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Marine Ecology of Seabirds in Polar Oceans¹

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SYNOPSIS. Patterns of seabird species' distributions differ between the Antarctic and the Arctic. In the Antarctic, distributions are annular or latitudinal, with strong similarities in species composition of seabird communities in all ocean basins at a given latitude. In the Arctic, communities are arranged meridionally, and show strong differences between ocean basins and, at a given latitude, between sides of ocean basins. These differences between the seabird communities in the Northern Hemisphere and the Southern Hemisphere reflect differences in the patterns of flow of major ocean current systems. At smaller spatial scales, in both hemispheres the species composition of seabird communities is sensitive to changes in watermass characteristics.

The distribution of avian biomass is affected by both physical and biological features of the ocean. In the Antarctic, much seabird foraging is over deep water, and within-season, small-scale patchiness in prey abundance and availability in ice-free waters is likely to be controlled primarily by the behavior of the prey, rather than by physical features. Thus, prey availability may be unpredictable in time and space. In contrast, in the Northern Hemisphere, most seabird foraging is concentrated over shallow continental shelves, where currents interact with bathymetry to produce predictable physical features capable of concentrating prey or making prey more easily harvested by seabirds.

Ice cover appears to be the most important physical feature in the Antarctic. An entire community of birds is specialized to use prey taken near the ice edge. These prey consist of a variety of species, some of which are normally found much deeper in the water than the birds taking them can dive. The open-water portion of the marginal ice zone is also an important foraging habitat for Antarctic marine birds. In the Arctic, a food web based on underice algae is used by marine birds, but few if any data exist on avian use of the open water segment of the marginal ice zone.

Recent simultaneous surveys of birds and their prey indicate that only rarely does the small-scale abundance of birds match that of their prey; correlations between predators and prey are generally stronger at larger scales. Evidence is accumulating in the Antarctic that the largest aggregations of krill may be disproportionately important to foraging seabirds.

INTRODUCTION

High-latitude oceans provide exceptional opportunities for studying the linkages between marine birds and the ocean ecosystems on which they depend. Avian populations are large, breeding colonies are accessible and the marine food webs of which the birds are a part are relatively simple. Taking advantage of these circumstances, we have learned a great deal about the reproductive ecology and energetics of Antarctic (*e.g.*, Croxall, 1984; Trivelpiece *et al.*, 1987) and Arctic (*e.g.*, Gaston and Nettleship, 1981; Hunt *et al.*, 1986) marine birds and how changes in the availability of prey are reflected by events in the colony

(*e.g.*, Nettleship *et al.*, 1984; Croxall and Prince, 1979; Prince, 1980; Croxall *et al.*, 1988b).

Large numbers of birds, and diets dominated by one to a few prey species have also simplified the tasks of studying foraging habitat selection and the circumstances under which seabirds take prey. Multidisciplinary cruises in which marine ornithologists have had access to acoustic records of the horizontal and vertical distribution of prey have greatly improved our understanding of factors controlling the availability of prey to birds. In this paper I focus on aspects of the marine ecology of seabirds in the Antarctic and draw examples from the Arctic where appropriate.

The importance of understanding the trophic ecology of marine birds in the Antarctic has practical as well as basic interest. Determination of the form of the linkages between the birds and their prey has gained

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TABLE 1. Comparison of coefficient of community (Pielou, 1977) of marine bird faunas at various latitudes in the northern and southern hemispheres (from Hunt and Nettleship, 1988).

Latitude	Pacific Ocean	Western No. Atlantic	Eastern No. Atlantic	South Atlantic	Indian Ocean
40–50° vs. 50–60° N	0.95	0.74	0.82	—	—
50–60° vs. 60–70° N	0.81	0.67	0.81	—	—
60–70° vs. 60–80° N	0.56	0.86	0.75	—	—
40–50° vs. 50–60° S	0.53	—	—	0.51	0.60
50–60° vs. 60–70° S	0.09	—	—	0.54	0.40

particular urgency with the nascent development of commercial fisheries for Antarctic krill (*Euphausia superba*), an important prey of many Antarctic marine predators (Croxall and Prince, 1980; Laws, 1985). Marine birds have been selected for monitoring, both to serve as models for populations of less easily studied Antarctic vertebrate predators, and also as a source of information on the size of krill stocks (CCAMLR, 1985, 1986; Croxall *et al.*, 1988b). For these monitoring efforts to be used effectively, we must understand the linkages in the marine ecosystem that determine the relationship between prey abundance, prey availability and prey use by seabirds (Hunt *et al.*, manuscript).

