The pelagic distribution of marine birds in a heterogeneous environment

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In this paper I review recent, small-scale, process-oriented studies of the pelagic distribution of marine birds. I examine the roles played by a variety of hydrographic features, including steep flow gradients (fronts) and water column stratification, in determining the abundance or availability of avian prey. The ice edge/marginal ice zone is a frontal area of particular interest in polar regions. In most oceanic systems we have examples of avian use of a feature, but only poor information on the importance of the feature for supporting the population as a whole. I review recent studies of the spatial and numerical concordance of marine birds and their prey, and find that these studies have yielded mixed results, with correlations stronger for piscivorous birds, particularly murres foraging on capelin, than for planktivores. Review of investigations of multispecies interactions during foraging shows that flock foraging has both beneficial and negative aspects. Interspecific facilitation of foraging occurs in numerous interactions involving both other species of birds and marine mammals. However, co-occurrence of predators may occur because both seek the same prey, and caution must be used in assessing mutualistic interactions between predatory species.

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Recently, Hunt & Schneider (1987) examined the similarities in distribution and abundance patterns of zooplankton and seabirds at a variety of spatial and temporal scales. In their review, it was apparent that mapping of seabird distributions at the scale of major portions of the world ocean has given way to more detailed studies of birds and oceanographic processes at the scale of tens to hundreds of kilometers. In this review, I focus on recent smaller-scale, process-oriented studies, many of which have been published since Hunt & Schneider (1987) was compiled.

The ultimate goal of pelagic studies of marine birds is to understand the processes underlying the observed distribution and abundance of birds at sea. These processes include three related elements: 1) aspects of the physical regime that result in either the passive accumulation of prey or increased production of prey, 2) the amount and type of prey present and its availability, and 3) interactions with other organisms that enhance a bird's ability to locate prey or that result in competition for the prey, once found. In the ideal study of seabirds at sea, we would like to measure simultaneously hydrographic structure and process, as well as the distribution and abundance of both predators and their prey. Usually it is not possible to obtain a complete suite of these data. Often, therefore, we must infer the processes responsible for the observed patterns. In particular, when we lack information on prey abundance and the behavior of foraging individuals, we must assume that variations in prey availability are responsible for the observed variations in seabird abundance.

Estimating the importance of features

Within the larger geographic areas that constitute the water types or habitats occupied by seabirds, seabirds are not uniformly distributed (Ashmole 1971; Shuntov 1974; Ainley & Boekelheide 1984; Schneider et al. 1988). This patchiness is frequently associated with physical processes that vary in spatial scale from relatively small Langmuir cells to fronts associated with continental shelf slopes and major ocean currents (Hunt & Schneider 1987; Brown 1988). When concentrations of foraging birds frequently associate with some feature, we infer that this feature is the location of a major trophic transfer of energy to birds. The question remains whether these foraging areas are the most important sites for trophic transfer, or if the majority of trophic transfer occurs through individual birds scattered, seemingly at random, over the ocean. For instance, in a study of birds in the vicinity of the ice edge in the Canadian High Arctic, McLaren (1982) found that the majority of birds were foraging offshore, even though densities were often higher along the edge of the land-fast ice.

We infer that we have identified correctly important trophic pathways and the physical processes responsible for creating the preferred foraging habitats when there is repeatability of results between locations with similar physical features, or between years at the same feature. For example, phalaropes (*Phalaropus*) during their 'pelagic' stage have been found to concentrate at frontal areas and upwellings associated with major boundary currents off California (Briggs et al. 1984), Peru (Brown 1980a), the southeastern (Haney 1985) and northeastern United States and Canada (Orr et al. 1982; Powers 1983) and the Canary Current in the eastern tropical Atlantic (Brown 1979; Cadee 1981) (see also Brown 1988 for other references). Several of these studies were based on multiple visits to an area over a period of two or more years. In this instance we can have considerable confidence that we have identified the most important marine habitat of this avian group.

Migrant shearwaters (*Puffinus* spp.) in the North Pacific, like the phalaropes, are associated with shelf waters offshore of coastal upwelling systems (Briggs & Chu 1986; Briggs et al. 1987). At least in California, these birds are not found in the coldest, most recently upwelled water, but farther offshore, possibly associated with convergences near the shelf edge (Briggs & Chu 1986). In the Bering Sea, their greatest numbers are generally in the vicinity of the front between the stratified waters of the middle domain and the well-mixed waters of the inner domain (Hunt et al. 1981; Schneider 1982; Schneider et al. 1986; Guzman & Myers 1987). Within this region of the Bering Sea, the shearwaters are extremely patchy in distribution and we have no data on the factors controlling patch size or the small-scale distribution of flocks.

