

S34.3: Physical processes, prey abundance, and the foraging ecology of seabirds

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We review the foraging ecology of seabirds at scales of 100s of m to 10s of km. We examine processes responsible for the distribution and availability of seabird prey, and how populations of foraging seabirds distribute themselves with respect to prey. Seabirds forage preferentially at physical processes that cause predictably located aggregations of prey, such as occur at fronts. Seabirds also exploit prey concentrated in the vertical dimension by strong density gradients (pycnoclines). Individual birds show foraging-site fidelity that emphasises the importance of learning where and how prey can be economically exploited. The ability of seabirds to locate prey patches varies with spatial scale and with prey dispersion, and new studies have revealed characteristics of prey distributions that influence prey choice. Threshold effects influence the numerical response of seabirds to prey abundance at both high and low prey densities. Understanding the causes of non-linear responses of foraging seabirds to the abundance of their prey is of basic interest and is an important goal for future research.

INTRODUCTION

In this review, we address two related questions: (1) what processes influence the distribution and availability of seabird prey? and (2) how do populations of foraging seabirds distribute themselves with respect to prey? We discuss how individual seabirds may exhibit preferences for specific foraging sites and suggest that learning is an important component of seabird foraging ecology. We focus on recent studies of seabird foraging ecology at spatial scales of 100s of m to 10s of km. The majority of at-sea studies at these spatial scales have investigated coastal and shelf processes that occur over time scales of hours to weeks.

Physical processes in the ocean affect the distribution and abundance of plankton and other marine organisms (Haurly *et al.* 1978; Wolanski & Hamner 1988; Franks 1992a,b). The influence of these processes on seabird foraging ecology varies in spatial and temporal scale (Hunt &

Schneider 1987; Schneider 1991, 1993, 1994). Recognition of the importance of physical processes in the ocean as major forces shaping the ecology and evolution of marine birds is relatively recent. The review by Brown (1980) focused attention on the need to understand factors that determine where and when seabirds can profitably harvest prey. Knowledge of marine processes and the constraints they impose provides the basis for understanding both the at-sea foraging ecology of seabirds and their breeding distributions and reproductive biology (Schneider 1991, 1993).

Studies of the foraging ecology of populations of seabirds with respect to prey have relied primarily on shipboard surveys, often in the vicinity of breeding colonies. In some cases these surveys have been coupled with investigations of prey distributions and physical processes that enhance the accessibility of prey. The development of echo-sounding instruments for underway surveys of prey distribution and abundance, coupled with use of opening-closing nets that allow discrete sampling of potential prey, has provided important advances in our ability to investigate the distribution and abundance of prey species. Because the use of ships equipped for oceanographic research is expensive, ship-based studies have focused on locations where large numbers of birds are present, and where foraging can be predicted to occur reliably. Thus, studies of topographically-controlled phenomena (Schneider *et al.* 1987) near large colonies have proven particularly attractive. Tidally-driven phenomena have received considerable attention because they occur over short spatial and temporal scales, thereby enhancing the possibility of efficient sampling.

Study of the foraging behaviour of free-flying individual seabirds has been revolutionised by the development of instruments small enough to be carried by a bird. Although some of the first generation of dive recorders could be used on the smaller species of diving birds (Wilson & Bain 1984; Burger & Wilson 1988), many of the early generations of instruments could be deployed on only the largest species. Recent miniaturisations of batteries, transmitters for tracking birds, and instruments that record underwater activity or time and location now permit study of the foraging tactics of a wide range of seabird species previously impossible to investigate. These studies are the focus of other papers in this symposium (Prince *et al.*; Kooyman *et al.*, *this volume*).

Populations of foraging seabirds with respect to physical processes

The abundance of prey in a given water mass may result from *in situ* primary production and passage of energy through a local food web, or from the advection of prey organisms produced elsewhere. In either case, at the scale of 10s to 100s of km, the distributions of birds at sea (e.g., Hunt *et al.* 1981b; Haney 1986; Elphick & Hunt 1993) and of seabird breeding colonies (Hunt *et al.* 1981a; Springer & Roseau 1985) reflect the distribution of water masses containing suitable prey. At spatial scales of m to 10s of km, seabird foraging distributions reflect locations of prey concentrations. The predictability of these concentrations in space and time depends on the processes responsible for their formation.

At scales of km to 10s of kms, seabirds forage at physical features where prey are concentrated, including fronts at the boundaries of water masses, at ice edges, and where currents interact with bathymetry (e.g., Bradstreet 1980; Ainley & Jacobs 1981; Schneider 1982; Haney & McGillivray 1985a,b; Cairns & Schneider 1990; Harrison *et al.* 1990; Hunt & Harrison 1990, Schneider *et al.* 1990a,b; Veit & Hunt 1991,1992; Hunt *et al.* 1996a). The presence of a strong pycnocline may also influence the accessibility or concentration of prey in the vertical dimension (Hunt *et al.* 1990; Haney 1991). When prey concentrations occur close to shore, they have the potential to be of considerable importance to breeding birds that make multiple daily foraging trips.

Tidal forcing

Within water masses, locations where tidal currents impinge on bathymetric features provide opportunities for seabird foraging. In some locations, prey are carried from depth to the surface where they are vulnerable to predation by surface-foraging seabirds. In island passes with exceptionally strong tidal currents, gulls *Larus* spp. and terns (*Sterna* spp.) forage at upwellings when normally deep-dwelling prey are forced to the surface (Braune & Gaskin 1982; Vermeer *et al.* 1987). When the currents relax at high and low water, i.e., during slack tide, prey are able to descend to depth, and the foraging flocks disperse. In other locations, currents not sufficiently strong to force prey to the surface may be sufficient to prevent weakly swimming organisms from descending. As a result, prey aggregations form where the downward swimming ability of the organism is matched by the upward movement of the water (Simard *et al.* 1986; Frank 1992b). Such aggregations are vulnerable to predation by pursuit-diving seabirds such as guillemots *Uria* spp. and auklets *Aethia* spp. (Hoffman *et al.* 1981; Coyle *et al.* 1992; Hunt *et al.* 1998). Small fish also assemble in tidally forced currents and rips and may then be vulnerable to seabird predation (Cairns & Schneider 1990, Safina & Burger 1985, 1989). Tidally forced variations in prey availability can be reflected in the types or amounts of food brought to chicks at colonies (Frank 1992; Frank & Becker 1992; Wendeln *et al.* 1994; Frick & Becker 1995).

