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SEABIRD FORAGING ECOLOGY

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Introduction

Though bound to the land for reproduction, most seabirds spend 90% of their life at sea where they forage over hundreds to thousands of kilometers in a matter of days, or dive to depths from the surface to several hundred meters. Although many details of seabird reproductive biology have been successfully

elucidated, much of their life at sea remains a mystery owing to logistical constraints placed on research at sea. Even so, we now know a considerable amount about seabird foraging ecology in terms of foraging habitat, behavior, and strategy, as well as the ways in which seabirds associate with or partition prey resources.

Foraging Habitat

Seabirds predictably associate with a wide spectrum of physical marine features. Most studies implicitly assume that these features serve to increase prey abundance or availability. In some cases, a physical feature is found to correlate directly with an increase in prey; in others, the causal mechanisms are postulated. To date, the general conclusion with respect to seabird distribution as related to oceanographic features is that seabirds associate with large-scale currents and regimes that affect physiological temperature limits and/or the general level of prey abundance (through primary production), and with small-scale oceanographic features that affect prey dispersion and availability.

Water Masses

In practically every ocean, a strong relation between sea bird distribution and water masses has been reported, mostly identified through temperature and/or salinity profiles (Figure 1). These correlations occur at macroscales (1000–3000 km, e.g. associations with currents or ocean regimes), as well as

mesoscales (100–1000 km, e.g. associations with warm- or cold-core rings within current systems). The question of why species associate with different water types has not been adequately resolved. At issue are questions of whether a seabird responds directly to habitat features that differ with water mass (and may affect, for instance, thermoregulation), or directly to prey, assumed to change with water mass or current system.

Environmental Gradients

Physical gradients, including boundaries between currents, eddies, and water masses, in both the horizontal and vertical plane, are often sites of elevated seabird abundance. Seabirds respond to the strength of gradients more than the presence of them. In shelf ecosystems, e.g. the eastern Bering Sea shelf and off the California coast, cross-shelf gradients are stronger than along-shelf gradients, and sea-bird distribution and abundance shows a corresponding strong gradient across, as opposed to along the shelf. At larger scales the same pattern is evident, e.g. crossing as opposed to moving parallel with boundary currents.

Physical gradients can affect prey abundance and availability to seabirds in several ways. First, they can affect nutrient levels and therefore primary production, as in eastern boundary currents. Second, they can passively concentrate prey by carrying planktonic organisms through upwelling, downwelling, and convergence. Finally, they can maintain property gradients (fronts, see below) to which prey actively respond. In the open ocean, where currents

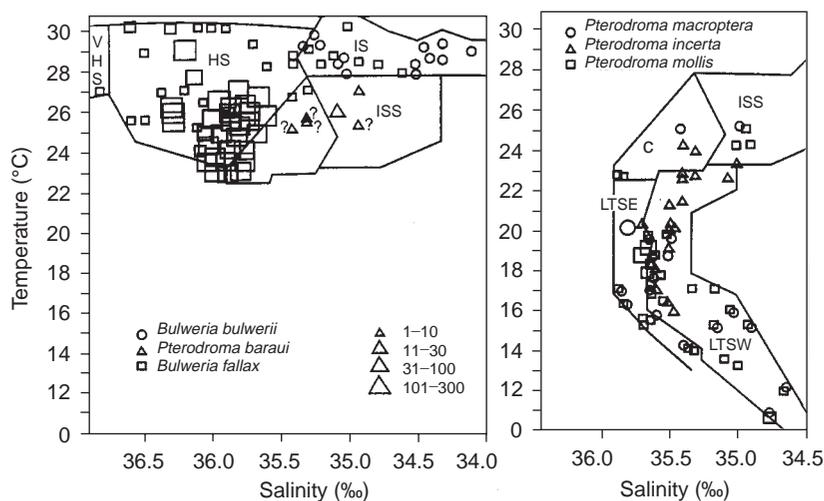


Figure 1 Distribution of gadfly petrels in the Indian Ocean corresponding to various regimes of surface temperature and salinity: (A) warm-water species, and (B) cool-water species. The relative size of symbols is proportional to the number of sightings. Symbols for water masses as follows: VHS, very high salinity; HS, high salinity; IS, intermediate salinity; ISS, intermediate salinity south; C, common water; LTSE, low temperature southeast; LTSW, low temperature southwest. (Redrawn from Pocklington R (1979) *Marine Biology* 51: 9–21.)

