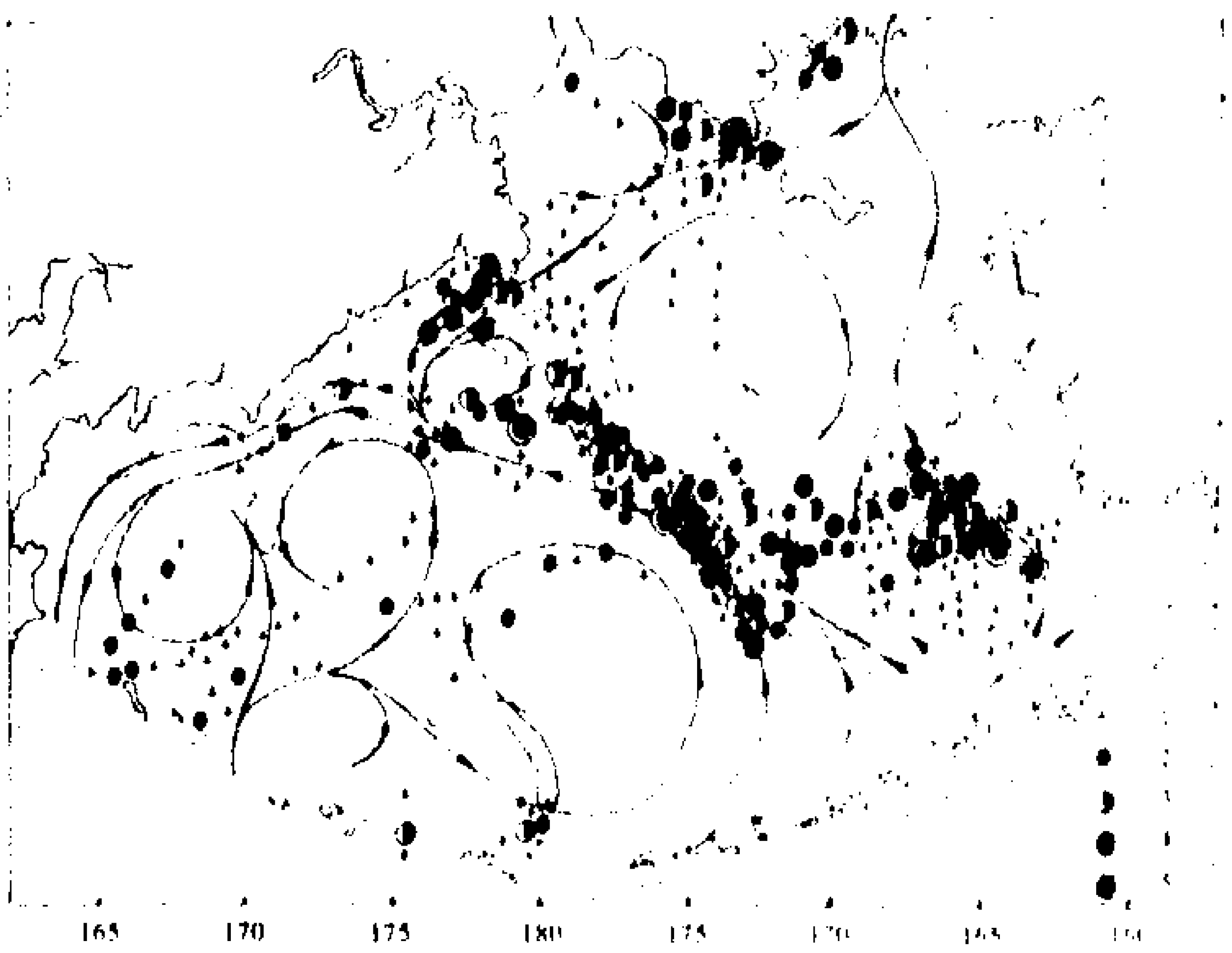


Figure 3
Average densities of seabirds in the Bering Sea during summer (1960s average data). The dotted line indicates the 200-m isobath; the solid line indicates the 1000-m isobath. Arrows show general current patterns. Density indices are as follows: 1 = less than 5/km^2, 2 = 5–10/km^2, 3 = 10–20/km^2, 4 = 20–100/km^2, 5 = more than 100/km^2.