In some locations, tidal currents create upwelling on the upstream side of submerged reefs and downwelling with accompanying zones of surface convergence on the downstream side. In the Bay of Fundy, migrant gulls and shearwaters *Puffinus* spp. ate euphausiids forced to the surface by strong tidal currents passing over a submerged reef (Braune & Gaskin 1982). Likewise, phalaropes *Phalaropus* spp. foraged for prey concentrated in both the divergences and convergences where tidal currents crossed a reef (Brown 1980; Brown & Gaskin 1988). In the Aleutian Islands, Hunt *et al.* (1998) found three species of auklets foraging in the vicinity of a submerged reef over which strong tidal currents passed. Crested Auklets *Aethia cristatella* ate upwelled euphausiids on the upstream side of the reef, Parakeet Auklets *A. psittacula* foraged for a wide variety of prey over the reef, and Least Auklets *A. pusilla* foraged downstream of the reef on copepods concentrated in zones of surface convergence. The sides of the reef occupied by the Least and Crested Auklets reversed when the tide reversed, and the strength of the tide was a good predictor of the number of birds present.

In each of these situations, birds foraged on prey advected to the site by currents, rather than on locally produced prey. The sites where prey were available were consistently confined to a particular region, and thus could be relocated readily. Also, foraging activity depended on current strength. In the studies of Braune and Gaskin (1982), Vermeer *et al.* (1987), Cairns and Schneider (1990), and Hunt *et al.* (1998), birds anticipated the time when prey would be available and assembled only when currents were sufficient to facilitate foraging. Braune and Gaskin reported the important observation that birds assembled at the appropriate phase of the tide even on days when prey were absent, and cited this observation as evidence that the seabirds were 'foraging by expectation,' a different use of the term than that employed by Gibb (1962). In the Wadden Sea, distinct foraging areas were visited by Common Terns *Sterna hirundo* during site-specific phases of the tidal cycle with the visits being deferred from day to day reflecting the daily tidal shift (Becker *et al.* 1993). Thus, an important aspect of tidal features is the spatial and temporal predictability of prey availability.

Shallow water tidal or structural fronts

When tidal currents interact with the sea floor, friction between the water and the bottom results in mixing. When the mixing is sufficiently vigorous, and the water sufficiently shallow, 'structural' or 'tidal' fronts result (Pingree *et al.* 1974; Simpson & Pingree 1978; Schumacher *et al.* 1979). These fronts can have both zones of convergence, at which buoyant materials may concentrate at the surface (Pingree *et al.* 1974), and enhanced vertical transport of nutrients (Sambroto *et al.* 1986; Whitledge *et al.* 1986, Whitledge & Walsh 1986), which support primary production in the vicinity of the front (Pingree *et al.* 1975; Richardson & Christoffersen 1991, Franks 1992a). Structural fronts are usually associated with gradually shoaling depths and do not require the strong tidal currents associated with violent mixing and upwelling commonly seen in narrow passes between islands or over shallow reefs.

At structural fronts, seabirds make use of both convergences and production-related increases in prey biomass. For example, at a structural front near the Pribilof Islands, Alaska, Schneider *et al.* (1990a) observed surface-foraging birds attracted to convergences. This frontal system also supports enhanced stocks of phytoplankton, zooplankton, fish, and subsurface-foraging seabirds such as guillemots *Uria* spp. and Short-tailed Shearwaters *Puffinus tenuirostris* (Kinder *et al.* 1983; Coyle & Cooney 1993; Decker & Hunt 1996; Hunt *et al.* 1996b). Decker & Hunt (1996) showed that patches of acoustically detected biomass associated with the fronts were more likely to be attended by guillemots than were patches closer to, or farther from, the colonies. Decker and Hunt hypothesised that patches at the fronts could be located more predictably than those elsewhere, and were therefore exploited preferentially. Short-tailed Shearwaters also forage near a structural front associated with the 50 m isobath in the southeastern Bering Sea (Troy *et al.* 1989; Schneider & Shuntov 1993). Structural fronts in the Irish Sea and near Bear Island in the Barents Sea are also important for foraging seabirds (Begg & Reid 1997; Mehlum *et al.* 1998b).

Physical processes and the spatial and temporal scale of aggregation

The tightness of spatial and temporal associations of seabirds with hydrographic features varies depending on whether physically forced aggregation or production is the mechanism responsible for elevated prey abundance. When physical processes force prey aggregation, the spatial association between the physical feature and foraging birds usually occurs at small spatial and temporal scales (*e.g.*, Hunt *et al.* 1998). When hydrographic processes at a front enhance nutrient availability and subsequent primary production, aggregations of foraging seabirds may be offset several km to one side or the other of the front. This offset may be the result of drift occurring while the energy made available from primary production passes through the food web to an organism suitable for seabird consumption (Ashmole 1971; Briggs *et al.* 1984; Croll 1990).

The spatial scale of hydrographic features, such as the width of fronts, is influenced by latitudinal variation in the strength of the Coriolis effect. The spatial scale of frontal features approximates the first internal Rossby radius, which is the characteristic scale of pycnocline bending in frontal regions (Franks 1992a). The Rossby radius is determined, in part, by the strength of the Coriolis effect, which increases with latitude. Thus, at high latitudes, all else being equal, the spatial scales of fronts are likely to be smaller than at mid- or low latitudes. A front with a small Rossby radius will have a sharp bend where the pycnocline deviates from the horizontal and the isopycnals will meet the surface at nearly a right angle. This will create a stronger surface front than where the isopycnals meet the surface at a shallow angle. In a limited number of studies, the spatial scales of prey aggregations and foraging seabirds associated with hydrographic features have been similar to the scale of the Rossby radius of the feature (Schneider & Methven 1988; Schneider *et al.* 1990b; Schneider 1994). Because seabirds are more likely to associate with strong than weak fronts (Schneider *et al.* 1987), it would be valuable to see if latitudinal variation in the strength of the Rossby radius or other physical attributes could be used to predict variations in the importance of hydrographic features as mechanisms for concentrating seabird prey.

The time scale of the predictability of prey concentrations varies from hours to seasons, depending on the processes involved (Haury *et al.* 1978, Hunt & Schneider 1987; Cairns & Schneider 1986; Wolanski & Hamner 1988; Schneider 1991). When tidal currents force prey aggregation, the duration of patches will be on the order of hours; when physical processes result in localised enhancement of production, elevated prey abundance may persist for months. If prey are concentrated as a layer on a pycnocline, the vertical location of this concentration will be predictable on time scales from days to months, varying with the frequency of mixing events that are sufficiently strong to disrupt the stratification.