Hydrographic structures

One of the most robust generalizations concerning the distribution of seabirds on continental shelves is that cross-shelf gradients in seabird distributions are consistently stronger than long-shelf gradients. This pattern reflects the underlying physical regimes. Recent studies in the Bering Sea (Iverson et al. 1979; Schneider & Hunt 1982; Schneider et al. 1986; Schneider et al. 1988), the eastern Pacific Ocean off California (Briggs et al. 1987; Briggs et al. 1988), the Western Atlantic Ocean off the southeastern United States (Haney & McGillivary 1985b) and the Benguela Current off southern Africa (Schneider & Duffy 1985; Schneider et al. 1988) provide examples of seabird distributions that change in response to frontal systems parallel to continental shelf bathymetry. In each of these systems, going from nearshore waters to offshore waters, one crosses a series of watermasses separated by fronts. The watermasses typically differ in their temperature and salinity characteristics. Additionally, hydrographic structure, driven by a combination of bathymetry and currents, may differ between watermasses. As a result, adjacent water masses frequently have different prey communities and trophic pathways.

The southeastern Bering Sea provides an example of a 500 km wide shelf system that is partitioned into three domains (Iverson et al. 1979; Coachman 1986). Plankton and fish communities trap a substantial portion of the primary production in a pelagic food web in the outer shelf domain, but in the middle domain much of the carbon settles to the bottom (Walsh & McRoy 1986). As a result, seabirds in the middle domain are primarily subsurface foragers and those in the outer domain are surface foragers (Schneider & Hunt 1982; Schneider et al. 1986).

Currents may also carry different prey communities into an area. In the northern Bering Sea, currents of different origin establish three distinct marine habitats (Coachman et al. 1975; Kinder & Schumacher 1981). Unlike the southeastern Bering Shelf, bathymetry is not the major determinant of watermass boundaries in the region between St. Lawrence Island and the Bering Strait. The various watermasses support strikingly different zooplankton communities. These differences are reflected in the foraging and breeding distributions of seabirds in the northern Bering Sea and the Chukchi Sea (Springer & Roseneau 1985; Springer et al. 1984, 1987; Hunt & Harrison unpublished).

Other ocean systems also provide examples of shifts in seabird food webs between water masses. In the Barents Sea, Belopol'skii (1961) showed that Arctic cod (*Boreogadus saida*) are of prime importance to seabirds in the eastern sector which is dominated by Arctic Water. In the western Barents Sea, in which warmer North Atlantic Current Water is present, Sandlance (*Amodytes spp.*), Capelin (*Mallotus villosus*) and Herring (*Clupea harengus*) are the primary fish taken by birds. Similarly, in the North Sea, there are dramatic changes in trophic paths to seabirds, depending upon whether the birds are foraging in North Atlantic or North Sea Water (Joiris 1983).

Within the above and other shelf systems, steep flow gradients (fronts) have frequently been identified as important foraging areas for birds (e.g. Brown 1980a; Schneider 1982; Kinder et al. 1983; Haney & McGillivary 1985a, b; Veit 1985; Schneider, Harrison & Hunt 1990; Schneider, Pierotti & Threlfall 1990; Abrams & Lutjeharms 1988). The importance of hydrographic features that enhance prey availability can be particularly great near colonies and foraging distributions around colonies are likely to be patchy (Ford et al. 1982), reflecting local oceanographic conditions. Competition for food near large colonies is strong (Gaston et al. 1983; Furness & Birkhead 1984; Birkhead & Furness 1985; Hunt et al. 1986) and in some instances prey abundance is depressed (Birt et al. 1987). Evidence is accumulating that alcids at many colonies concentrate their foraging at a limited number of sites near the colony where currents or tidal flows concentrate or force prey toward the surface often in a frontal structure (Kinder et al. 1983; Cairns & Schneider 1990; Schneider, Harrison & Hunt 1990; Schneider, Pierotti & Threlfall 1990). In polar regions, ice edge habitats near colonies may be particularly important 'frontal' areas in which prey availability is enhanced (Brown & Nettleship 1981). Understanding factors affecting seabird foraging in the vicinity of colonies is particularly important, as a lack of success can affect reproductive success. Thus, this area of research is of interest not only to students of the pelagic biology of marine birds, but also to a growing number of workers on colonies (e.g. Wanless et al. 1985; Trivelpiece et al. 1986; Croxall et al. 1988).