Species distribution

The at-sea distribution of marine birds is related to physical and biological aspects of the ocean environment over a wide range of spatial scales that vary from whole ocean basins to mesoscale changes in watermass (Ashmole, 1971; Brown, 1980; Hunt and Schneider, 1987). At the largest scales, the distribution of bird species in the Southern Ocean have a striking annular or latitudinal pattern around the Antarctic Continent reflecting the dominant pattern of Southern Ocean currents (Croxall, 1984). Hunt and Nettleship (1988) found that the breeding distribution of Southern Hemisphere seabirds varies more strongly with latitude than with ocean basin (compare Tables 1 and 2). Latitude also has more influence on the at-sea distribution of Southern Ocean seabirds than does ocean basin (Watson, 1975; Shuntov *et al.*, 1981; Harrison, 1983). Particularly at high latitudes, the species composition of seabird communities is strikingly similar around the

circumference of Antarctica (Hunt and Veit, 1983; SCAR, 1985; Veit, 1988). Although change in species composition as a function of latitude remains a dominant factor in seabird communities between the Antarctic divergence and the subtropical convergence, there is nonetheless considerable overlap in bird species composition between latitudes. Thus, except for the southernmost seabird communities associated with ice, there are no clear oceanic boundaries demarcating seabird distribution in the sub-Antarctic and Antarctic (Ainley and Boekelheide, 1983; Ainley *et al.*, 1984; SCAR, 1985). Latitudinal variation also exists in the flight characteristics of Southern Ocean birds. Seabirds found over warmer, windier ice-free waters of sub-Antarctic latitudes are, in most cases, species which use dynamic soaring for flight, a type of flight pattern relatively rare over ice-filled waters (Ainley and Boekelheide, 1983; SCAR, 1985).

In contrast to the Southern Ocean, in the Northern Hemisphere seabird species' distributions differ considerably between ocean basins and even between sides of ocean basins at similar latitudes (Tables 1 and 2) (Hunt and Nettleship, 1988). Within these regions, seabird community composition may be similar over wide ranges of latitude (Table 1). These differences between and within northern ocean basins stem from the position of the continents and the consequent meridional flow of the major current systems of the north; north-south oriented currents create similar oceanographic habitats over wide ranges of latitude. In response, the nesting and foraging distributions of marine bird species in the north often have much wider latitudinal ranges and narrower longitu-

TABLE 2. Comparison of coefficients of community (Pielou, 1977) of marine bird faunas between ocean regions at similar latitudes in the northern and southern hemispheres (from Hunt and Nettleship, 1988).

Ocean regions	40-50°	50-60°	60-70°	70-80°
No. Pacific vs. West Atlantic	0.27	0.37	0.47	0.71
NW Atlantic vs. NE Atlantic	0.63	0.54	0.61	0.72
NE Atlantic vs. No. Pacific	0.17	0.18	0.42	0.61
So. Pacific vs. So. Atlantic	0.38	0.76	0.71	—
So. Atlantic vs. So. Indian	0.53	0.58	0.62	—
So. Indian vs. So. Pacific	0.33	0.58	0.89	—

dinal ranges than those of their Southern Hemisphere counterparts (Hunt and Nettleship, 1988).