and dynamic processes are less active, prey behavior should be the principal mechanism responsible for seabird aggregation. In these cases, locations of aggregations are unpredictable, and this has important consequences for the adaptations necessary for seabirds to locate and exploit them. In contrast, in continental shelf systems, currents impinge upon topographically fixed features, such as reefs, creating physical gradients predictable in space and time to which seabirds can go directly. Thus, the first and second mechanisms are the more important in shelf systems, and aggregations are so predictable that seabirds learn where and when to be in order to eat.

Fronts

Much effort has been devoted successfully to identifying correlations between seabird abundance and fronts, or those gradients exhibiting dramatic change in temperature, density, or current velocity (Figure 2). Results indicate a considerable range of variation in the strength of seabird responses to fronts. This may be due to the fact that fronts influence sea-bird distribution only on a small scale. The factors behind the range of response is of interest in itself.

Nevertheless, fronts are important determinants of prey capture. Two hypotheses have been proposed to account for this: (1) that frontal zones enhance primary production, which in turn increases prey supply, e.g. boundaries of cold- or warm-core rings in the Gulf Stream; and (2) that frontal zones serve to concentrate prey directly into exploitable patches, e.g. current rips among the Aleutian Island passages.

Topographic Features

Topographic features serve to deflect currents, and can be sites of strong horizontal and vertical changes in current velocity, thus, concentrating prey through a variety of mechanisms (Figure 2). For example, seamounts are often sites of seabird aggregation, likely related to the fact that they are also sites of increased density and heightened migratory activity for organisms comprising the deep scattering layer. A second example are topographic features in relatively shallow water, including depressions in the tops of reefs and ridges across the slope of marine escarpments, which may physically trap euphausiids as they attempt to migrate downward in the morning. A third example is the downstream, eddy effect of islands that occur in strong current systems.

Depth gradient itself is sometimes correlated with increased abundance of seabirds, and water depth in

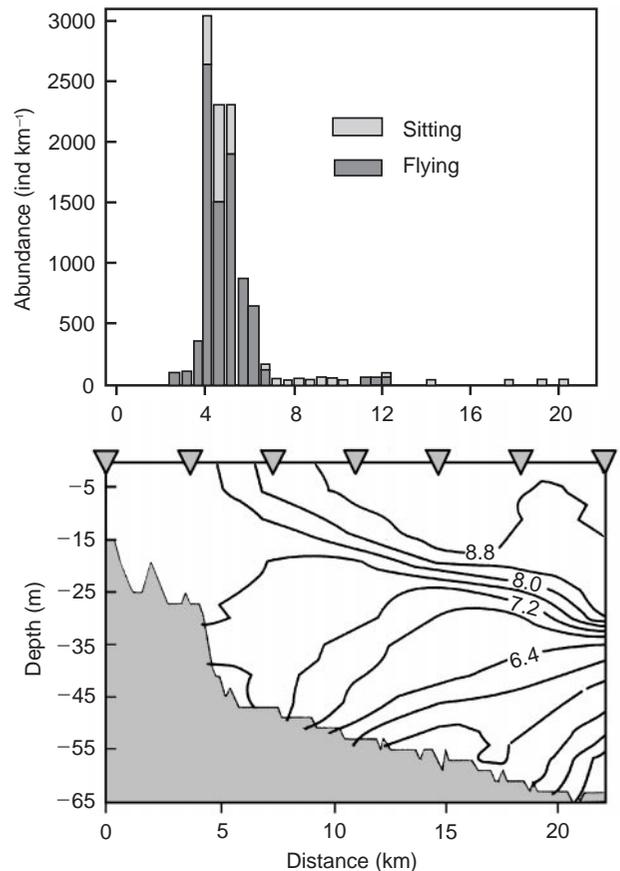


Figure 2 The aggregation of foraging shearwaters at fronts, in this case the area where an elevation in bottom topography forces a transition between stratified and well-mixed water. The bottom panel shows isotherms. (Redrawn from Hunt GL *et al.*, *Marine Ecology Progress Series* 141: 1-11.)