Many studies of birds at fronts rely on one to a few crossings of the physical structure in question, and the possibility that the reported observation of elevated numbers of birds was a coincidence or a rare event cannot be ignored, Schneider et al. (1987) addressed this question by testing whether larger numbers of birds were found at Bering Sea shelf fronts than over adjacent waters. In an examination of 62 crossings of fronts, densities of birds were not significantly greater at the fronts, on average, than over nearby waters. However, these authors found that those fronts with the steepest flow gradients had elevated numbers of birds present more frequently than weaker flow gradients. Although this result provides an important insight into habitat use by marine birds, it is not clear whether strength or predictability of strong flow gradients is the more important factor. Numerous examples exist of predictable, but temporally varying tidally generated flow gradients that are important foraging areas for local populations (e.g. Brown 1980a, b; Braun & Gaskin 1982; Vermeer et al. 1987; Brown & Gaskin 1988; Cairns & Schneider 1990).

Hydrographic structure may be important in the vertical dimension as well as the horizontal. When water of a lower density rests atop more dense water, the result is increased stability and reduced mixing in the vertical dimension. Stable vertical structure has important consequences for planktonic organisms which may concentrate at sharp property gradients (Harder 1968; Barroclough et al. 1969). Hunt et al. (1990) have shown that Least Auklets (*Aethia pusilla*) in the northern Bering Sea forage in stratified water where echosurveys have revealed concentrations of zooplankton at and above a shallow pycnocline. When the water lacks stratification, even if prey are apparently abundant close to a colony, the auklets fly to more distant but stratified waters where the prey are at higher densities close to the surface.

Strong winds are capable of mixing surface waters to considerable depth, thereby deepening the pycnocline and diluting near surface concentrations of plankton. Lasker (1979) suggested that such mixing decreased recruitment of first-feeding larval northern anchovies (*Engraulis mordax*) (Peterman & Bradford 1987), a prey of Xantus' Murrelets (*Synthliboramphus hypoleuca*) (Hunt & Butler 1980). Hunt & Butler found that in a year of high winds and low anchovy survival, murrelet breeding was considerably delayed (see also Lasker 1979). Decreased foraging rates of both plunge divers (e.g. Salt & Willard 1971; Dunn 1973) and pursuit divers (e.g. Birkhead 1976) as a function of wind speed may reflect increased difficulty in obtaining prey from a greater volume of water as well as greater difficulty in flying or spotting prey. The potential importance of vertical as well as horizontal structure in defining seabird foraging habitats is only just becoming apparent.

The ice edge and marginal ice zone

Ice cover is a physical feature of major importance to marine birds in high latitude oceans. Ice cover determines access to resources, provides a refuge from aquatic predators, and in some situations contributes to enhanced prey abundance. In the last decade, our understanding of the processes whereby sea ice influences marine bird populations has increased greatly, but overall, we still lack sufficient data to assess the magnitude of the contribution of ice-related productivity to seabird populations.

The presence of extensive ice cover can prevent marine birds from acquiring adequate food resources. Unlike seals that maintain breathing holes through the ice, marine birds at high latitudes do not maintain openings, and with the occasional exception of some gulls (*Laridae*) and skuas (*Stercorariidae*), marine birds are rarely present in areas of 100 percent ice cover. When not breeding, marine birds can shift their distribution to avoid excessive ice cover, and in some cases they aggregate near the edge of the ice while waiting for it to melt (Divoky 1979, 1981). In areas of heavy ice cover, polynyas (areas of open water surrounded by ice) may be of critical importance to breeding (and wintering) birds (Stonehouse 1967; Stirling 1980; Brown & Nettleship 1981; Dunbar 1981). In the Northern Hemisphere, virtually all large colonies of seabirds in the North American and European Arctic are adjacent to recurring polynyas (Brown & Nettleship 1981). The importance of open water near colonies is emphasized by the observations of Nettleship et al. (1984); in a year of unusually heavy ice cover in Lancaster Sound, Canadian High Arctic, breeding of Thick-billed Murres (*Uria lomvia*) was delayed by three weeks.