Seabird distributions in the Antarctic in some cases reflect mesoscale and large-scale variation in water masses. In Drake Passage and Bransfield Strait, Hunt *et al.* (1990) found concordance between the distribution of water masses of various origins and the distribution of seabird species groupings. The geographic distributions of most species in Hunt *et al.*'s 1985 study were similar to those recorded in 1981 by Starck and Wyrzykowski (1982). This similarity suggests that the mesoscale distribution patterns of birds in the region are relatively stable. We do not know why these Bransfield Strait region seabird communities varied between water masses. In the Northern Hemisphere, differences in seabird communities between water masses often reflect dependence upon different food webs and water-column structure (*e.g.*, Joiris, 1983; Springer and Roseneau, 1985; Schneider *et al.*, 1986), or are related to upwelling systems (*e.g.*, Brown, 1980; Briggs *et al.*, 1987). In both the Bering Sea and the North Sea, the species composition and trophic dependencies of the seabird community change between water masses. Likewise, in the Greenland Sea, there are striking changes in the seabird community between the Greenland Current in the west and the Atlantic water in the east (Mehlum, 1989).

Patterns of abundance

The distribution of most species of seabirds at sea is patchy. This patchiness results both from patchiness in the availability of prey and from social interactions, particularly the habit of forming flocks when

abundant prey is present (Hoffman *et al.*, 1981; Obst, 1985). In turn, spatial variation in the abundance and availability of prey is controlled by the physical and biological environment of the prey, including social interactions among prey individuals.

Differences between the Northern and Southern Hemispheres in the availability of shallow continental shelf waters to foraging seabirds influence the extent to which physical features *versus* social interactions determine prey availability to seabirds. In the Antarctic, the continental shelf is relatively deep (500-700 m) and, except in a few areas (*e.g.*, Ross Sea, Antarctic Peninsula, Scotia Arc), the shelf is mostly, if not completely, ice covered throughout the year. The result is that much of the ocean habitat available to foraging marine birds in the Southern Ocean is over abyssal depths. Between years, fluctuations in major ocean currents influence the distribution and abundance of prey (Priddle *et al.*, 1988). However, within seasons, it is unlikely that physical processes, with the exception of Langmuir circulation cells (Brown, 1980; Barstow, 1983) and subsurface temperature structures (Brinton, 1985), determine the patchiness of prey in Southern Ocean waters over abyssal depths. Rather, over short time periods clumping of prey is more likely the result of social interactions between prey organisms (*e.g.*, the aggregation of krill, Marr, 1962; Hamner, 1984). We know little about the processes that determine the size or location of aggregations of krill, let alone those of other prey species such as squid, but these social interactions are clearly of importance in determining the small-scale availability of prey to seabirds in the deep waters of the Antarctic.