general has long been related to seabird abundance and species composition. Depth-related differences in primary productivity explain large-scale patterns between shelf and oceanic waters. Within shelf systems themselves, several hypotheses explain changes in species composition and abundance with depth. First, primary production may be diverted into one of two food webs, benthic or pelagic, and this may explain differences in organisms of upper trophic levels in inner versus outer shelf systems, e.g. the eastern Bering Sea. Alternatively, the fact that interactions between flow patterns in the upper water column and bottom topography will be strong in inner shelf areas but decoupled in outer shelf areas, may result in differences in predictability of prey and consequently, differences in the species that exploit them, e.g. most coastal shelf systems. Finally, depending on diving ability and depth, certain seabirds may be able to exploit bottom substrate, whereas others may not.

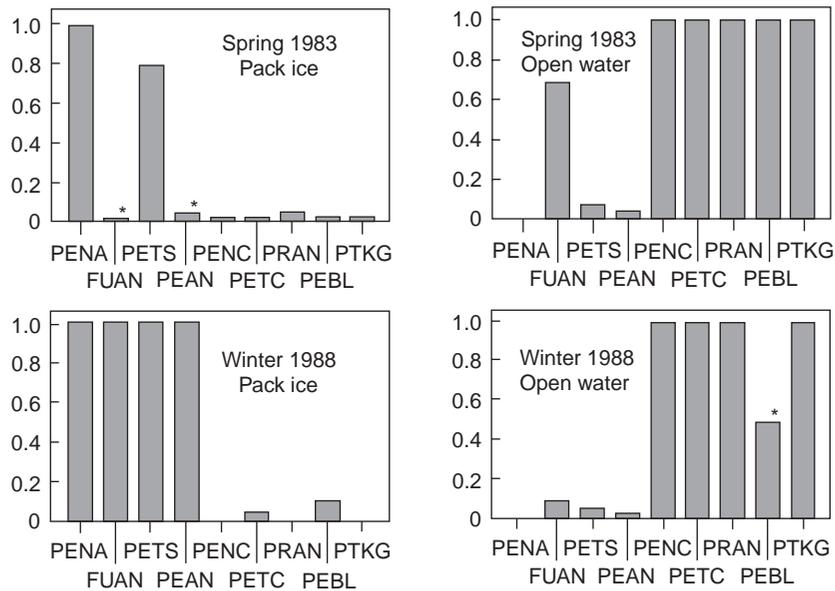


Figure 3 The correspondence of various seabird species either to pack ice or open water immediately offshore of the ice; Scotia-Weddell Confluence, Southern Ocean. Abbreviations: PENA, Adélie penguin; FUAN, Antarctic fulmar; PETS, snow petrel; PEAN, Antarctic petrel; PENC, chinstrap penguin; PETC, pintado petrel; PRAN, Antarctic prion; PEBL, blue petrel; PTKG, Kerguelan petrel. (Redrawn from Ainley *et al.* (1994) *Journal of Animal Ecology* 63: 347–364.)

Sea Ice

A strong association of individual species and characteristic assemblages exists with sea ice features. On one hand, certain species are obligate associates with sea ice; on the other, sea ice can limit access to the water column, and in some cases, aggregation of seabirds near the ice margin is a simple response to this barrier (Figure 3).

Sea ice often enhances foraging opportunities. First, there is an increased abundance of mesopelagic organisms beneath the ice, believed to be a phototactic response of these organisms to reduced light levels. Second, primary production is enhanced beneath the ice or at its edge, and in turn leads to increased abundance of primary and secondary consumers. The abundance and degree of concentration of this sympagic fauna varies with ice age, ice structure, and depth to the bottom. As a result, Arctic ice, often multi-year in nature, has a speciose sympagic fauna as compared to Antarctic ice, which is often annual. The ice zone can be divided into at least three habitats, a region of leads within the ice itself, the ice edge, and the zone seaward of the ice. Each zone is exploited by different seabird species, and the relative importance of zones appears to differ between Arctic and Antarctic oceans, with the seaward zone being particularly important in Antarctic systems.