Under certain circumstances, sea ice may enhance foraging opportunities for marine birds. In both the Arctic and the Antarctic, there is a diatom flora associated with sea ice and an under-ice or epontic community of zooplankton that forages on exposed ice algae (Alexander & Chapman 1981; Dunbar 1981; Bradstreet & Cross 1982; Smith et al. 1985; Garrison et al. 1986). Additionally, in the late winter and early spring, these ice algae provide an innoculum for an algal bloom that occurs in the open water of the marginal ice zone (McRoy & Goering 1974; Schandelmeier & Alexander 1981; Smith & Nelson 1985, 1986). The melting of ice creates water column stability via a sharp pycnocline below low-salinity meltwater (Buckley et al. 1979; Alexander & Niebauer 1981; Niebauer & Alexander 1985; Smith & Nelson 1986; Müller-Karger & Alexander 1987; Smith 1987). Additionally, at least in the Arctic, upwelling of nutrients at the ice edge occurs due to wind forcing, thereby creating the physical conditions conducive to a strong algal bloom. Marine birds in the Arctic and the Antarctic forage on food webs based on the epontic algae (Bradstreet 1980, 1988; Bradstreet & Cross 1982; Fraser & Ainley 1986). Birds also take mesopelagic organisms that come near the surface under the ice, possibly due to reduced light levels (Gulliksen 1984; Ainley et al. 1986). Birds foraging near the ice edge presumably benefit from a concentration of prey organisms at the ice-water interface beneath the ice, a situation in which prey cannot easily escape avian predators (Bradstreet 1988).

In the Antarctic, marine birds forage on a food web based on the algal bloom seaward of the ice edge (Fraser & Ainley 1986). Use of this portion of the marginal ice zone by birds has not been studied in the Arctic. However, given the potentially vast size of the open water portion of the marginal ice zone (up to 250 km wide in the Antarctic, Smith & Nelson 1986), one might expect that its contribution to marine birds would be even greater than that of the ice edge and epontic system. This prediction is based on the assumption that algal production is cropped by pelagic zooplankters. If these primary consumers are scarce and pelagic fish largely unavailable (e.g. the middle domain of the Bering Sea, Iverson et al. 1979; Cooney & Coyle 1982; Coyle & Cooney 1988), foraging in the open sea portion of the marginal ice zone should not be especially profitable and enhanced numbers of birds would not be expected.

Considerable evidence points to the importance of the ice edge as a foraging zone for high latitude seabirds. In the Canadian High Arctic, foraging seabirds concentrate at the ice edge (Bradstreet 1979, 1982, 1988; Divoky 1981) and Thick-billed Murres fly up to 100 km from their colonies over open water to forage at the ice edge (Bradstreet 1979). In the Barents Sea, there are similar long distance movements over water to the ice edge (V. Bakken pers. comm.). In the Antarctic, evidence is accumulating that the ice edge is an area in which birds concentrate, but the picture appears less clear than it is in the Arctic. In the Weddell Sea, Fraser & Ainley (1986) observed concentrations of birds and avian biomass near the ice edge, but in the Ross Sea, Ainley & Jacobs (1981) found peaks in avian biomass at the ice edge on only one of five transects (their Fig. 3a-e). Because the Ross Sea ice edge was over the edge of the continental shelf, it is difficult to assess the relative importance of the ice or shelf edge to birds. Ainley & Jacobs suggest that both factors work together, as did Eppley & Harrison (1985), who found an elevated number of birds when the ice edge was coincident with the shelf edge near Wilkes Land. Seabird distributions are patchy along the ice edge (Bradstreet 1982; Bakken & Hunt unpublished), and vary in response to factors such as wind velocity and the amount of pack ice present seaward of the edge of land-fast ice (Bradstreet 1979; McLaren 1982). This patchiness confounds our ability to assess the importance of the ice-edge habitat when survey efforts are limited to one or a few transects across the ice edge zone.