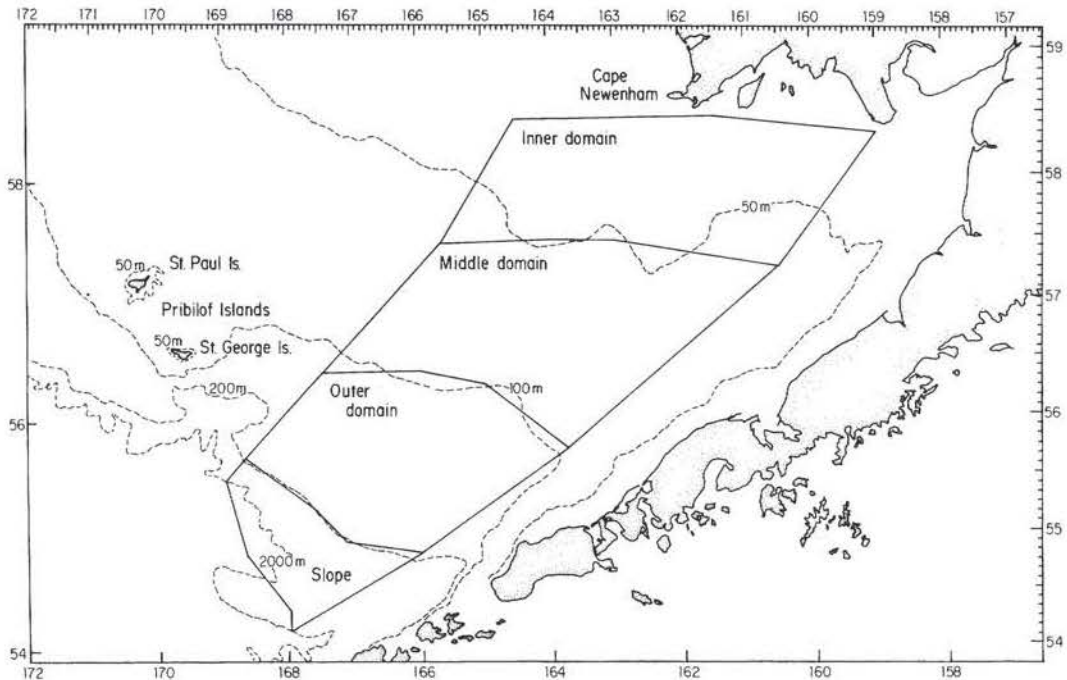


FIG. 1. Southeastern Bering Sea showing the broad, shallow continental shelf and the location of oceanographic domains defined by bathymetrically fixed fronts (Iverson *et al.*, 1979).

In contrast, in the Northern Hemisphere, there are large areas of shallow (100–200 m) water over the continental shelves available to foraging birds (*e.g.*, Fig. 1). Here currents interact with bottom features and often determine critical aspects of the physical regime in which birds forage (Iverson *et al.*, 1979; Pingree *et al.*, 1974). For example, on the continental shelf systems of both the southeastern Bering Sea and the Labrador Current, variability in seabird numbers is greater across than along the shelf (Schneider *et al.*, 1988). In both cases, fronts are parallel to the shelf. In the Bering Sea trophic pathways to birds vary between domains (Table 3), and 62% of the variation in energy flow to seabirds was explained by the cross-shelf salinity gradient (Schneider *et al.*, 1986). In this system, aggregations of birds were not found at fronts (in general) more frequently than expected by chance, but the extent to which fronts were attended by birds varied with the strength of the front (Schneider *et al.*, 1987). Near the Pribilof Islands, strong, nearshore fronts are of

importance in the foraging of breeding seabirds (Ford *et al.*, 1982; Kinder *et al.*, 1983; Schneider *et al.*, 1990).

Over the Antarctic continental shelf, there is the possibility for bathymetrically determined fronts to influence the availability of prey to marine birds. For instance, shelf-slope fronts may be important for foraging birds in the Antarctic (Ainley and Jacobs, 1981; Ainley *et al.*, 1984), even though the shelf-slope front, at least where studied, has a sub-surface expression (Ainley and Jacobs, 1981; Veit, 1988), and there is no obvious connection between processes at depth and prey availability at the surface. One source of evidence that this frontal system is important for marine bird

TABLE 3. Ratio of estimated energy flux to non-diving versus diving species of seabirds foraging in the Southeastern Bering Sea (from Schneider *et al.*, 1986). See Figure 1 for location of domains.

Year	Slope	Outer	Middle	Inner
1980	6.60	1.38	0.79	0.05
1981	4.01	3.09	0.36	0.03

foraging comes from the Ross Sea. On three of five crossings of the shelf break, Ainley and Jacobs (1981) found elevated numbers of birds. However, on two of these transects there was also a change in the extent of pack-ice cover at the shelf break which may have influenced the density of birds present. Veit (1988) examined the importance of the shelf-slope during a circumnavigation of Antarctica, and found significantly elevated numbers of birds associated with the shelf-slope. The relationship found by Veit was driven by only four species of birds, each of which had large aggregations at only one or two locations over slope waters. Given this result, the importance of the Antarctic Shelf Break Front as a foraging zone for birds in the absence of ice is not entirely clear.

In the shallower waters of the Antarctic continental shelf, particularly near islands, there is the possibility for currents to interact with bathymetry and form fronts and eddies as have been described for other shallow seas (Uda and Ishino, 1958; Fernhead, 1975; Pingree *et al.*, 1978; Alldredge and Hamner, 1980; Schneider *et al.*, 1990). Eddies that concentrate krill have been identified in the vicinity of the South Orkney Islands (Bogdanov *et al.*, 1969) and near South Georgia Island (Everson, 1984), and krill swarms may be disproportionately common near islands (Brinton, 1985). However, the importance to birds of small-scale features for concentrating prey in the Antarctic has not been examined.