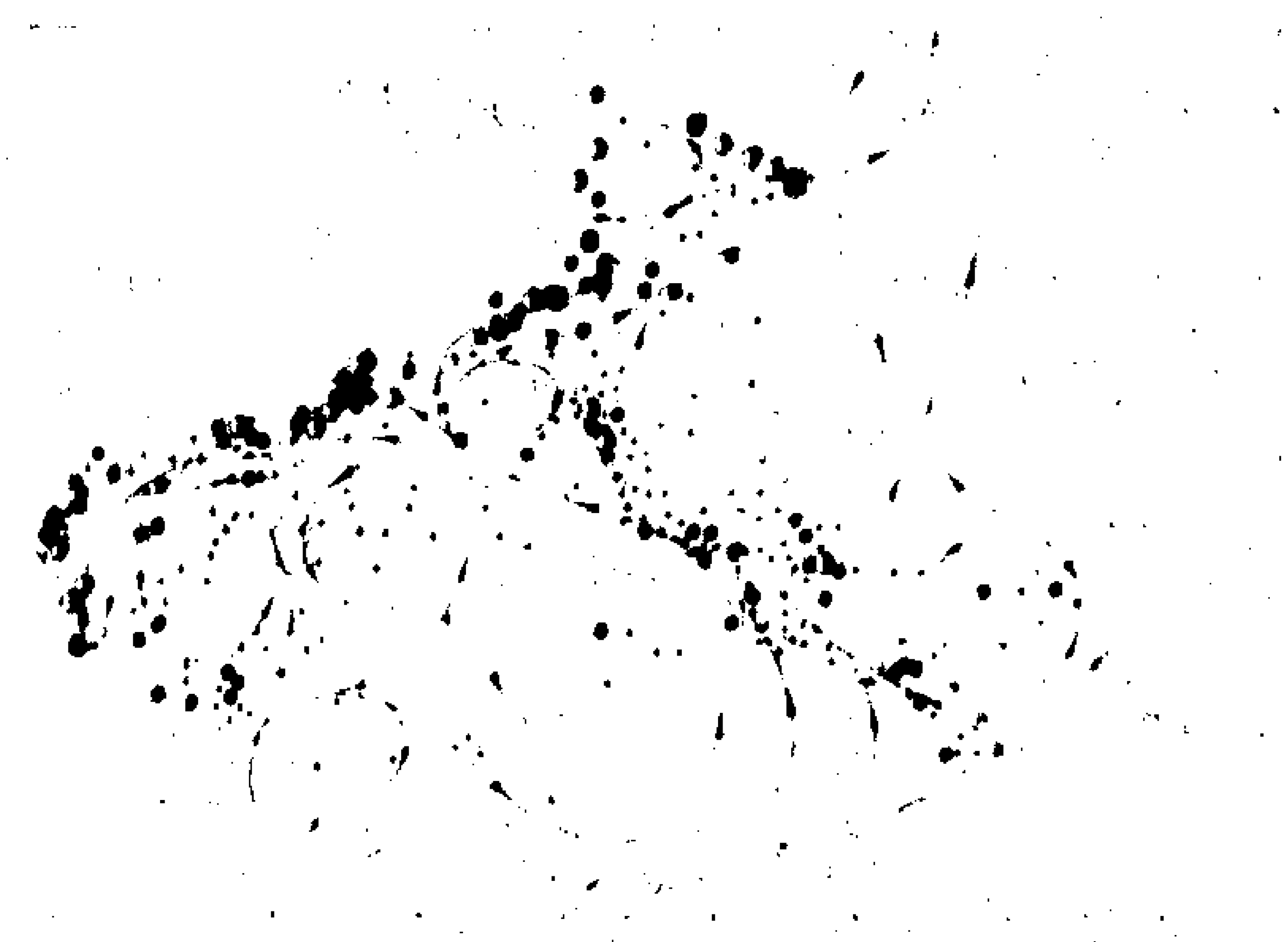


Figure 4
Average densities of seabirds in the Bering Sea during fall (1960s average). Data on the western Bering Sea, obtained in 1986, are also included. See Figure 3 for density codes.