Assessment of the importance of the ice edge as a foraging zone for seabirds is complicated by the difficulty in delimiting the area of concern from adjacent areas. When there is a sharply defined interface between open water and continuous land-fast ice, only the seaward boundary of the 'ice edge' zone need be defined. When ice is breaking up and extensive areas of pack ice are involved, there may be a wide zone grading from open water to solid ice cover with no clearly defined edge. The term marginal ice zone has been used to refer to this zone (see Smith 1987). However, the zone of stratified water seaward of the ice edge that results from stability imposed by low-density melt-water is also a part of the physical regime that results in enhanced productivity in the marginal ice zone. Thus, in examining the contribution of sea ice to avian food resources, it is necessary to include the entire region from the seaward edge of this zone of stratified water to water completely covered by ice. To date, there are no published data, of which I am aware, that compare the relative importance to bird populations (total bird use) of unstratified waters seaward of the marginal ice zone, stratified water in the marginal ice zone and the use of open water within the pack ice. Regardless of this lack, it is increasingly clear that the marginal ice zone is a frontal system of great significance to marine birds.

Marine birds in relation to prey resources

In recent examinations of the distribution and abundance of birds in relation to prey resources, the working hypothesis has been that predators should aggregate where prey are most abundant. Several assumptions are implicit in the formulation of this hypothesis: (1) There is a close coupling between prey abundance and prey availability, (2) the predators are good at detecting prey and evaluating the relative value of prey patches, and (3) predators do not deplete prey patches prior to measurement of prey abundance. The validity of these assumptions has not been tested.

Correlation between predator and prey abundance has been sought for both planktivorous and piscivorous species of birds, using a variety of echosounding techniques for measuring prey abundance. For the most part, measures of the abundance of plankton prey explain only a small portion of the variance in seabird abundance, while in contrast, measures of fish abundance have explained large portions of the variance in the abundance of avian piscivores. The strength of correlation in most cases is sensitive to the scale at which measurements are taken.

One of the first studies of marine bird distribution with respect to planktonic prey was Obst's (1985) investigation of the abundance of marine birds in Bransfield Strait, Antarctica, with respect to the abundance of Antarctic krill (*Euphausia superba*). Obst used a ship's depth finder as a semi-quantitative measure of krill abundance. He found that avian density and biomass were higher in waters where krill were present, and, for three species of birds and for all birds combined, the probability that krill was present increased with increasing bird density. However, Obst was unable to predict bird density on the basis of relative abundance or depth of krill. In contrast, Woodby (1984) in a study of murres (*Uria spp.*) in relation to prey in the Bering Sea, found significant rank correlations between the density of murres and that of euphausiids (*Thysonoessa spp.* and *Euphausia pacifica*) in one of two years.

In the second year, no correlation was found between murres and euphausids, and Woodby concluded that murres were able to catch sufficient prey in the low density aggregations of prey. He suggested that it might not be energetically efficient for murres to seek the densest patches of prey.

Subsequent to these early studies of seabirds and euphausiids, Heinemann et al. (1989) and Hunt et al. (unpublished) undertook studies of seabirds and krill in Antarctica, and Hunt et al. (1990) examined the abundance of Least Auklets with respect to the abundance of copepods (*Neocalanus spp.*) in the northern Bering Sea. Using quantitative echosurveys of krill in conjunction with counts of birds in Bransfield Strait, Antarctica, Heinemann et al. (1989) determined the frequency of miles of survey in which both birds and krill were present (spatial concordance) and correlations of abundance within the spatial units in which both predators and their prey were present (numerical concordance). They found that seabirds of two species, Cape Petrels (*Daption capensis*) and Antarctic Fulmars (*Fulmarus glacialoides*), showed spatial concordance with krill but only Adelie Penguins (*Pygoscelis adeliae*) and Cape Petrels showed significant correlations with krill abundance. Correlations were found over a range of spatial scales from nautical mile intervals to scales of hundreds of nautical miles. Generally, correlations (up to 0.99) were stronger at the larger scales, but few were statistically significant.

Near Bird Island, South Georgia, Hunt et al. (unpublished) found positive correlations between Antarctic krill and Antarctic fur seals (*Arctocephalus gazella*), Macaroni Penguins (*Eudyptes chrysolophus*) and Black-browed Albatrosses (*Diomedia melanophris*). However, when the confounding variables of distance and direction from the colony on Bird Island were factored out, Hunt et al. were able to demonstrate an additional influence of krill abundance on predator abundance for fur seals only.