Foraging Behavior

Most seabird species take prey within a half meter of the sea surface. This they accomplish by capturing prey that either are airborne themselves (as a result of escaping subsurface predators, see below), or are shallow enough that, to grasp prey, the bird dips its beak below the surface (dipping) or crashes into the surface and extends its head, neck and upper body downward (surface plunging, contact dipping). Other species feed on dead prey floating at the surface. Another group takes prey within about 20 m of the surface either by flying into the water to continue flight-like wing movements below the surface (pursuit plunging) or by using the momentum of an aerial dive (plunging).

Finally, a number of seabirds can dive using either their wings or feet for propulsion. Dive depth is related to body size, which in turn relates to physiological capabilities of diving. The deepest dives recorded by a bird (penguin) reach 535 m, but most species are confined to the upper 100 m. A highly specialized group of species capture prey by stealing them from other birds.

Foraging Strategies

The issue of how seabirds locate their prey is far from completely understood. Below is a summary of known strategies, most of which depend on

sea-birds locating some feature which itself serves to reliably concentrate prey.

Physical Features

Physical features are important to foraging sea-birds, because they serve to concentrate prey in space and time, and because they often occur under predictable circumstances (Figure 2). This issue was addressed above.

Subsurface Predators

Subsurface predators commonly drive prey to the surface because the air-water interface acts as a boundary beyond which most prey cannot escape. Under these circumstances, seabirds can access these same prey from the air. A wide array of subsurface predators are important to seabirds: large predatory fishes (e.g. tuna), particularly in relatively barren waters of the tropics; marine mammals, both cetaceans and pinnipeds; and marine birds themselves.

Subsurface predators increase the prey available to birds in at least three ways. First, they drive prey to the surface. Second, they injure or disorient prey, which then drift to the surface and are accessible to surface foragers. Third, they leave scraps on which seabirds forage, particularly when the prey themselves are large.

Feeding subsurface predator schools can be highly visible and the degree of association of birds with these prey patches is often great. One investigation found 79% of the variability in seabird density could be explained by the number of gray whale mud plumes; this visibility may have been responsible for the higher correlation than typically reported for other studies attempting to relate seabird and prey abundance (see below).

Feeding Flocks

Seabirds in most of the world's oceans exploit clumped prey by feeding in multispecies flocks. Studies in all latitudes report that seabirds in flocks, often in a very few disproportionately large aggregations, account for the majority of all individuals seen feeding. Although flocks can result from passive aggregation at a shared resource, evidence indicates that seabirds benefit in some way from the presence of other individuals. First, as noted above, some seabird species act as subsurface predators, making prey available to surface-feeding seabirds, e.g. alcid driving prey to the surface for larids in coastal Alaska. Second, a small number of seabird species are kleptoparasitic, obtaining their prey from other seabirds, e.g. jaegers, skuas and a few other species.

Third, vulnerability of individual fish in a school may increase with the number of birds feeding in the flock. Finally, flocks are highly visible signals of the location of a prey patch, e.g. species keying on frigate birds circling high over tuna schools.

Certain species are disproportionately responsible for these signals, simply through their highly visual flight characteristics. Such species are termed 'catalysts'. There is strong evidence that seabirds follow these visual signals, in some cases distinguishing between searching and feeding catalyst species, and between those feeding on a single prey item and those feeding on a clumped patch.

Nocturnal Feeding

Many fishes and invertebrates remain at depth during the day and migrate to the surface after dark. During crepuscular or dark periods, surface densities of prey can be 1000 times greater than during the day. This migration is more significant in low than high latitudes, and in oceanic than neritic waters. Many studies indirectly infer nocturnal feeding from the presence of vertically migrating species in seabird diets or from circadian activity patterns. Little direct evidence exists.

Among the indirect data on how seabirds might locate prey at night is a considerable body of information on olfaction. In particular, members of the avian order Procellariiformes possess olfactory lobes disproportionately large compared to the total brain size and compared to most vertebrates. Experiments show a marked ability of these birds to differentiate among odors and, especially, to find sources of odors that are trophically meaningful.

Maximization of Search Area

Feeding opportunities in the open ocean are often patchily distributed requiring seabirds to travel over large areas in search for prey. This ability to search large areas is tightly linked to adaptations for flight proficiency. Seabirds capable of wide-area search exhibit morphological adaptations of the wing and tail that enhance energy-efficient flight. They also modify their flight behavior to take advantage of wind as an energy source. Penguins, loons, grebes, cormorants and alcid, the pre-eminent seabird divers (see above), sacrifice wide-area search capabilities for what is needed for diving: high density and small wings. Therefore, divers are limited to areas of high prey availability.