St. Matthew Island, and a smaller-scale cyclonic gyre is located to the east of the Pribilof Islands. Figures 3 and 4 demonstrate that bird density is lower inside than outside of the boundaries of all of the macro-gyres; and in addition that the density as a rule is low outside the boundaries of gyres located in the deep-water part of the sea. All of the stable areas of higher concentration mentioned above are located either at the periphery or outside of the boundaries of macro-gyres, namely in the vicinity of islands, along the continental slope, and at the periphery of coastal currents.

Data collected in the 1970s (Hunt et al. 1981a; Gould et al. 1982) show that the quantitative bird distribution in fall resembles that of summer. During fall, higher densities of birds occur along the continental slope and the outer part of the shelf, as well as locally in northern parts of the shelf. During fall, a steep reduction in numbers of birds in Bristol Bay results largely from the departure of shearwaters. The fall distribution and density of birds are also greatly influenced by the southward migration, which generally follows the configuration of the coastline and shelf (i.e., movements to the southwest in the western Bering Sea and to the southeast in the east). The densities of birds found over the shelf in summer average seven- to 10-fold higher than over the deep-water basin, and fourfold higher in fall (Shuntov 1972; Hunt et al. 1981a; Gould et al. 1982).

Two large areas that contain the lowest biomass are evident in the quantitative distribution of phytoplankton in the Bering Sea, based on multi-year averages (Markina and Khen 1990). Both areas correspond to the locations of large-scale gyres, one occupying nearly all of the deep-water part of the sea, the other occupying the central region of the northeastern shelf. The areas containing larger amounts of phytoplankton are located along the perimeter of the sea (i.e., along the coast and the interior part of the shelf, and along the ridge of the Commander and Aleutian islands bordering the sea). These areas form a "bridge" of high phytoplankton biomass between the Navarin region and the eastern part of the Aleutian Islands. This bridge divides two vast areas of large-scale gyres impoverished of phytoplankton. The existence of the bridge corresponds well to the concept concerning the circulatory structure of the central Bering Sea at the shelf break. The complex relief of the continental slope perturbs the current, forming cross-wave oscillations, meanders, and eddies. Ascent and mixing of waters from a great depth caused by those disturbances promote, and are the principal prerequisites for, the formation of productive areas above the continental slope and the outer part of the shelf (Markina and Khen 1990). Multi-year averages of the distribution of zooplankton reveal two vast areas of a low productivity: one in the deep-water basin, and the other in the northern part of the sea shelf between St. Lawrence Island and St. Matthew Island.

The basic correspondence of the quantitative distribution of birds with oceanographic and biological conditions has a general character. Even in the deep-water parts of the sea, there are enormous quantities of plankton, small fish, and squid. This apparent contradiction is a result of the spatial and volumetric magnitude of the zone. For instance, zooplankton contained in epipelagic waters of the Russian economic zone in the western Bering Sea has been estimated at 95.3 million tonnes; of that, the shelf and continental slope contain 41.1 million tonnes, whereas waters of the deep-water area contain 54.2 million tonnes. Therefore it is highly unlikely to be coincidental that a significant portion of the adults of the most widespread fish species (walleye pollock) migrate for fattening not to the shelf but to the deep-water area of the Bering Sea (Shuntov et al. 1988; Sobolevskiy et al. 1989).

As already noted, some bird species are limited partly or completely to the deep-water part of the Bering Sea. These are the albatrosses, storm-petrels, Mottled Petrels, dark-phase fulmars, and Red-legged Kittiwakes. A few of these (Fork-tailed Storm-Petrels *Oceanodroma furcata*, Red-legged Kittiwakes, and dark-phase fulmars) form dense aggregations at the shelf break, but most birds do not reach the inner shelf.