Both Obst (1985) and Heinemann *et al.* (1990) have suggested that the placement of the colonies of near-shore-foraging penguins might reflect the predictable presence of krill in nearby waters. Additionally, in places where space is not limiting colony growth, colony size could be a predictor of the local availability of prey. To date, these hypotheses have not been tested. However, the majority of penguin colonies on the Antarctic Peninsula and in the Scotia Sea are either on small islands, or on points extending from large islands (Croxall and Kirkwood, 1979). It appears that the colonies are situated in locations to which currents could transport prey (*e.g.*, Everson and Murphy, 1987), or where prey avail-

ability might be influenced by bathymetrically controlled flow gradients or eddies (*e.g.*, Fernhead, 1975; Pingree *et al.*, 1978). However, without data on the availability of potential colony sites, it is impossible to determine if this distribution represents a non-random selection of colony sites. Understanding the extent to which local physical features influence the availability of krill to these colonies would be of considerable importance in the selection of predator colonies for monitoring of krill populations.

Seabirds and ice

The marginal ice zone, which in some cases contains a well defined ice edge, varies in extent depending on the type of ice, the dispersion of the ice by wind and current, and the seaward extent of stratified water resulting from meltwater-induced stability (Smith, 1987). In land-fast ice there may be few, if any open leads within the ice and, depending on currents and wind, a very sharply defined ice edge may result. In contrast when a large ice field disintegrates in a short period of time (*e.g.*, Bering Sea, Divoky, 1981), there may be no clear interior boundary to the marginal ice zone. The zone of stratified water seaward of the ice edge is of key importance for the enhanced algal productivity associated with the spring melting of the ice (Alexander and Niebauer, 1981; Niebauer and Alexander, 1985; Smith and Nelson, 1985, 1986). It is thus the region over which ice melt derived productivity might be expected to have its maximum localized impact on secondary and higher level consumers. The extent of this meltwater influenced area can be vast; in the Weddell and Ross seas the meltwater induced stability may extend 250 km from the "ice edge" (Smith and Nelson, 1986). Delimitation of the marginal ice zone is necessary when assessing the contribution of these processes to the regional carbon budget (*e.g.*, Smith and Nelson, 1986), or the extent to which populations of higher-trophic-level organisms such as seabirds depend on the marginal ice zone.

Ice cover could arguably be considered the single most important variable influ-

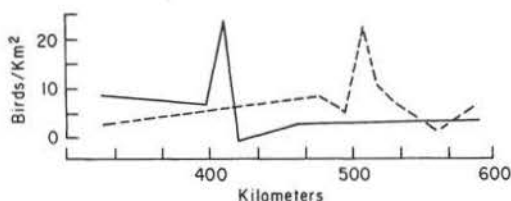


FIG. 2. Distribution of seabirds in the Weddell and Scotia seas along two transects obtained two weeks apart in the austral spring of 1983. The first distribution (broken line) was obtained when the ice edge was at about 300 km north of 63°S, the second when the ice edge had retreated to about 230 km north of 63°S. Fraser and Ainley (1986) suggested that the southward shift in bird abundance was tracking the retreat of the ice edge. From Fraser and Ainley (1986), with permission.

encing the distribution of marine birds in the Antarctic. Investigators who have examined the distribution of Antarctic marine birds have consistently identified striking differences between the species of birds associated with open water and those associated with ice (Ainley and Boekelheide, 1983; Ainley *et al.*, 1984; Veit, 1988). Investigators have also found high concentrations or high biomass of birds associated with the marginal ice zone in the Antarctic. In the Weddell Sea, Fraser and Ainley (1986) reported peaks in avian abundance and biomass near the ice edge, as well as inside the pack. They also provided the first evidence of elevated bird numbers seaward of the ice edge (Fig. 2). They found a high concentration of birds about 250 km north of the ice edge, approximately the width of the zone of water with meltwater induced stratification; the location of this concentration shifted southward as the ice melted. It is tempting to speculate that this peak corresponded to a frontal zone where the pycnocline beneath the fresh meltwater approached the surface. In the Ross Sea, Ainley and Jacobs (1981) found increased avian biomass near the edge of the pack ice in one of five transects, but the ice edge was over the shelf-slope front. Consequently it is difficult to assess the importance of the ice edge as the cause of the increase in biomass. They suggest that both factors work together, an idea supported by Eppley and Harrison's (1985) finding of elevated numbers of birds when

the ice edge was coincident with the shelf edge off the Wilkes Land Coast.