Foraging behaviour of individual birds

Radio-tracking of individual birds has revealed subtleties of behaviour not obvious from ship-based studies of populations (Morris & Black 1980). For example, site-fidelity in foraging seabirds has been demonstrated for several species. As hypothesised by Irons (1998), foraging-site-fidelity should be strongest in situations where prey availability is predictable, and where prey are unlikely to be depleted quickly (*e.g.* Birt *et al.* 1987). Among near-shore surface-

foraging species, Common Terns defended foraging territories and individuals foraged in them repeatedly (Nisbet 1983). In the Wadden Sea, Common Terns adjusted their site-specific foraging activities to coincide with particular phases of the tide, with some sites favoured on the flooding tide and others on the ebbing tide (Becker *et al.* 1993). Common Terns nesting on the mainland coast switched to inland waters to forage during flood and high tide when marine prey were less available (Frank 1992; Wendeln *et al.* 1994). This tidal switch resulted in a corresponding change in food composition: Marine fish were fed to chicks mainly during ebb, and freshwater fish during flood and high water, with individual terns preferring different foraging areas (Becker *et al.* 1993) and food sources (Wendeln *et al.* 1994). In Prince William Sound, Alaska, Irons (1998) showed that individually radio-tracked Black-legged Kittiwakes *Rissa tridactyla* showed strong individual preferences for particular foraging sites. Arrival times at these sites were adjusted daily to coincide with a particular phase of the tide. In the Southern Hemisphere, Wandering *Diomedea exulans* and Black-browed Albatrosses *D. melanophris* made repeat visits to areas previously exploited, but also explored new areas (Weimerskirch *et al.* 1993, 1997).

Among pursuit-diving species, Kuletz (1983) showed that colour-marked Pigeon Guillemots *Cephus columba* in Prince William Sound, Alaska, exhibited individual preferences for different foraging areas and prey types. The recent work of Benvenuti *et al.* (1998) suggests that individual Brünnich's Guillemots *Uria lomvia* may repeatedly visit the same general foraging area. In contrast, the results of Wanless *et al.* (1990, 1991) showed that individual Common Guillemots *U. aalge* and Razorbills *Alca torda* sometimes visited sites on consecutive days, but overall showed little foraging site fidelity, as was also the case for the Shag *Phalacrocorax aristotelis*, a species which is capable of depleting its epibenthic prey (Birt *et al.* 1987).

Learning

The use of physical features that result in prey aggregations requires site-specific knowledge of their location, and for small-scale features that are temporally variable, the times when they are economically exploitable. Learning is an important component of foraging behaviour (Smith & Sweatman 1974; Curio 1976; Lima 1983; Kacelnik & Krebs 1985). Seabirds develop skills for obtaining prey (e.g. Orians 1969; Porter & Sealey 1982; Greig *et al.* 1983) throughout the nonbreeding season without regard to a particular location. However, for birds at breeding colonies, the opportunity to learn about foraging locations near the colonies and the occasions when they are profitable to exploit is confined to the breeding season. Immature seabirds attend colonies for one to several years before commencing to breed (e.g., Hudson 1985), and this period of pre-breeding colony attendance may provide an important opportunity to learn where prey can be harvested profitably. Striking individual differences in use of foraging sites by birds from the same colony (e.g. Kuletz 1983; Gorke & Brandl 1986; McCleary & Sibly 1986; Becker *et al.* 1993; Irons 1998) suggest that learning where, when, and how best to exploit prey around a colony is an individual process, rather than one dependent solely on information transfer within a colony (Ward & Zahavi 1973; Irons 1998). Thus, seabird species dependent on prey resources that are distant from colonies or which exhibit high variability at small scales might be expected

to require more time to learn of foraging sites accessible from breeding colonies, and therefore to commence breeding at an older age (Irons 1998).

Responses of foraging seabirds to the distribution and abundance of prey

How predator populations are distributed with respect to prey populations is a fundamental question in ecology (Fretwell & Lucas 1970; Morris 1987; Kotliar & Wiens 1990). Seabirds are useful organisms with which to study predator-prey interactions because it is possible to obtain information on the distribution and abundance of both predators and prey over a wide range of spatial and temporal scales. Understanding the cues and constraints influencing foraging site selection by seabirds offers tests of theory, as well as information essential for incorporating the foraging requirements of seabirds in ocean management schemes.

To understand the basis for variability in the at-sea distribution and abundance of marine birds, it is necessary to examine not only the variability in prey distributions, but also variability in the associations between seabirds and their prey. When prey are aggregated at the sea surface or there are surface cues about the location of prey concentrations, seabirds can focus their foraging at these sites and aggregations of seabirds and their prey are tightly coupled (Brown 1980; Decker 1995; Goss *et al.* 1996; for a discussion of the use of prey forced to the surface by subsurface foragers, see Ballance & Pitman, this volume). However, when prey are not apparent from a distance or are deep in the water, the spatial relationships between predator and prey may be less tight. Seabird associations with subsurface prey have been investigated using shipboard surveys of seabird populations combined with hydroacoustic surveys of the horizontal and vertical distributions of prey. The results have been mixed, with some studies finding strong positive relationships between seabird predators and their prey, and others demonstrating negatively correlated distributions.

Hydroacoustic methods for delineating the distribution and abundance of prey have revolutionised our ability to examine seabird-prey interactions. Acoustic measures now permit determination of the size of an organism responsible for a particular echo pattern (Madureira *et al.* 1993), and software algorithms allow separation of echoes from different classes of targets, such as zooplankton and small fish (Mitson *et al.* 1996; Swartzman *et al.* 1998). There are also important limitations to the use and interpretation of acoustic surveys. For example, when prey are dispersed among other organisms, it may be difficult to determine either prey distribution or abundance. Because echosounders are deployed at depths of 5 to 10 m, they generally cannot detect prey within 8 to 15 m of the surface. It is particularly difficult to interpret acoustic data from the upper 10 m of the water column because bubbles and turbulence from waves often dominate echo returns.

The ability to detect fine-scale aggregative responses of predators to prey in the field depends, in part, on the investigator's ability to discriminate that portion of the biomass of potential prey to which the predators are responding. For example, in the southeastern Bering Sea in April, Woodby (1984) distinguished between echoes from fish and zooplankton. He found that

guillemot *Uria* spp. density on the water was spatially correlated with zooplankton density in one of two years, but that in neither year did guillemot density reflect fish abundance. In the Barents Sea, Mehlum *et al.* (1996, 1999) separated acoustic returns into those from aggregated prey and those from diffusely distributed prey. They found that correlations between Brünnich's Guillemot numbers and echo strength were stronger when only signals from the aggregated prey were analysed; inclusion of returns from diffuse prey resulted in weaker correlations of a strength similar to those found in a number of earlier studies that integrated all echoes from prey (Hunt *et al.* 1992).