Only light-phase fulmars nest in colonies near the northern Bering Sea shelf. About a dozen previously unkaown colonies were discovered on the Chukotskii Peninsula in the 1980s (Bogoslovskaya and Konyukhov 1988). Dark-phase fulmars were not recorded in the northern Bering Sea during observations made during the 1960s (Shuntov 1972), whereas they constituted between 5 and 10% of the total number of birds observed in Anadyr Bay in September 1986 (Shuntov 1988a). The northern expansion of these dark-phase fulmars is most likely linked to climatic changes and warming in the 1970s and 1980s.

Common to those species of birds that prefer oceanic waters is a limited diving ability, forcing them to obtain their food in the surface waters. Because of the low concentrations of prey, these bird species must forage over large areas.

5. Species assemblages, biomass, and productivity

Three groups of species—a neritic group found over shallow waters, an offshore group above the outer shelf, and an oceanic group in deep-water areas beyond the shelf—were described by Shuntov (1972). Shuntov (1988a) observed that in the western Bering Sea during fall, nondiving birds that obtain food from the sea surface made up approximately 15–30% of the total over the shelf, 35–60% over the continental slope, and 80–85% over the deep-water areas. These trends in the distribution of marine birds have also been documented for the eastern Bering Sea by Schneider and Hunt (1982) and Schneider et al. (1986). Diving murres (in spring) and shearwaters foraging in the upper layer (in summer) predominate over the inner shelf. Nondivers such as fulmars, kittiwakes, and storm-petrels predominate over the outer shelf, where they feed mostly on squid, medusae, hyperiids, and some fish.

In general, data on biological productivity do not correlate well with seabird distribution. This is readily demonstrated, for example, by comparing the Bering Sea with the Sea of Okhotsk. In general, the total volume of plankton and the productivities of these seas are quite similar. The amount of plankton is roughly 1.5 times greater per unit area in the Sea of Okhotsk than in the Bering Sea (Volkov and Chuchukalo 1985; Markina 1986). In contrast, however, biomass and productivity of the highest trophic levels (e.g., fish and squid) per unit area are considerably higher in the Bering Sea than in the Sea of Okhotsk. Biomass is 19.3 and 16.8 t/km^2 respectively, whereas productivity is 12.3 and 8.5 t/km^2 respectively (Shuntov 1987, 1988b). This suggests that high trophic level animals are utilizing energy far more effectively in the Bering Sea than in the Sea of Okhotsk.

A similar result emerges when comparing the western with the eastern parts of the Bering Sea. Multi-year averages of the biomass and productivity of zooplankton per unit area are approximately 1.5 times greater in the western Bering Sea than in the eastern (Markina and Khen 1990). Biomass of benthos per unit area in the southeastern shelf area is the lowest of all of the Bering Sea (Neiman 1963). In contrast, biomass of fish and some species of nektonic invertebrates is several times greater in the eastern Bering Sea; this is most likely a result of a milder oceanographic regime.

August in the Anadyr Bay and the Bering Strait corresponds phenologically to June in the southeastern Bering Sea. Thus, when zooplankton biomass is already decreasing in the south, the maximum is reached in the north. Some species of pelagic birds drift north, presumably following these changes in zooplankton biomass (Shuntov 1972). In the second half of the summer, as some shearwaters and phalaropes begin their migration south, other shearwaters and Fork-tailed Storm-Petrels increase in the northern half of the sea. By August the numbers of shearwaters have declined markedly in Bristol Bay and contiguous waters of the southeastern shallows, from the vast numbers present during the early summer (Bartonek and Gibson 1972). Large aggregations of Fork-tailed Storm-Petrels are not found north of the continental slope and contiguous areas of the outer shelf, whereas high numbers of shearwaters penetrate as far north as the Chukchi Sea. It has been considered that only Short-tailed Shearwaters *Puffinus tenuirostris* occur in the northern Bering Sea. Although this species does predominate, low numbers of Sooty Shearwaters *P. griseus* do occur in the northern Bering Sea (Harrison 1979; Shuntov 1988a).