An investigation into the relationship between wind and foraging behavior has revealed taxon-specific preferences in flight direction dependent on wind direction, and in turn, to wing morphology

and presumed prey distribution. Procellariiformes, primarily oceanic foragers, preferentially fly across the wind, whereas Pelecaniformes and Charadriiformes, the majority of which forage over shelf and slope waters, preferentially fly into and across headwinds. Because prey on a global scale are more patchy in oceanic than shelf and slope waters, across-wind flight may allow Procellariiformes to cover more area at lower energetic cost, whereas headwind flight allows slower ground speeds, possibly increasing the probability of detecting prey and decreasing response time once a prey item is detected. Flying up- or across-wind among procellariids also maximizes probabilities of finding prey using olfaction.

Associations With Prey

Positive or significant correlations have been identified between seabird and prey abundance, in the Bering Sea, eastern North Atlantic, Barents Sea, and in locations throughout the Antarctic, although rarely at scales smaller than about 2–3 km. In some studies, however, the correlation is weak to nonexistent, or a negative correlation is reported. From these results, several general principles have arisen. First, the strength of the correlation increases with the spatial scale at which measurements are made. Second, correlations between planktonic-feeding seabirds and their prey are lower than correlations between piscivorous seabirds and their prey. The reasons for this pattern may relate to differences in patch characteristics dependent on prey species, or to differences in search mode of various predators. Third, correlations are not as strong as expected and in many cases, a correlation is found only with repeated surveys. Many hypotheses have been proposed to explain the latter, including: (1) seabirds are unable consistently to locate large prey patches; (2) prey are sufficiently abundant that seabirds do not need to locate largest prey patches; (3) prey are actively avoiding seabirds; (4) prey patches are continuously moving so that a time lag exists between patch formation, discovery by the seabird, and measurement by the researcher; (5) extremely large prey patches are disproportionately important to seabirds so that they spend much of their time searching for or in transit to and from such patches; and (6) our means to measure prey patches (usually hydroacoustically) is a mismatch to the biology and attributes of the predators. Finally, different seabird species may respond on the basis of threshold levels of prey abundance, and these thresholds vary seasonally as well as with reproductive status of the bird (breeders require more food than

nonbreeders, which comprise at least half the typical sea-bird population).

Resource Partitioning

Food is considered to be an important resource regulating seabird populations. Accordingly, much research has focused on identifying differences in the way coexisting species exploit prey. At sea, the fact that different oceanic regimes or currents support different prey communities as well as different sea-bird communities has been used to support the idea that the geographic range of seabird species is a response to the presence of specific prey. Contrasting these patterns, however, several colony-based studies report high diet overlap between species, leading to speculation that dietary differences may reflect differences in foraging habitat as opposed to prey selection. Evidence from at-sea research indicates broad overlap in the species and/or sizes of prey taken by coexisting seabird species, often despite species-specific feeding methods, body size or habitat segregation.

Prey Selection

Under certain circumstances seabirds do make choices as to what prey they will attempt to capture (Figure 4). Among breeding species of the western North Atlantic and North Sea, in cases where a prey stock, such as capelin or sandlance, are being exploited by a large array of species, birds key in on fish that provide the highest energy package, in this case fish in reproductive condition. In the Bering Sea, breeding auklets have been observed to ignore smaller zooplankton to take the most energy-dense copepod species available. Finally, in the Antarctic, during winter with almost constant darkness or near-darkness when the mesopelagic community is near the surface most of the time, seabirds have been documented to avoid smaller prey (euphausiids) to take larger and more energy-rich prey (myctophids; Figure 5). However, although this is evidence for active prey selection, in these cases there is broad dietary overlap among seabird predators.