The depth distribution of prey has a significant effect on the responses of foraging seabirds because prey depth affects whether the prey are economically exploitable. Prey below the maximum dive depth of the predator are unlikely to be exploited unless they vertically migrate into the predator's foraging range. At depths shallower than the maximum dive depth of the predator, the economic exploitability of prey will depend on, among other factors, the energetic cost of diving to the prey, the amount of light present, which in part determines the predator's search radius at depth, and the density of prey. Although there is a large body of information on the physiology and cost of diving, there is relatively little information how these costs affect the minimal prey encounter rates needed for profitable foraging dives (Lovvorn & Gillingham 1996). The amount of light available at depth and the optical properties of the water will influence the distance at which prey are visible, and thus the rate at which diving seabirds encounter prey (Eriksson 1985; Wilson *et al.* 1989; Thetmeyer & Kils 1995; Van Eerden & Voslamber 1995). Thus, there are important interactions between depth, prey visibility and prey density that will influence seabird foraging decisions.

The ability to conduct continuous surveys of predators and prey over distances of 100s of km now allows examination of interactions between predators and prey over a wide variety of spatial scales (Schneider 1990, 1993, 1994). Most studies have revealed scale-dependent relationships in the magnitude of the correlations. However, our ability to measure the distributions and abundances of both seabirds and their prey is scale-dependent. Determining the distribution and abundance of foraging seabirds is straightforward at spatial scales of 100s of m to 100s of km. At smaller scales, seabird reactions to ships may prevent determination of foraging locations at scales of m to 100s of m. Additionally, at small scales the distance between where the birds are foraging and where the prey biomass can be measured is often large when compared to the scale of the interaction under study. Because the resolution of patch size is a function of the time or distance over which echo returns are integrated, delineation of prey patches at scales < 100s of m requires slow ship speeds and recording of echoes on a ping by ping basis. When the densest prey patches are on the order of a few m, but echo returns are integrated over distances of 100s of m to km, the importance of these patches is obscured (Dolphin 1987).

Schneider and Duffy (1985) provided one of the first demonstrations of scale-dependency in the aggregative responses of seabirds by showing that the patchiness of seabirds along transects across the Benguela Current system varied with the length of the distance-interval over which survey data were aggregated. During the same period, Safina and Burger (1985, 1989), working

with Common Terns foraging on small fish in tidal inlets in New Jersey showed associations between birds and fish at spatial scales on the order of 10s to 100s of m. Soon thereafter, Schneider and Piatt (1986) and Piatt (1990) showed that the strength of correlations between seabird predators and forage fish prey increased with increasing measurement scale; Atlantic Puffins *Fratercula arctica* and Common Guillemots in Witless Bay, Newfoundland, were associated with the intensity of echoes from capelin *Mallotus villosus* at scales of 5 km or more, but not at smaller scales. In contrast, in Hudson's Bay, Canada, Cairns and Schneider (1990) found that correlations between Brünnich's Guillemots and their prey were insensitive to changes in measurement scale over a range of 50 to 2000 m. In the Antarctic, Heinemann *et al.* (1989) found that correlations between seabirds and krill varied among seabird species and with the spatial scale of the measurement interval.

Although some of the scale-dependence of correlations between seabirds and their prey may reflect a reduction in variance that results from aggregating data, new information derived from spectral and wavelet analyses confirms the scale-dependence of seabird associations with prey. Logerwell *et al.* (1998) have shown that the spectral densities of both guillemot *Uria* spp. and prey biomass in the vicinity of the Pribilof Islands showed peaks at similar measurement scales. Investigation of phase and coherency spectra along individual transects showed that correlations between guillemots and their prey, which were present in extensive layers, were weak at scales below which prey biomass was relatively uniform. Logerwell *et al.* (1998) suggested that at these small scales there would have been only a minimal increase in foraging return if predators had sought to discriminate differences in prey resources. This is the scale at which predators become 'indifferent' to variations in prey density (Kotliar & Wiens 1990). Similarly, Mehlum *et al.* (1999) showed that over distances of 100 m to 10 km correlations between Brünnich's Guillemots and their prey in Størfjorden, Spitsbergen, were weak below the scale of the distance between the centres of prey patches. Wavelet variance for guillemots peaked at a scale similar to the distance between patches (600 m to 2.3 km) and was interpreted as indicating spatial structure in the guillemot distributions at these scales.

An alternative approach has been to examine the fractal geometries of planktivorous auklets and their prey (Russell *et al.* 1992). An object or process is said to be fractal if it exhibits similar patterns regardless of the scale at which it is measured. This property results when variability is autocorrelated across a continuum of spatial scales. Recent work on copepods has shown that their distribution is fractal (Tsuda 1995). Plankton distributions can therefore be viewed as complex resource landscapes with many local peaks and troughs evident at any scale of measurement. For planktivorous seabirds, fractal prey distributions should be desirable because local foraging success should be a useful predictor of foraging success in nearby areas, with the degree of predictability delimited by the fractal dimension. Recent work around the Aleutian Islands has confirmed that the fine-scale correlation between Least Auklets and their prey is stronger when the fractal dimension of the prey distribution is smaller (Russell *et al.* unpublished)

The regional or meso-scale abundance and availability of prey appears to influence the strength of relationships between predators and prey at smaller spatial scales. At a scale of 10s of km, if prey are scarce, isolated dense patches of prey at the scale of 100s of m will be under-utilised. Near Bird Island, South Georgia, Veit *et al.* (1993) showed that the strength of correlations between Macaroni Penguins *Eudyptes chrysolophus* and their prey, Antarctic Krill *Euphausia superba* along radial transects of 98 to 120 km in length were correlated with the biomass of krill along the transect as a whole. Likewise, at a scale of 10 km, Mehlum *et al.* (1998a) showed that the strength of correlations between Brünnich's Guillemots and biomass in the upper water column was positively correlated with the biomass of prey present on 70 km-long transects. These results suggest that at the scale of 10s to 100s of km, seabirds adjust their search patterns depending on the overall likelihood of encountering prey. Proximity of patches of intermediate quality to patches of high quality may also influence predator attendance in the former (Milne *et al.* 1989), although this phenomenon has not been explored in seabirds.