Shearwaters, murres, and auklets predominate in summer and fall over the entire Bering Sea shelf. Among the nondiving species, only light-phase fulmars, Black-legged Kittiwakes, and phalaropes reach high densities in local areas.

Figures 5a–5d demonstrate no clear relationships between birds and the biomass and productivity of either plankton or fish, although there is a weak correlation between herbivorous zooplankton levels and avian density. This suggests that numerical concentrations of birds depend on prey availability, which is in part determined by local patterns of circulation and by the structure of the water mass. Similar trends have been observed in the eastern Bering Sea (Schneider 1982; Kinder et al. 1983; Schneider et al. 1987).

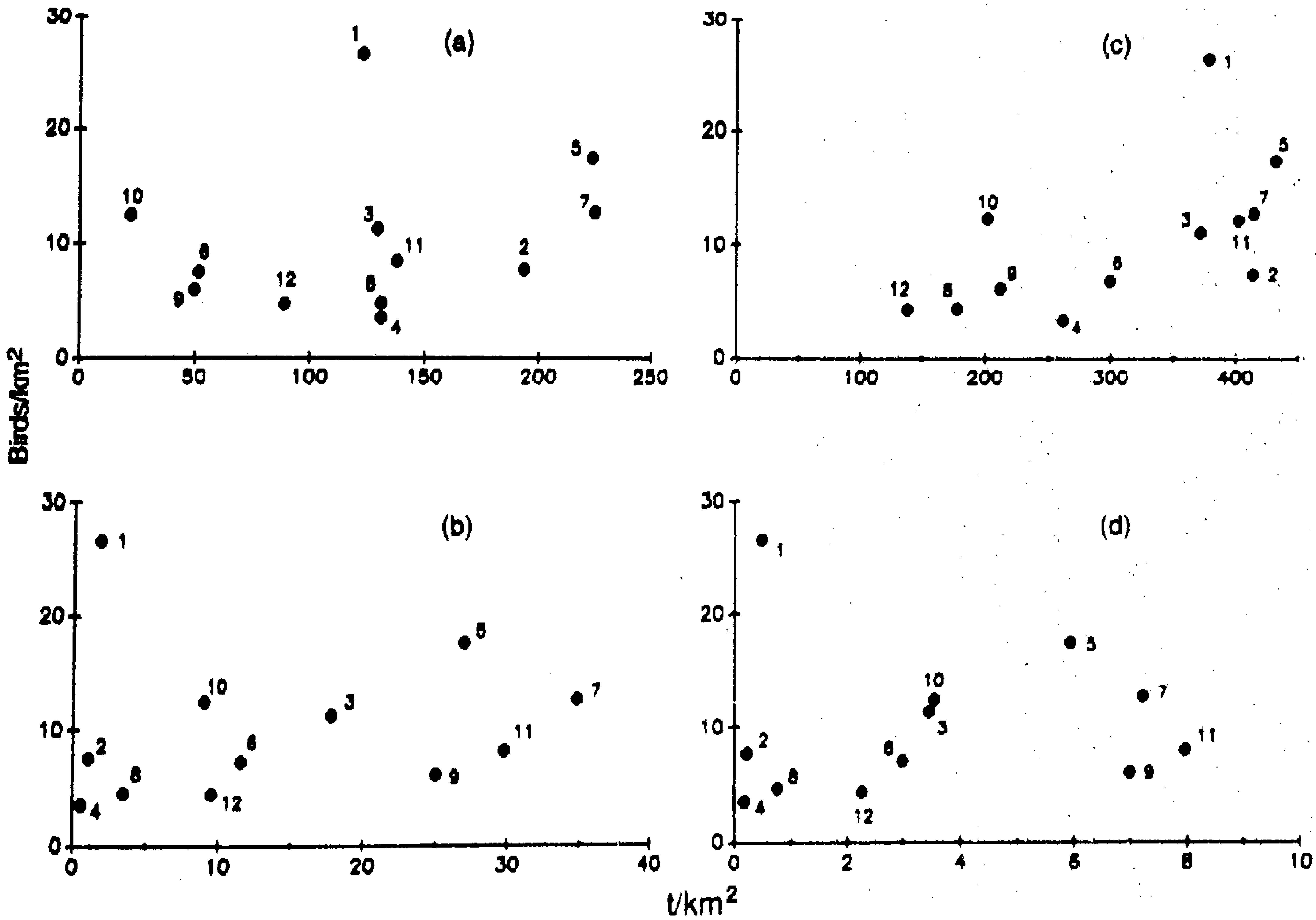
Secondary oceanic fronts, formed at the boundary between coastal isothermal waters and stratified waters of the middle shelf, are also important in the formation of seabird aggregations. Such frontal formations in the Bering Sea are oriented approximately along the 50-m isobath. Murres and shearwaters are most abundant along this front during spring in the eastern Bering Sea. Prey at these fronts are primarily euphausiids, obtainable only by diving (Schneider and Hunt 1982; Schneider et al. 1986). Apparently, the same frontal zones form at similar depths locally along the inner perimeter of Anadyr Bay. Specifically, in the areas located along the coast of Chukotskii Peninsula and in the western part of Anadyr Bay, where euphausiids form the major part of macroplankton, large accumulations of shearwaters are found during the second half of the year (Shuntov et al. 1988).