In the northern Bering Sea, Least Auklets forage on copepods and other small zooplankton found in stratified water 15–55 km offshore of their island colonies (Hunt et al. 1990). Rank correlations between the abundance of these predators and echosounder estimates of prey abundance were strongest for prey in the portion of the water column above the thermocline. In four out of five cases, correlations between bird and prey abundance appeared stronger when scales of measurement were increased from 1–2 nautical miles to 5–12 nautical miles, although due to sample size considerations, the number of statistically significant correlations dropped at the larger measurement interval. At a measurement interval of 1–2 nautical miles the average of five R^2 values was 0.25, while for the 5–12 nautical mile intervals it was 0.68. Thus, as in the case with the Heinemann et al. (1989) study of seabirds and krill in Bransfield Strait, explained variances were improved at larger measurement intervals.

In the northern hemisphere, several investigators have attempted to determine the strength of correlations between seabirds and forage fish. Safina & Burger (1988), after an initial failure to detect an influence of forage fish density on Common Tern (*Sterna hirundo*) density (Safina & Burger 1985), found in a multiyear study that Common Tern flock size increased with a number of measures of increasing prey abundance and prey availability (e.g. density, relative abundance in the upper water column). This study is the first to demonstrate statistically significant correlations between a surface foraging seabird and forage fish, although the correlations are generally fairly weak, and the statistical significance of the correlations was driven by the large numbers of tern flocks investigated. The study did not address the problem of the correlation between seabirds and their prey throughout a potential foraging area because their study was focused on foraging flocks and sampling was not independent of bird distribution. In general, we may expect difficulties in associating surface foraging birds with prey density using echosounding surveys of prey because the echosounders are unable to record prey in the top one to ten meters of the water column, depending upon the system used.

Two investigations of the distribution and abundance of Common Murres (*U. aalge*) and Atlantic Puffins (*Fratercula arctica*) with respect to capelin abundance have yielded strong correlations between these birds and their prey (Schneider & Piatt 1986; Piatt 1990; Erikstad this volume). In work in the Avalon Channel between Newfoundland and the Grand Banks, Schneider & Piatt found significant positive correlations between murre and capelin abundance on four out of six transects. Scale-dependent correlations between predators and prey occurred on two transects for murres and three transects for puffins, with correlations increasing at larger measurement distances. Piatt (1990), reporting on a longer series of observations, including many in the immediate vicinity of the large Common Murre and Atlantic Puffin colonies (about 74,000 pairs of each) in Witless Bay, Newfoundland, found that the abundance of both murres and puffins increased each year in late June when spawning schools of capelin arrived inshore. Thereafter, there was a strong temporal correlation between the abundance of capelin and the abundance of these alcids. Piatt found that murres (68% of 63 surveys) and puffins (54% of 70 surveys) were significantly correlated with capelin at a measurement scale of 0.5 km and correlations grew increasingly stronger with increasing measurement interval on 35% of murre and 27% of puffin surveys. Interestingly, Piatt also found evidence for a threshold effect in prey density. A maximum correlation in the regression of bird and capelin densities occurred at an intermediate density of capelin; the value of the threshold was higher for murres than it was for puffins. The value of the threshold also varied with background values of prey abundance. Erikstad (this volume) also has found scale-dependent correlations between Common Murres and capelin wintering in the Barents Sea. In contrast, in the Bering Sea, Woodby (1984) found no indication that murre abundance varied in response to the large-scale distribution or abundance of schooling fish.

In some cases, most of the individual birds seen in a long-term, wide-ranging study may be concentrated in one or more very large foraging aggregations. For instance, Hunt et al. (1985) found 76% of all Adelie Penguins seen during a 20 day period in one foraging flock and 62% of all Cape Petrels and 62% of all Antarctic Fulmars seen over the same period in another foraging flock. In this instance, rare large aggregations of foraging birds associated with unusually large patches of Antarctic krill were responsible for the vast majority of foraging seen over an extended period. Thus, large patches of prey may be of disproportionate importance to foraging birds.