When regional densities of prey are sufficiently high, predators may not invest the time necessary to locate the richest prey patches. Letcher & Rice (1997) modelled the importance of prey patchiness as a function of overall food availability for larval fish. They found that predators benefit most by concentrating foraging in prey patches when overall prey densities are low, and that at high overall prey densities, the importance of concentrating foraging in patches declines. Seabirds appear to follow a similar rule in determining their use of patches. Hunt *et al.* (1990) found that Least Auklets near St. Lawrence Island, Bering Sea, foraged in regions where prey biomass in the upper water column was high (spatial scale of 5 to 8 km), but within these regions, failed to select the densest patches of prey at spatial scales < 1.2 km. Wright & Bailey (1993), in a three year study of the small-scale relationships between foraging seabirds and sandeels *Ammodytes marinus*, found that in two years when regional stocks of sandeels were large, small-scale correlations between foraging seabirds and prey were weak. In the third year, when sandeel stocks were low, there were significant correlations between the densities of sandeels and foraging Shags and Arctic Terns *Sterna paradisaea*. These results imply that when overall prey abundance is above some threshold, seabirds may cease to seek prey patches of the highest biomass.

Evidence for threshold foraging has been found by Piatt (1990) for Common Guillemots and Atlantic Puffins foraging on capelin in the northwest Atlantic, and by Erikstad *et al.* (1990) for guillemots *Uria* spp. foraging on capelin in the Barents Sea. Piatt (1990) found that, at scales of 2 to 6 km, seabirds showed a sigmoidal response to prey density. Among vertebrate predators, the numerical response curve between predator aggregation and prey density is usually sigmoidal (Holling 1959, 1965; Goss-Custard 1970, 1977; Hassell & May 1974; Murdoch & Oaten 1975; Piatt & Methven 1992). A sigmoidal aggregative response suggests that, at low prey densities, it does not pay for a predator to search for prey, whereas above some higher level of prey density, predator satiation occurs and no further aggregation occurs (Hassell & May 1974). Overall high levels of prey may explain why, in the Bransfield Strait region of Antarctica, Obst (1985) was unable to show, at spatial scales of 100s of m, significant correlations between the numbers of foraging storm-petrels and the biomass of Antarctic Krill.

At small spatial scales, correlations between predators and their prey may be negative if the predators deplete local prey patches, or if the prey show a strong escape response that removes them from the vicinity of the predator. In seabirds, Birt *et al.* (1987) demonstrated depletion of epibenthic fish by Shags in the vicinity of a colony. Logerwell & Hargraves (1996) invoked prey escape behaviour to explain a negative correlation between Common Guillemot numbers and the catch of juvenile herring *Clupea harengus* in nets fished within 10 m of the sea surface. These authors found that, at a large spatial scale, there was a positive correlation between guillemots and their prey. They suggested that, at small scales, fish went deeper in the water to avoid the guillemots, and were therefore below the depth at which they were vulnerable to being caught in the near-surface trawls.

OVERVIEW

Evidence from the Northern Hemisphere increasingly supports the importance of small-scale to coarse-scale physical processes that are predictable in time and space for providing foraging opportunities for breeding and migrating seabirds. It is also apparent that seabird foraging aggregations are more likely at features with strong flow gradients (Schneider *et al.* 1987), perhaps because prey patches are more predictably concentrated in a smaller area. As Cairns and Schneider (1990) discuss, the distance at which most Northern Hemisphere seabirds forage from their colonies is 200 km or less, and lateral predictability in ocean systems at this spatial scale is typically high only in shallow water where currents interact with topography to produce predictable surface features that can aggregate prey. In the Southern Hemisphere, seabirds also forage at physical features, such as shelf-edge fronts and the Polar Front (Jouventin & Weimerskirch 1990; Weimerskirch *et al.* 1988, 1993; Brost *et al.* 1997; Guinet *et al.* 1997), but in many instances these features occur over larger spatial scales (10s to 100s of km) than the nearshore features commonly used by breeding seabirds in the Northern Hemisphere. The more economical flight patterns (Pennycuik 1982, 1987) and longer duration of provisioning trips of many Southern Hemisphere species may facilitate economical use of these large-scale features that are often distant from colonies.

There are a number of features of seabird foraging that may work against foraging distributions reflecting an ideal free distribution with respect to prey abundance. Colony location presents constraints on the selection of foraging sites by breeding birds. Subsurface-foraging seabirds forage under the constraint of imperfect knowledge of prey distributions. Prey depth, water clarity and ambient light levels will all affect the ability of seabirds to assess prey stocks. Sub-surface foragers also face considerable costs in gaining information about the quality or quantity of food beneath them, and in moving to a new location should prey abundance be less than the regional mean. Not only are flight costs great, but the effort expended in taking flight appears considerable for many species. Seabirds gain knowledge about foraging opportunities from prior experience during which they may select preferred foraging sites or prey types, and from watching other birds (Hunt *et al.* 1991; Haney *et al.* 1992). In either case, the likelihood of a full appraisal of prey abundance in the foraging arena is compromised.

Given the above constraints, and no doubt others, it is perhaps surprising that seabirds, in particular subsurface foragers, show significant spatial and numerical correlations with the abundance of prey over a wide range of spatial scales. Although some of these studies have been conducted in areas with strong physical features that may have provided clues about the location of prey, many were conducted in water that was relatively uniform in the horizontal over the spatial scales investigated. In these cases seabirds must have adjusted their distributions with respect to that of their prey, possibly over a considerable period of time. Whereas we are now beginning to develop the survey and statistical tools to investigate relationships between foraging seabirds and their prey, we know remarkably little about how birds find their prey and the constraints on the formation of associations with prey.

FUTURE WORK

Past work has focused on small-scale, predictably locatable foraging sites near colonies. We have little information on seabird foraging that relies on areas of the open sea where predictably locatable prey concentrations may be lacking. For species restricted to inshore or shelf waters, the presence of numerous physical features at which prey might concentrate makes it likely that these processes play an important role in seabird foraging ecology. Although seabird species that range widely over the open ocean may forage more opportunistically than inshore species, it is likely that they concentrate their foraging at meso-scale hydrographic features where prey biomass is elevated (e.g., Briggs *et al.* 1984; Prince *et al.* 1988; Weimerskirch *et al.* 1993). Knowledge about the foraging behaviour of seabirds over the open ocean is more likely to come from tracking the movements of individual birds than from shipboard surveys.

We also know little about the foraging strategies and habitat selection of seabirds in winter. There are a modest number of studies of transequatorial migrants that use summer foraging conditions in another hemisphere (e.g., Brown 1980; Brown *et al.* 1981; Hoffman *et al.* 1981; Haney & McGillivray 1985a; Briggs *et al.* 1987; Troy & Johnson 1989; Troy & Bradstreet 1991; Hunt *et al.* 1996b), but information on winter distribution and especially foraging ecology under winter conditions is scarce (Brown 1988; Divoky 1979; Irving *et al.* 1970; Powers & Brown 1987; Briggs *et al.* 1987). Many species of zooplankton descend to depth in winter and are unavailable to near-surface-foraging seabirds. Thus it is not clear what prey are available to planktivores in winter. Likewise, fish and other nekton may be deeper in the water column in winter. A combination of winter ship-board surveys and long-range tracking of known individuals is needed to fill this important gap in our knowledge about how seabirds survive winters.