Secondary fronts around islands appear to have the same origin: i.e., they form between coastal isothermal waters and stratified offshore waters. For instance, a front of this kind forms along the 50–70-m isobaths in the vicinity of the Pribilof Islands (Kinder et al. 1983; Schneider et al. 1990). The existence of this front creates favourable foraging conditions for murres, but apparently other factors are involved in determining the distribution of prey and of birds. For example, there are no marked increases in fulmars or auklets at the front near the Pribilof Islands. The composition of food differs strongly within bird species that nest on the two main Pribilof Islands, St. George and St. Paul. Walleye pollock are the dominant prey of birds nesting on St. Paul Island, whereas euphausiids are most frequently taken by birds from St. George Island (Schneider and Hunt 1984). This suggests that the factors that influence the formation of food aggregations differ between islands.

Another frontal zone in the northern shelf area is located along the 100-m isobath. It is formed as a result of an interaction between warm waters of the central Bering Sea continental slope current and the cold waters of the stagnant zone, located between the 50-m and 100-m isobaths (Khen 1989; Markina and Khen 1990). However, this front has less of an influence on the quantitative distribution of birds than the front at the shelf break (Schneider 1982; Schneider et al. 1987).

It is clear that the existence of the boundary between waters of the continental slope and the shelf edge results in increased numbers of birds (Gould et al. 1982; Schneider and Hunt 1982; Schneider et al. 1987). As shown in Figures 3 and 4, the zone of elevated bird density closely follows the continental slope throughout the central part of the sea. As

Figure 5
Quantity of birds (birds/km²) and biomass (tonnes/km²) of macroplankton (a) and pelagic fish (b), seasonal productivity (tonnes/km²) of herbivorous zooplankton (c) and pelagic fish (d) in the western Bering Sea in autumn in 1986. Birds are shown on the ordinate, plankton and fish are shown on the abscissa. Numbers, beside each dot, refer to the following areas: 1. Bering Strait; 2. Western Anadyr Bay; 3. Central Anadyr Bay; 4. Eastern Anadyr Bay; 5. Southeastern Navarinskii area; 6. Inner shelf of the Olutorski-Navarin area; 7. Shelf edge and continental slope of the Olutorski-Navarin area; 8. Deep-water basin of the Olutorski-Navarin area; 9. Shelf edge and continental slope of the Olutorskii Bay; 10. Inner shelf of the Karaginskii and the Olutorskii areas; 11. Shelf edge and continental slope of Karaginskii Bay; 12. Commander Basins (Shuntov 1988a).