Two features are common to the results of most studies of seabirds in relation to prey abundance. First, in all studies where measurement scale was investigated, correlations between these predators and their prey were scale dependent and showed stronger correlations at measurement intervals greater than the minimum. Consequently, survey designs must be large enough to encompass the largest scales at which interactions between seabirds and their prey are likely and single measurement distances may fail to reveal significant interactions (Schneider & Piatt 1986). Secondly, in several studies it was apparent that significant correlates between predators and prey were intermittent and that repeated surveys were necessary for detection of correlations (Schneider & Piatt 1986; Safina & Burger 1988). Additionally, studies focusing on diurnally foraging birds (e.g. alcids) appear to have been more successful in finding positive correlations than those focusing on Southern Hemisphere predators that take krill. Many of these krill predators take the majority of their prey at night (Croxall et al. 1985, 1988; Fraser et al. unpublished) when krill migrate to near-surface waters (Mauchline 1980; Everson 1983; Loeb & Shulenberger 1987). Most hull-mounted echosounders are unable to detect krill within 10–20 m of the water's surface. Thus given the difficulties of detecting krill near the surface and counting foraging birds at night, it is possible that surveys of krill predators and krill are unlikely to yield strong correlations at small scales of measurement except under unusual circumstances (e.g. Hunt et al. 1985). These problems not withstanding, efforts to correlate avian predators and zooplankton prey seem to yield lower correlation values, particularly at small scales, than surveys of fish-eating birds and their prey. It is possible that the planktivorous birds are less able to locate the densest patches of prey. Alternatively, they may not need to seek the densest patches if background densities or the frequency of micropatches of prey at high densities are sufficiently great (Woodby 1984; Hunt et al. 1990).

Multispecies interactions during foraging

Although seabirds in many cases search for food over very large areas, feeding events occur at the very small scales of individual prey patches (Duffy 1983; Hunt & Schneider 1987). The location of individual prey patches in a comparatively vast area of foraging habitat is particularly challenging if the prey sought are out of sight well beneath the surface. Surface manifestations of the presence of prey are important to searching birds; for instance, the presence of feeding birds can often be detected from a long distance (Simmons 1972; Bayer 1983; Götmark et al. 1986). Foraging birds can locate feeding birds either directly by observing the behavior of nearby birds that have located prey, or indirectly by responding to changes in the behavior of birds moving toward a foraging flock (network foraging, Wittenberger & Hunt 1985). Birds at a colony also obtain information about the location of prey from birds returning to or departing from the colony (e.g. Gaston & Nettleship 1981).

The importance of using foraging birds as indicators of available food should not be underestimated. In at least some situations, foraging flocks account for the majority of all individuals seen feeding (e.g. Duffy 1983; Hunt et al. 1985, 1988). The dynamics of these flocks are thus of importance in determining the trophic linkages between seabirds and the marine environment. In particular, to the extent that birds choose to join others that are already foraging in preference to foraging independently, the first birds to commence feeding will influence the type of prey taken and the size of patch exploited by the joiners.

Many foraging flocks consist of more than one species, and the roles played in the flocks differ between species (Sealy 1973; Hoffman et al. 1981; Duffy 1983). Some bird species serve as 'nuclear' (Sealy 1973) or 'catalyst' species (Hoffman et al. 1981), while others are late joiners or even disrupters of the flocks. In some cases, there is evidence that subsurface foragers drive prey to the surface, which is then available to surface foragers (Sealy 1973; Grover & Olla 1983); in other cases organisms injured by birds foraging deep in the water column drift to the surface where they are taken by nondiving species (Hunt et al. 1988; Schneider, Harrison & Hunt 1990). Götmark et al. (1986) found that, for captive gulls foraging on live fish in a shallow pool, fishing success of individual gulls improved with increasing flock size up to at least eight gulls. The presence of numerous foraging birds broke up the protective schooling of the fish (Shaw 1978). Additionally, they found that a greater proportion of captures was from the front or side of the prey when the flock was present than when a single gull was foraging. Thus, a variety of synergistic interactions is possible within foraging flocks.

Interactions between bird species in foraging flocks can also lead to displacement of one species by another. Hoffman et al. (1981) describe how large numbers of shearwaters (*Puffinus spp.*) joining a flock can disrupt foraging by other bird species present. Likewise, Duffy (1986) provides evidence of Common Terns displacing Roseate Terns (*S. dougalli*) to the edge of dense foraging flocks. Larger-sized birds may monopolize the center of foraging flocks where food is densest, but smaller species are still able to forage at the periphery (Duffy 1983). Kleptoparasitism (Hatch 1975) is a highly visible negative effect of joining a flock for the bird that loses its prey. However, the percentage of attacks that result in the attacked bird losing its prey may be fairly small, and thus this penalty for joining a flock may be relatively small compared to the advantages of flock foraging (Bayer 1983).