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REFERENCES

- Ainley, D.C. & Jacobs, S.S.** 1981. Seabird affinities for ocean and ice edge boundaries in the Antarctic. *Deep Sea Research* 28: 1173-1186.
- Ashmole, N.P.** 1971. Seabird ecology and the marine environment. In: Farner, D.S. & King, J.R. (eds). *Avian Biology* Vol. I; New York; Academic Press: 223-286
- Becker, P.H., Frank, D. & Sudmann, S.R.** 1993. Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389-393.
- Begg, G.S. & Reid, J.B.** 1997. Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES Journal of Marine Science* 54: 552-565.
- Benvenuti, S., Bonadonna, F., Dall'Antonia, L. & Gudmundsson, G.A.** 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115: 57-66.
- Birt, V.L., Birt, T.P., Cairns, D.K. & Montevecchi, W.A.** 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40: 205-208.
- Bradstreet, M.S.W.** 1980. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. *Canadian Journal of Zoology* 58: 2120-2140.
- Braune, B.M. & Gaskin, D.E.** 1982. Feeding ecology of nonbreeding populations of Larids off Deed Island, New Brunswick. *Auk* 99: 67-76.
- Briggs, K.T., Dettman, K.F., Lewis, D.B. & Tyler, W.B.** 1984. Phalarope feeding in relation to autumnal upwelling off California. In: Nettleship, D.N., Sanger, G.A., & Springer, P.A. (eds.) *Marine birds: Their feeding ecology and commercial fisheries relationships*. Ottawa; Canadian Wildlife Service Special Publication: 51-64.
- Briggs, K.T., Tyler, W.B., Lewis, D.B. & Carlson, D.R.** 1987. Bird communities at sea off California: 1975-1983. *Studies in Avian Biology* 11.
- Brost, C.A., Georges, J.Y., Guinet, C., Cherel, Y., Puetz, K., Charrassin, J.B., Handrich, Y., Zorn, T., Lage, J. & Le Maho, Y.** 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology Progress Series* 150: 21-33.
- Brown, R.G.B.** 1980. Seabirds as marine animals. In: Burger, J., Olla, B.L., & Winn, H.E. (eds.) *Behavior of marine animals*. Vol. 4; New York; Plenum Press: 1-39.
- Brown, R.G.B.** 1988. Oceanographic factors as determinants of the winter range of the Dovekie (*Alle alle*) off Atlantic Canada. *Colonial Waterbirds* 11: 176-180.
- Brown, R.G.B., Barker, S.P., Gaskin, D.E. & Sandeman, M.R.** 1981. The foods of the Great and Sooty Shearwaters *Puffinus gravis* and *P. griseus* in eastern Canadian waters. *Ibis* 123: 19-30.
- Brown, R.G.B. & Gaskin, D.E.** 1988. The pelagic ecology of the Gray and Red-necked Phalaropes *Phalaropus fulicarius* and *P. lobatus* in the Bay of Fundy, eastern Canada. *Ibis* 130: 234-250.
- Burger, A.E. & Wilson, R.P.** 1988. Capillary-tube depth gauges for diving animals: an assessment of their accuracy and methods of deployment. *Journal of Field Ornithology* 59: 345-354.

- Cairns, D.K. & Schneider, D.C.** 1990. Hot spots in cold water: feeding habitat selection by Thick-billed Murres. *Studies in Avian Biology* 14: 52-60.
- Coyle, K.O. & Cooney, R.T.** 1993. Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea. *Continental Shelf Research* 13: 803-827.
- Coyle, K.O., Hunt, G.L., Jr., Decker, M.B. & Weingartner, T.J.** 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. *Marine Ecology Progress Series* 83: 1-14.
- Croll, D.A.** 1990. Physical and biological determinants of the abundance, distribution, and diet of the Common Murre in Monterey Bay, California. *Studies in Avian Biology* 14: 139-148.
- Curio, E.** 1976. *The Ethology of Predation*. Berlin; Springer-Verlag: 250pp.
- Decker, M.B.** 1995. Influences of oceanographic processes on seabird ecology. PhD Thesis, University of California, Irvine, California, USA.
- Decker, M.B. & Hunt, G.L., Jr.** 1996. Foraging by murres (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Marine Ecology Progress Series* 139: 1-10.
- Divoky, G.J.** 1979. Sea ice as a factor in seabird distribution and ecology in the Beaufort, Chukchi and Bering seas. In: Bartonek, J.C. & Nettleship, D.N. (eds.) *Conservation of marine birds of northern North America*. U.S. Fish and Wildlife Service Wildlife Research Report 11: 9-18.
- Dolphin, W.F.** 1987. Prey densities and foraging of Humpback Whales, *Megaptera novaeangliae*. *Experientia* 43: 468-471.
- Elphick, C.S. & Hunt, G.L., Jr.** 1993. Variations in the distributions of marine birds with water mass in the northern Bering Sea. *Condor* 95: 33-44.
- Erikstad, K.E., Moum, T. & Vader, W.** 1990. Correlations between pelagic distribution of Common and Brünnich's Guillemots and their prey in the Barents Sea. *Polar Research* 8: 77-87.
- Eriksson, M.O.G.** 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. *Ornis Scandinavica* 16: 1-7.
- Frank, D.** 1992. The influence of feeding conditions on food provisioning of chicks in Common Terns *Sterna hirundo* nesting in the German Wadden Sea. *Ardea* 80: 45-55.
- Frank, D. & Becker, P.H.** 1992. Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. *Ardea* 80: 57-69.
- Franks, P.J.S.** 1992a. Phytoplankton blooms at fronts: patterns, scales and physical forcing mechanisms. *Reviews in Aquatic Science* 6: 121-137.
- Franks, P.J.S.** 1992b. Sink or swim: accumulation of biomass at fronts. *Marine Ecology Progress Series* 82: 1-12.
- Fretwell, S.D. & Lucas, H.L., Jr.** 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.