Prey/Predator Size

Body-size differences among coexisting sea bird species have been used to imply diet segregation by prey size (Figure 5). In general, discounting penguins but realizing there are a number of exceptions, the larger seabirds (i.e. those > 1500 g) tend to take fish and squid; the smaller species tend to take juvenile or larval fish and squid, along with zoo-

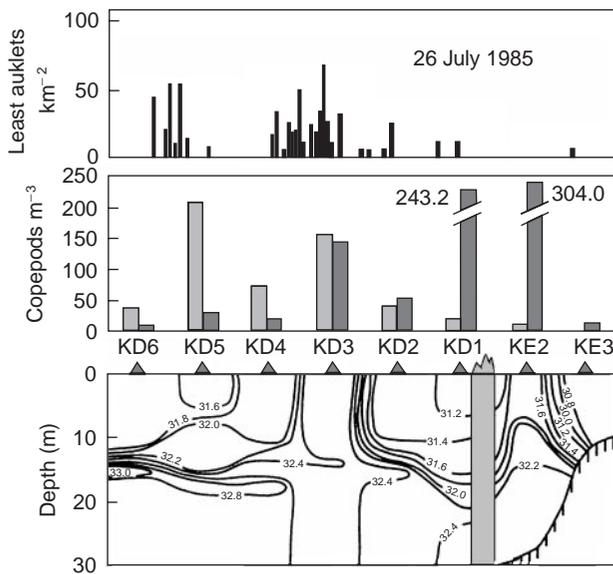


Figure 4 Aggregation of least auklets over concentrations of the copepods *Eucalanus bungii* and *Neocalanus* spp. (light bars), and *Calanus marshallae* (dark bars). All three are confirmed prey of least auklets. Birds virtually ignored huge concentrations of *C. marshallae*, which were much closer to the breeding colony on King Island to preferentially feed on larger and presumably more energy-rich *Neocalanus* spp. (Redrawn from Hunt GL Jr and Harrison NM (1990) *Marine Ecology Progress Series* 65: 141–150.)

planktonic invertebrates. It comes down to energetic cost-efficiency of foraging and the morphology of the seabird foraging apparatus: the bill, which picks one prey item at a time (the lone exception, perhaps, being one or two species groups, e.g. prions, that may filter-feed). Some degree of dietary size segregation is apparent among the few studies that have investigated all species breeding at single sites, e.g. a tropical oceanic island. Other studies at sea report little, if any, dietary separation, even though a 1000-fold difference in seabird size can exist. The implication is that seabirds often forage opportunistically depending on the availability of prey in their preferred habitat, and that differences in habitat are more important than differences in prey selection in facilitating predator coexistence.

Habitat Type/Time

Species or assemblages often segregate according to habitat with little evidence of interactions among seabirds that significantly influence their pelagic distributions. Instead, the implication is that species respond to physical and biological characteristics of environments according to their individual needs and flight or diving capabilities. Spatial segregation can occur with respect to simple habitat features. For example, the Antarctic avifauna is divided into

one assemblage associated with pack-ice covered waters and the other with ice-free waters (Figure 3). The species composition of these assemblages changes little over time; assemblage distribution tracks the distribution of ice features in the absence of differences in prey communities between the two habitat types, and there is little spatial overlap between the two assemblages. Spatial segregation, with respect to species or assemblages, can also occur along environmental gradients with respect to physical, chemical, and biological features of a seabird's habitat, in both the horizontal and vertical dimension. This has been well documented especially in shelf waters, where differences in foraging habitat, particularly as determined by depth, lead to differences in diet; it is also evident in the pelagic tropical waters along productivity gradients.

A recurrent theme is that seabird species sort out along prey density gradients, regardless of prey identity. Such segregation has been recorded even within the same prey patch, with certain species exploiting the center and others the periphery. The idea that oligotrophic waters, having reduced prey availability, can only be exploited by highly aerial species with efficient locomotion, whereas productive waters are necessary for diving species is one that occurs in a wide variety of studies conducted in tropical, temperate, and polar systems.

Finally, segregation can occur with respect to time, specifically with respect to those species that feed at night versus during the day. A few seabird species are adapted to feed only at night.

Mutualism and Kleptoparasitism

The sea bird flocking community in the North Pacific comprises species having complementary foraging behaviors, thus, indicating a degree of integration within the community. In particular, the feeding behavior of catalyst and diving species could be interpreted as mutualistic, catalysts signaling the location of a prey patch, and divers increasing or maintaining prey concentration. Certain authors have speculated that this relationship could have resulted from coevolution of behavior designed to increase the mutualistic benefit of the association. Kleptoparasitism was also proposed to stabilize these feeding flocks by forcing alcids to forage at the edges of a prey patch where they are less vulnerable to piracy, thus, maintaining patch density and ultimately, increasing prey availability to all flock members.