In the Weddell Sea, the diets of birds in the pack-ice and in the open water were similar; krill and myctophid fish predominated in both groups (Ainley *et al.*, 1984, 1986, 1987). Mesopelagic micronekton was also found in near-surface-foraging birds foraging deep in the pack ice, and Ainley *et al.* (1986) suggested that these normally deep-dwelling species shifted their distribution to surface waters in response to lower levels of light beneath the ice. In the Ross Sea, Ainley *et al.* (1984) found that, in addition to krill, fish, squid and crustaceans other than krill were taken by birds. When associated with ice, krill are known to forage on ice diatoms (Hamner *et al.*, 1983; Garrison *et al.*, 1986), and thus at least part of the food web on which birds depend derives from the sea ice microbial community.

The marginal ice zone (including the "ice edge") is also an important habitat for birds in the Arctic. In the Canadian High Arctic, marine birds aggregate near the ice edge to forage upon a food web based upon epontic (underice) algae (Bradstreet, 1980, 1982, 1988; Bradstreet and Cross, 1982). In this system, the characteristics of the undersurface of the ice are important as a refuge and as a foraging area for the prey organisms (Bradstreet, 1982). It is the proximity of this substrate, rather than a meltwater supported algal bloom seaward of the ice edge that determines the availability of avian prey. Thus, the ice edge provides the point of access to birds using this underice-dwelling community (Bradstreet, 1979, 1982, 1988; Stirling, 1980; Brown and Nettleship, 1981).

Avian use of the ice-water interface in winter presumably is unrelated to any bloom. In the Barents Sea, marine birds, particularly Thick-billed Murres (*Uria lomvia*), use leads in the ice throughout the winter and spring (Bakken and Mehlum, 1988). There, Bakken (unpublished data) has wintertime observations of Thick-billed Murres moving between leads deep in the ice during the day and open water at the ice edge at night, but the significance of these diel movements is not known. A food

web based on epontic algae may be used in winter, or normally deeper-dwelling organisms may be more available if they migrate toward the surface in response to reduced light levels under the ice (Gulliksen, 1984; Ainley *et al.*, 1986). In the Bering Sea, marine birds, particularly murrens (*Uria* spp.), forage at the ice edge in winter, but move into the disintegrating pack in spring (Divoky, 1981). This situation differs from that in the Canadian Arctic where, in spring, birds fly up to 100 km over open water to forage at the ice edge (Bradstreet, 1979), or the Barents Sea where birds cross large expanses of open water within the pack ice to reach the ice edge (V. Bakken, personal communication).

Other factors may influence avian use of the ice edge and marginal ice zone. For instance, many Antarctic bird species commonly associated with the ice edge spend considerable time roosting on ice, either for safety or energy conservation. Likewise, in the Arctic, many if not most species of birds frequenting the ice edge occasionally roost on ice. The energetic consequences of this behavior have not been investigated.

The ice edge and marginal ice-zone habitats in polar oceans involve two related food webs, one based on epontic (underice) algae growing on a fixed substrate, and one based on an algal bloom seaward of the ice edge in water stratified by a surface layer of relatively fresh meltwater. Marine birds in spring use both of these systems in the Antarctic, and at least the epontic system in the Arctic. Avian use of the food web seaward of the ice edge in the Arctic has not been investigated. In fall and winter marine birds also forage in association with ice, but little information is available on the food webs used. We also lack information on the relative importance of ice-related food webs for marine birds compared to food webs based on pelagic systems. Because there have been few studies that have examined concurrently bird use of the marginal ice zone and the ocean beyond the influence of the meltwater (*e.g.*, McLaren, 1982; Fraser and Ainley, 1986), we have little information on the relative importance of these habitats to marine

birds. One would anticipate that the enhanced productivity of the marginal ice zone would support greater numbers of birds. This prediction presupposes a coupling between the algal production and tertiary consumers via zooplankton. When primary consumers are relatively scarce, as is the situation over the middle domain of the southeastern Bering Sea (an uncoupled system) (Cooney and Coyle, 1982; Coyle and Cooney, 1988), foraging in the marginal ice zone should not be especially profitable.