- Frick, S. & Becker, P.H.** 1995. Unterschiedliche Ernährungsstrategien von Fluss- und Küstenseeschwalbe (*Sterna hirundo* und *S. paradisaea*) im Wattenmeer. *Journal für Ornithologie* 136: 47-63.
- Gibb, J.A.** 1962. Tinbergen's hypothesis of the role of specific search images. *Ibis* 104: 106-111.
- Gorke, M. & Brandl, R.** 1986. How to live in colonies: spatial foraging strategies of the black-headed gull. *Oecologia* 70: 288-290.
- Goss, C., Bone, D.G., Peck, J.M., Everson, I., Hunt, G.L., Jr. & Murray, A.W.A.** 1997. Small-scale interactions between prions *Pachyptila* spp. and their zooplankton prey at an inshore site near Bird Island, South Georgia. *Marine Ecology Progress Series* 154: 41-51.
- Goss-Custard, J.N.** 1970. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *Journal of Animal Ecology* 39: 91-113.
- Goss-Custard, J.N.** 1977. Responses of redshank, (*Tringa totanus*), to the absolute and relative densities of two prey species. *Journal of Animal Ecology* 46: 867-874.
- Greig, S.A., Coulson, J.C. & Monaghan, P.** 1983. Age-related differences in foraging success in the herring gull (*Larus argentatus*). *Animal Behavior* 31: 1237-1243.
- Guinet, C., Khouidil, M., Bost, C.A., Durbec, J.P., Georges, J.Y., Mouchot, M. & Jouventin, P.** 1997. Foraging behaviour of satellite-tracked King Penguins in relation to sea-surface temperatures obtained by satellite telemetry at Crozet Archipelago, a study during three austral summers. *Marine Ecology Progress Series* 150: 11-20.
- Haney, J.C.** 1986. Seabird segregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series* 28: 279-285.
- Haney, J.C.** 1991. Influence of pycnocline topography and water-column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, Northern Bering Sea, Alaska. *Marine Biology* 110: 419-435.
- Haney, J.C., Frstrup, K.M. & Lee, D.S.** (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica* 23: 49-62.
- Haney, J.C. & McGillivray, P.A.** 1985a. Aggregations of Cory's Shearwaters (*Calonectris diomedea*) at Gulf Stream fronts. *Wilson Bulletin* 97: 191-200.
- Haney, J.C. & McGillivray, P.A.** 1985b. Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. *Biological Oceanography* 3: 401-430.
- Harrison, N.M., Hunt, G.L., Jr. & Cooney, R.T.** 1990. Front affecting the distribution of seabirds in the northern Bering Sea. *Polar Research* 8: 29-31.
- Hassell, M.P. & May, R.M.** 1974. Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43: 567-594.
- Haury, L.R., McGowan, J.A. & Wiebe, P.H.** 1978. Patterns and processes in the time-space scales of plankton distribution. In: Steele, J.H. (ed.) *Pattern in plankton communities*. New York; Plenum Press: 277-327.
- Heinemann, D., Hunt, G.L., Jr. & Everson, I.** 1989. The distribution of marine avian predators and their prey, *Euphausia superba*, in Bransfield Strait and Southern Drake Passage, Antarctica. *Marine Ecology Progress Series* 58: 3-16.

- Hoffman, W., Heinemann, D., Weins, J.A.** 1981. The ecology of seabird feeding flocks in Alaska. *Auk* 98: 437-456.
- Holling, C.S.** 1959. The components of predation as revealed by a study of small mammal predation on the European pine sawfly. *Canadian Entomologist* 91: 293-320.
- Holling, C.S.** 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45: 1-60.
- Hudson, P.J.** 1985. Population parameters for the Atlantic Alcidae. In: Nettleship, D.N. & Birkhead, T.R. (eds) *The Atlantic Alcidae*. London, UK; Academic Press: 233-261.
- Hunt, G.L., Jr., Bakken, V. & Mehlum, F.** 1996a. Marine Birds in the marginal ice zone of the Barents Sea in late winter and spring. *Arctic* 49: 53-61.
- Hunt, G.L., Jr., Coyle, K.O., Hoffman, S., Decker, M.B. & Flint, E.N.** 1996b. Foraging ecology of Short-tailed Shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series* 141: 1-11.
- Hunt, G.L., Eppley, Z. & Drury, W.H.** 1981a. Breeding distribution and reproductive biology of eastern Bering Sea marine birds. In: Hood, D.W. & Calder, J.A. (eds) *The Bering Sea Shelf: Oceanography and Resources*. Washington D.C.; NOAA: 649-687.
- Hunt, G.L., P. Gould, D.J. Forsell, and H. Peterson.** 1981b. Pelagic distribution of marine birds in the eastern Bering Sea. In: Hood, D.W. & Calder, J.A. (eds) *The Bering Sea Shelf: Oceanography and Resources*. Washington D.C.; NOAA: 689-718.
- Hunt, G.L., Jr., & Harrison, N.M.** 1990. Foraging habitat and prey taken by Least Auklets at King Island, Alaska. *Marine Ecology Progress Series* 65: 141-150.
- Hunt, G.L., Jr., Harrison, N.M. & Cooney, R.T.** 1990. Foraging of Least Auklets: the influence of hydrographic structure and prey abundance. *Studies in Avian Biology* 14: 7-22.
- Hunt, G.L., Jr., Heinemann, D. & Everson, I.** 1992. Distributions and predator-prey interactions of Macaroni Penguins, Antarctic Fur Seals and Antarctic Krill near Bird Island, South Georgia. *Marine Ecology Progress Series* 86:15-30.
- Hunt, G.L., Jr., Piatt, J.F., Erikstad, K.E.** 1991. How do foraging seabirds sample their environment? *Acta XX Congressus Internationalis Ornithologi* : 2272-2279.
- Hunt, G.L., Jr., Russell, R.W., Coyle, K.O. & Weingartner, T.** 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* : In Press.
- Hunt, G.L., Jr. & Schneider, D.C.** 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall, J. P. (ed.) *Seabirds: feeding biology and role in marine ecosystems*. Cambridge; Cambridge University Press: 7-41.
- Irons, D.B.** 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647-655.
- Irving, L., McRoy, C.P. & Burns, J.J.** 1970. Birds observed during a cruise in the ice-covered Bering Sea. *Condor* 72: 110-112.