Marine birds also associate with marine mammals (Evans 1982; Burger 1988). Evans (1982) cites several examples of birds obtaining prey that whales had concentrated and driven to the surface. He describes instances in which various species of dolphins herding fish near or at the surface were converged upon by gannets (*Sula bassana*) which then dove in the areas where the prey were concentrated. Seabirds near the subantarctic Crozet Islands join killer whales (*Orcinus orca*) in order to scavenge floating offal (Ridoux 1987), but in other areas killer whales are not usually joined by birds (Evans 1982; Bering Sea, Hunt personal observation). Grey whales (*Eschrictius robustus*) in the Bering Sea forage on amphipods living in the bottom sediment and expel clouds of mud containing amphipods and fragments of amphipods at the surface. Several species of birds take advantage of this otherwise unavailable resource (Harrison 1979; Obst & Hunt 1990). In the Chirikov basin, 87% of all Red Phalaropes (*Phalaropus fulicarius*) and Black-legged Kittiwakes (*Rissa tridactyla*) seen foraging were at grey whale mud plumes, suggesting that, for at least some bird species in this region, whales provide access to a significant source of food (Obst & Hunt 1990).

In many instances, birds and mammals take similar prey, and their presence together may result from independent aggregation to forage on a particular prey (Evans 1982). For instance, Au & Pitman (1986) conclude that the statistically significant positive association between birds and dolphins is the result of a 'common attraction to food made available by feeding yellowfin tuna (*Thunnus albacares*)'. Interestingly, only in the eastern tropical Pacific, where surface-foraging schools of yellowfin commonly occur, were birds frequently found with dolphins. Elsewhere in the central and western Pacific where surface foraging yellowfin are rare, birds were not commonly associated with dolphins. Birds also seldom flock with species of dolphins that rarely associate with yellowfin. The flocks associated with the dolphins in the tropical waters of the eastern tropical Pacific were generally multispecies aggregations of boobies (*Sula spp.*), Wedge-tailed Shearwaters (*Puffinus pacificus*), Sooty Terns (*Sterna fuscata*) and jaegers (Au & Pitman 1988). In contrast to the multispecies flocks of the eastern tropical Pacific, Au & Pitman (1988) found that Equatorial and Southern Subtropical Waters supported primarily single-species flocks of Sooty Terns which were not associated with dolphins. These reports suggest that extreme care must be exercised in assuming that interactions between seabirds and marine mammals are the result of birds following the mammals in order to locate food.

Summary

Over the past decade, marine ornithologists have made considerable progress in relating variations in the pelagic distribution and abundance of marine birds to physical and biological aspects of the marine environment. Attendance of birds at fronts in the open sea and at the ice edge are well documented, and at least in some cases, water-column stratification is important. However, for most of these features, we have little information on their overall significance for trophic transfer to marine birds. In at least one case, the inter-domain fronts of the southeastern Bering Sea, fronts were not attended by higher numbers of birds than expected by chance. Although we assume that birds attend various physical features because prey is either more abundant or more available at them, we have relatively few data on the distribution of prey at an appropriate measurement scale. Those studies investigating the spatial and numerical concordance between marine birds and their prey have found some instances of strong concordances and others in which prey distribution and abundance were of little or no value in predicting bird abundance. This is an area of study in which we need more information linking birds, prey and physical features. Additionally, study of systems in which prey abundance has been severely reduced (such as the Barents Sea capelin fishery) and predators are abundant relative to prey stocks should be of particular interest for revealing the ability of predators to locate prey. In comparison, when prey are abundant relative to predators, the extent to which predators seek the densest prey patches appears to be reduced. Under these circumstances, correlations between avian abundance and prey abundance are often considerably stronger at large than at small scales of measurement. The propensity of marine birds to join foraging birds or marine mammals can influence the extent to which the abundance of foraging marine birds will correlate with prey abundance at small scales. Participation in mixed-species foraging assemblages may result from chance associations while pursuing the same prey. Although in some cases the result is competitive interactions, in a number of mixed-species flocks interactions are beneficial to one or more species. Our knowledge of the extent and persistence of mixed-species assemblages is as yet poor. We need to know which species regularly co-occur over wide portions of their ranges and how these species interact when foraging. In many of the areas of study reviewed, we have only begun to answer the larger questions of how the observed interactions with physical and biological aspects of the marine environment influence trophic transfer at the level of populations. Beyond this, we have not yet begun to relate the foraging success of the birds to the ultimate question of their survival or reproductive success.

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