Spatial concordance of marine birds and their prey

In recent years, we have learned a great deal about the diets of Antarctic seabirds. Both colony-based studies (*e.g.*, Croxall and Lishman, 1987; Prince and Morgan, 1987; Trivelpiece *et al.*, 1987) and ship-based studies (*e.g.*, Kock and Reinsch, 1978; Ainley *et al.*, 1984) have contributed to this knowledge. Two important generalizations have emerged. First, diets of bird species vary from one part of their Antarctic distribution to another (Ainley *et al.*, 1984) and it is not safe to assume information gathered in a restricted portion of a species' range can be extrapolated to the whole range (*e.g.*, Abrams, 1985). Second, while krill is the most important prey for a number of species, some species in some parts of their ranges will take considerable amounts of other prey (*e.g.*, Ainley *et al.*, 1984). For other species, krill is seldom if ever taken. Krill is an important direct or indirect link in the food web of Antarctic marine predators (Everson, 1984; Laws, 1985), but it is not the only one.

Two recent advances in methodology have increased greatly our understanding of the foraging behavior of birds. The use of various types of activity and dive recorders has provided useful information on the allocation of time and effort by foraging birds (*e.g.*, Kooyman *et al.*, 1982), and simultaneous observations of birds and echosounder surveys of prey have begun to elucidate the circumstances under which prey are taken. Croxall *et al.* (1988a) showed that Gentoo Penguins (*Pygoscelis papua*) took fish to greater depths than those at

which they took krill, and that Macaroni Penguins (*Eudyptes chrysolophus*) dived to greater depths during the day than during the night when foraging on krill. Similar diel changes in diving patterns were also recorded for the krill foraging Antarctic Fur Seal (*Arctocephalus gazella*), patterns presumably driven by diel vertical migrations of krill (Kalinowski and Witek, 1980; Everson, 1982, 1983; Croxall *et al.*, 1988a). However, the diel movements of krill are complex, and do not invariably follow a simple migration rhythm of daytime descent and nightly ascent (Everson, 1983). Thus, caution must be exercised in assuming that diel variations in predator diving depth reflect changes in prey distribution, rather than, for instance, changes in the ability of krill to avoid predators at certain light levels. Using radio transmitters, Trivelpiece *et al.* (1986) have shown that both Gentoo and Chinstrap Penguins (*P. antarctica*) differ in their diving patterns depending on whether they are traveling, searching for food or catching prey. The next step in the study of seabird foraging behavior will be to relate these individual foraging patterns to the distribution and abundance of prey where the predators are foraging (Fraser *et al.*, manuscript).

The direct comparison of the spatial distributions of marine birds and their prey has been the recent focus of several investigations. Previously, marine ornithologists trying to explain the at-sea distribution of birds were restricted to relating bird distribution to a variety of physical features that were assumed to affect prey community structure (Jehl, 1974; Brown *et al.*, 1975; Ainley and Boekelheide, 1983; Schneider *et al.*, 1986) or prey availability (Ainley *et al.*, 1984; Kinder *et al.*, 1983). These assumptions were largely untested because of the lack of reliable, synoptic measures of the distribution and abundance of the birds' prey. The advent of quantitative echosounder surveys of prey has provided a major improvement in our ability to test hypotheses concerning the foraging distribution and behavior of marine birds in relation to prey availability. High latitude oceans are particularly favorable sites for echosounder studies of sea-

bird prey. Determination of the source of echoes can be difficult, particularly in areas with a high diversity of mobile prey that are hard to sample using nets. In the polar oceans this problem is minimized, as usually the same one or two species predominate in both the birds' diets and in the ocean, and acoustically measured biomass can be a useful measure of prey abundance and distribution.