Morphological or Physiological Factors

Differential resource use is sometimes ascribed to species-specific morphological or physiological

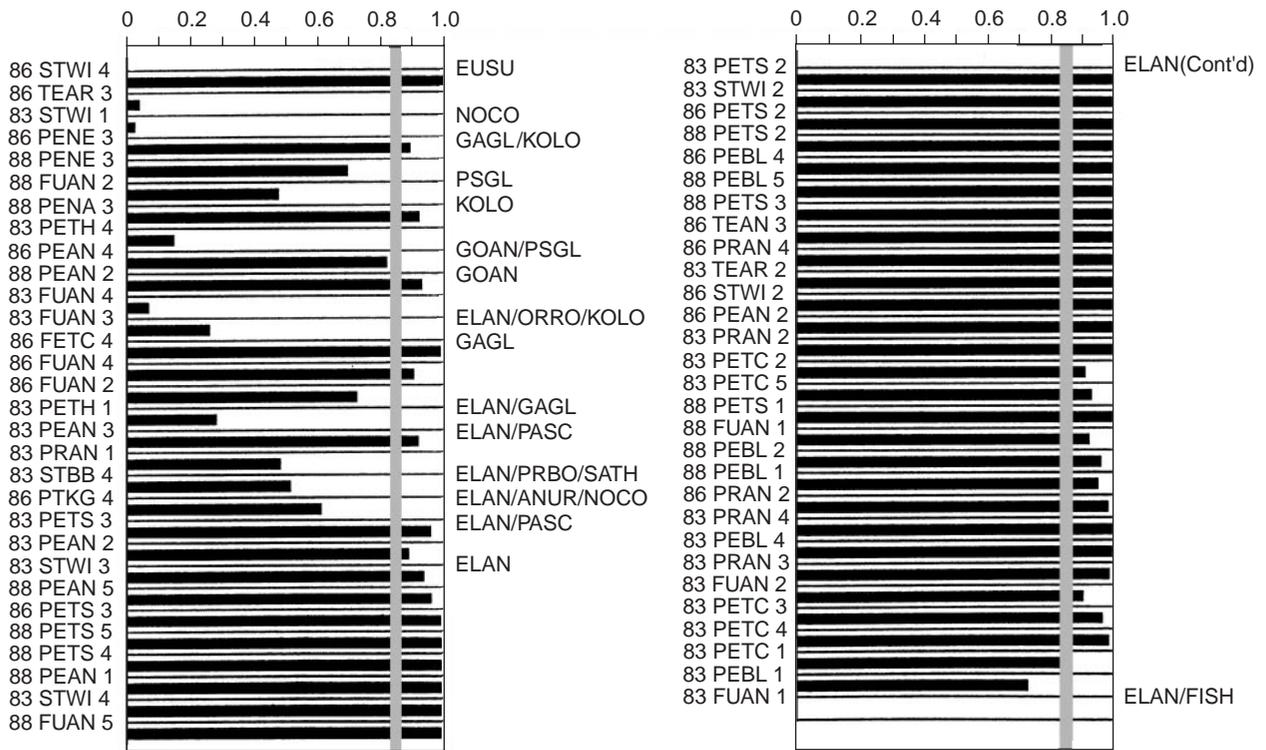


Figure 5 Diet overlap among Antarctic seabirds. Even though a 1000-fold difference in predator size existed, there was no appreciable separation of diet for many sea-bird species. The vertical stippled line indicates the level at which diet is considered to be similar on the basis of prey species overlap. Bird species to the left of bars, prey species to the right. Each bird species name is preceded by the year in which collection was made, and followed by a number that denotes habitat (1, open water; 2, sparse ice; 3, heavy ice). Bird species: PENE, emperor penguin; PENA, Adélie penguin; FUAN, Antarctic fulmar; PETS, snow petrel; PEAN, Antarctic petrel; PENC, chinstrap penguin; PETC, pintado petrel; PRAN Antarctic prion; PEBL, blue petrel; PTKG, kerguelen petrel; STWI, Wilson's storm-petrel; STBB, black-bellied storm-petrel; TEAR, Arctic tern; TEAN, Antarctic tern. Prey names: ANUR, *Anuropsis* spp.; EUSU *Euphausia superba*; ELAN, *Electrona antarctica*; GAGL, *Galiteuthis glacialis*; GOAN, *Gonatus antarcticus*; KOLO, *Kondakovia longimana*; NOCO, *Notolepis coatsi*; ORRO, *Orchomene rossii*; PASC, *Pasiphaea scotia*; PRBO, *Protomyctophum bolini*; PSGL, *Psychroteuthis glacialis*; SATH, *Salpa thompsoni*. (Redrawn from Ainley DG *et al.* (1992) *Marine Ecology Progress Series* 90: 207–221.)

factors affecting flight or diving capabilities. Several examples exist. First, terns differ in their ability to feed successfully in dense flocks over predatory fishes as a function of a given species' ability to hover for prolonged periods of time. Second, differential metabolic demands may be responsible for species-specific differences in the threshold prey density to which alcid respond. Finally, differential flight costs correlate with species-specific patterns in resource use, e.g. along productivity gradients in the tropics, or the amount of foraging habitat that can be exploited (near-shore vs. offshore).

Ultimately, many of these morphological and physiological adaptations are driven by body size. Body size influences depth of dive capabilities, cost of transport, and basal metabolic rate. Additionally, body size can frequently be used to predict the outcome of interference competition (below).

Competition

Interference competition apparently does occur between seabirds at sea. It is referred to most often in the context of feeding flocks, taking the form of aggressive encounters, and collisions between feeding birds. The proximate limiting resource identified in many of these cases is access to prey, i.e. space over the prey patch. In another situation, shearwaters in the North Pacific feed by pursuit plunging in large groups, by which they disperse, decimate, or drive prey deeper into the water column thereby reducing the availability of prey to surface-feeding species. This same mechanism has been proposed for tropical boobies, which by plunge diving may also drive prey beyond the reach of surface feeders.