mentioned above, the increased productivity in these waters may be explained by a highly dynamic circulation caused by disturbances in the flow field under the influence of the complex bottom relief of the shelf break. Apparently, a band of productive waters formed at the shelf break converges locally into a frontal zone along the 100-m isobath; this in turn is reflected by the quantitative distribution of birds. The species that obtain food at the sea surface (i.e., fulmars, Fork-tailed Storm-Petrels, and gulls) form the major part of avian populations in the areas of the shelf edge and the continental slope.

In general, the mechanisms controlling the formation of high densities of plankton and other aquatic life have been insufficiently studied. However, it is known that plankton accumulate in convergences, local fronts, and eddies. Stable formations of conditions favouring high prey densities can be expected where circulation structures are caused by orographic effects. The Navarin area is one such place; high productivity of waters in this area is caused in part by a highly dynamic circulation that maintains a supply of nutrients to the photosynthetic zone, and in part by plankton accumulations in the area of the stable anti-cyclonic gyres and in the area where the Navarin Current moves onto the shelf (Khen 1989; Markina and Khen 1990). Likely in response to the above, large aggregations of planktivorous walleye pollock remain year-round in the Navarin area. In fact, one of the highest fish densities in the Bering Sea occurs in this area (Shuntov et al. 1988). In summer and fall, large numbers of birds, especially shearwaters, accumulate in the shelf and shelf-break areas in the Navarin region (Figs. 3 and 4). In contrast, beyond the shelf, numbers and overall density of birds decrease. In the zone of the anti-cyclonic gyre, elevated densities of fulmars and Fork-tailed Storm-Petrels are observed locally, largely due to the year-round presence of the fishing fleet on the shelf and at the shelf break in the vicinity of Cape Navarin.

Birds feeding on the sea surface also use other methods of obtaining prey that are not available under usual circumstances. Gulls and other species are frequently found near grey whales *Eschrichtius robustus* that feed at shallow depths in the northern Bering Sea (Harrison 1979). The more or less continual accompaniment of birds is most likely because of the many benthic animals and their fragments that are brought to the surface by the whales (Obst and Hunt 1990). During the summer there may be as many as 15 000 grey whales in the northern Bering Sea: their activity likely represents an important, alternate source of food for many birds.

Flocks of surface-feeding species frequently form temporary aggregations with diving species. Such aggregations feeding together have been described, for instance, in the vicinity of St. Matthew and St. George islands (Hunt et al. 1988; Schneider et al. 1990). Diving species such as murres, pursuing prey many metres below the surface, will often drive the prey animals to the surface, where they become accessible to kittiwakes, fulmars, and phalaropes.

Except for some avian species that feed mostly on benthos, most seabirds in the Bering Sea feed upon abundant planktivorous fish (young walleye pollock, capelin, sand lance, herrings) and/or crustaceans (euphausiids, amphipods, copepods, and others) and/or squid (Ogi and Tsujita 1973; Ainley and Sanger 1979; Schneider and Hunt 1984). Indicative of how enormous these stocks are, between 10 and 20 million shearwaters migrate each year from the southern hemisphere to the Bering Sea to exploit the abundant prey. However, the highly dynamic distribution and abundance of birds, even within a season, suggest that the richness and availability of prey do not always remain high.

As emphasized throughout this paper, the actual foraging conditions depend to a large degree not only on the general oceanic background and the specific biology of each species, but also on the fine-scale oceanographic features. The study of seabird ecology in this sense has just begun; large-scale surveys that are currently practised are ineffective, even if they are of a sophisticated design. Further progress in the study of patterns in seabird distribution and formation of aggregations will largely depend on the results of detailed field tests and small-scale surveys. In order for future studies to successfully determine the mechanisms responsible for the observed patterns of seabird and prey distribution, a multidisciplinary approach must be adopted.

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