The earliest studies using echosounders relied upon the depth recorders or "fish-finders" commonly found on vessels, and compared counts of birds with semi-quantitative measures of prey abundance (Obst, 1985; Safina and Burger, 1985). These studies showed that the presence of birds was a good predictor of the presence of prey, a relationship relied on by fishermen for centuries. However, in these studies the abundance of prey was not a good predictor of bird abundance because many prey patches were not exploited.

Attention to the spatial scales at which processes in the ocean environment influence the distribution and abundance of marine birds is important and affects our ability to relate the distribution of predators and their prey (Schneider and Duffy, 1985; Schneider and Piatt, 1986; Hunt and Schneider, 1987). In particular, the spatial scale over which one attempts to relate the distribution of seabirds and their prey (measurement-distance) can have a critical effect on the results. For example, in Bransfield Strait, Antarctica, Heinemann *et al.* (1990) examined both spatial and numerical concordance of seabirds with krill. They found stronger numerical correlations between marine birds and the acoustically measured biomass of Antarctic krill when they used the average of hundreds of nautical miles within a large area than when they attempted correlations at the scale of single, mile-long, transect segments. Seabird-krill correlations in this study were strongest over areas thousands of square miles in extent defined either by their seabird species composition or by the average depth distributions of krill. Bird species that were known to have a dietary specialization on krill showed the highest spatial correlation with krill. Studies in the

Arctic have shown scale-dependent correlations between seabirds and their prey. In the Bering Sea, Hunt *et al.* (1990) found that the strength of correlation between Least Auklets (*Aethia pusilla*) and prey were stronger at a measurement scale of 8–12 nautical miles than at a scale of 1–2 nautical miles. Piatt (1990) found that Common Murres (*Uria aalge*) and Atlantic Puffins (*Fraticula arctica*) had their strongest correlations at a scale of 2–6 km with a minimum measurement interval of 0.25 km. He also found that murres required a minimum threshold of prey abundance (which is adjusted in response to overall prey abundance) before the distribution of Common Murres begins to show a positive correlation with their prey, capelin. This finding supports, in part, hypotheses put forward by Obst (1985), Heinemann *et al.* (1990) and Hunt *et al.* (1990) that marine birds in many cases may not be adept at finding localized prey patches, but that they are able to learn which ocean regions (habitats) have, on average, sufficient densities of prey for their needs.

In the case of some avian consumers of krill [e.g., Antarctic Fulmar [*Fulmarus glacialisoides*], Cape Petrel [*Daption capense*] and Adelie Penguin [*Pygoscelus adeliae*]), the meager data available suggest that the largest krill patches may be disproportionately important. In a 20-day study of foraging seabirds with respect to krill abundance in Southern Drake Passage and Bransfield Strait, 62% of all Antarctic Fulmars, and 62% of all Cape Petrels seen were at one very large aggregation of krill, and 76% of all Adelie Penguins seen were at another aggregation (Hunt *et al.*, 1985; Heinemann *et al.*, 1990). Similarly, in a 42 day circumnavigation of the Antarctic continent, an estimated 1×10^6 Antarctic Petrels (*Thalassipica antarctica*), the majority of all Antarctic Petrels seen, were foraging over a single large krill patch off Enderby Land (Hunt and Veit, 1983; Veit, 1988). The two aggregations in Bransfield Strait were in areas where gyres or bathymetrically influenced currents could have affected the accumulation of krill (Heywood and Pridde, 1987). However, Everson and Murphy (1987) suggest that krill were carried

through the region in the prevailing currents and were not concentrated or retained.

We need to learn a great deal more about the circumstances that influence the concentration and availability of prey to marine birds. At large scales, we need to explore the relationship between the coupling of marine trophic levels and the availability of prey to marine birds. For example, the extent of coupling between primary producers and secondary consumers varies between marginal ice zones in various oceans. We need to investigate the extent to which this variation is reflected by birds. At a smaller scale, there is often considerable patchiness and variation in bird species composition along ice edges. We have no information on the cause of this patchiness. Several possible mechanisms include (1) differences in the physical structure of the ice which may provide differential access to prey, (2) differences in the abundance of prey along the ice edge, (3) competitive interactions between bird species in the ice-edge community which may result in spatial structuring of distributions. Polar seas provide a wealth of opportunities for studying how marine birds use their ocean habitats.

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