Despite widespread discussion of trophic competition, supporting data are sparse and some evidence indicates it to be not important in structuring some

sea-bird communities. For example, one study in the Antarctic found no habitat expansion of the pack-ice assemblage into adjacent open waters seasonally vacated by another community (Figure 3), a shift that might be expected if competition affected community structure and habitat selection. In that study, sufficient epipelagic prey were available in the ice-free waters to be exploited successfully by sea birds (Figure 5).

Competition with Fisheries

Many of the forage species sought by sea birds are the same sought by industrial fisheries. The result is conflict, particularly in eastern boundary currents, where clupeid fishes are dominant and are of ideal size and shape to be consumed by sea birds. The tracking of bird populations with fish stocks has been especially well documented in the Benguela and Peru currents, where not only have fish stocks been heavily exploited but so have guano deposits accumulated by the sea birds. The bird populations have responded closely to geographic, temporal and numerical variation in the fish stocks. Well documented, also, have been fish stocks and avian predator populations in the North Sea. There, commercial depletion of predatory fish benefited seabird populations by reducing competition for forage fish; when fisheries turned to the forage fish themselves, seabird populations declined. In some areas, it has been proposed to use statistical models of predator populations as an indicator of fish-stock status independent of fishery data, for instance, the Convention for the Conservation of Antarctic Living Marine Resources. Much information is needed to calibrate seabird responses to prey populations before seabirds can be used reliably to estimate prey stocks.

See also

Benguela Current. Canary and Portugal Currents. Seabird Migration. Seabird Responses to Climate Change. Seabirds and Fisheries Interactions. Sea Ice: Variations in Extent and Thickness.

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SEABIRD MIGRATION

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Introduction

Bird migration is one of the most fascinating phenomena in our living environment, and accordingly

has been studied since ancient times, particularly among nonmarine species. Studies of migration and navigation of nonmarine species have become quite sophisticated, examining in detail subjects including orientation and navigation, and physiological and morphological adaptations. In contrast, studies of migration among marine birds have been fewer and more simplistic. Indeed, until recently, much of the information on migration of seabirds had come