- Jouventin, P. & Weimerskirch, H.** 1990. Satellite tracking of Wandering Albatrosses. *Nature* 343: 746-748.
- Kacelnik, A. & Krebs, J.R.** 1985. Learning to exploit patchily distributed food. In: Sibley, R.M., Smith, R.H. (eds) *Behavioural Ecology*. Oxford; Blackwell: 189-205.
- Kinder, T.H., Hunt, G.L., Jr., Schneider, D.C. & Schumacher, J.D.** 1983. Correlation between birds and oceanic fronts around the Pribilof Islands, Alaska. *Estuarine Coastal and Shelf Science* 16: 163-299.
- Kotliar, N.B. & Wiens, J.A.** 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260.
- Kuletz, K.J.** 1983. Mechanisms and consequences of foraging behavior in a population of Pigeon Guillemots. M.Sc. Thesis, University of California, Irvine, California, USA.
- Letcher, B.H. & Rice, J.A.** 1997. Prey patchiness and larval fish growth and survival: inferences from an individual-based model. *Ecological Modeling* 95: 29-43.
- Lima, S.** 1983. Downy Woodpecker foraging behavior: foraging by expectation and energy intake rate. *Oecologia* 58: 232-237.
- Logerwell, E.A. & Hargraves, N. B.** 1996. The distribution of seabirds relative to their fish prey off Vancouver Island: opposing results at large and small scales. *Fisheries Oceanography* 5: 163-175.
- Logerwell, E.A., Hewitt, R. & Demer, D.A.** 1998. Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography*: In Press.
- Lovvorn, J.R. & Gillingham, M.P.** 1996. Food dispersion and foraging energetics: A mechanistic synthesis for field studies of avian benthivores. *Ecology* 77: 435-451.
- Madureira, L.S.P., Ward, P. & Atkinson, A.** 1993. Differences in backscattering strength determined at 120 kHz and 38 kHz for three species of Antarctic macrozooplankton. *Marine Ecology Progress Series* 93: 17-24.
- McCleary, R.H. & Sibly, R.M.** 1986. Feeding specialization and preference in Herring Gulls. *Journal of Animal Ecology* 55: 245-259.
- Mehlum, F., Hunt, G.L., Jr., Klusek, Z., Decker, M.B. & Nordland, N.** 1996. The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. *Polar Biology* 16: 537-547.
- Mehlum, F., Hunt, G.L., Jr., Klusek, Z. & Decker, M.B.** 1999. Scale-dependent correlations between the abundance of Brünnich's Guillemots and their prey. *Journal of Animal Ecology* 68: 60-72.
- Mehlum, F., Nordlund, N. & Isaksen, K.** 1998. The importance of the 'Polar Front' as a foraging habitat for guillemots *Uria* spp. breeding at Bjørnøya, Barents Sea. *Journal of Marine Systems* 14: 27-43.
- Milne, B.T., Johnston, K. & Forman, R.T.T.** 1989. Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. *Landscape Ecology* 2: 101-110.
- Mitson, R.B., Simard, Y. & Goss, C.** 1996. Use of two-frequency algorithm to determine size and abundance of plankton in three widely spaced locations. *ICES Journal of Marine Science* 53: 209-215.
- Morris, D.W.** 1987. Ecological scale and habitat use. *Ecology* 68: 362-369.

- Morris, R.D. & Black, J.E.** 1980. Radiotelemetry and Herring Gull foraging patterns. *Journal of Field Ornithology* 51: 110-118.
- Murdoch, W.W. & Oaten, A.** 1975. Predation and population stability. *Advances in Ecological Research* 9: 1-125.
- Nisbet, I.C.T.** 1983. Territorial feeding by Common Terns. *Colonial Waterbirds* 6: 64-70.
- Obst, B.S.** 1985. Densities of Antarctic seabirds at sea and the presence of the krill *Euphausia superba*. *Auk* 102: 540-549.
- Orians, G.H.** 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). *Animal Behavior* 17: 316-319.
- Pennycook, C.J.** 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Philosophical Transactions of the Royal Society London B* 300: 75-106.
- Pennycook, C.J.** 1987. Flight of auks (Alcidae) and other northern seabirds as compared with southern Procellariiformes: ornithological observations. *Journal of Experimental Biology* 128: 335-347.
- Piatt, J.F.** 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *Studies in Avian Biology* 14: 36-51.
- Piatt, J.F. & Methven, D.A.** 1992. Threshold foraging behavior of baleen whales. *Marine Ecology Progress Series* 84: 205-210.
- Pingree, R.D., Forster, G.R. & Morrison, G.K.** 1974. Turbulent convergent tidal fronts. *Journal of the Marine Biological Association of the UK* 54: 469-479.
- Pingree, R.D., Pugh, P.R., Holligan, P.M. & Forster, G.R.** 1975. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature, London* 258: 672-677.
- Porter, J.M. & Sealey, S.G.** 1982. Dynamics of seabird multispecies flocks: age-related feeding behaviour. *Behaviour* 81: 91-109.
- Powers, K.D. & Brown, R.G.B.** 1987. Seabirds. In: Backus, R.H. & Bourne, D.W. (eds) *Georges Bank*. Cambridge, Massachusetts; MIT Press: 359-371.
- Prince, P.A., Croxall, J.P., Trathan, P.N., & Wood, A.G.** 1998. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. In: Robertson, G. & Gales, R. (eds) *Albatross biology and conservation*. Chipping Norton, Australia; Surrey Beatty & Sons: 137-167.
- Richardson, K. & Christoffersen, A.** 1991. Seasonal distribution and production of phytoplankton in the southern Kattegat. *Marine Ecology Progress Series* 78: 217-227.
- Russell, R.W. & Hunt, G.L., Jr. Coyle, K.O., Cooney, R.T.** 1992. Foraging in a fractal environment: spatial patterns in a marine predator-prey system. *Journal of Landscape Ecology* 7: 195-209.
- Safina, C. & Burger, J.** 1985. Common Tern foraging: seasonal trends in prey fish densities and competition with blue-fish. *Ecology* 66: 1457-1463.

- Safina, C. & Burger, J.** 1989. Ecological dynamics among prey fish, bluefish, and foraging Common Terns in an Atlantic coastal system. In: Burger, J. (ed) Seabirds and other marine vertebrates. New York; Columbia University Press: 95-173.
- Sambroto, R.N., Niebauer, H.J., Georing, J.J. & Iverson, R.L.** 1986. Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. *Continental Shelf Research* 5: 161-198.
- Schneider, D.C.** 1982. Fronts and seabird aggregations in the southeastern Bering Sea. *Marine Ecology Progress Series* 10: 101-103.
- Schneider, D.C.** 1990. Spatial autocorrelation in marine birds. *Polar Research* 8: 89-97.
- Schneider, D.C.** 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanography and Marine Biology, Annual Review* 29: 487-521.
- Schneider, D.C.** 1993. Scale-dependent spatial dynamics: marine birds in the Bering Sea. *Biological Review* 68: 579-598.
- Schneider, D.C.** 1994. Scale-dependent patterns and species interactions in marine necton. In: Giller, P.S., Hildrew, A.G. & Raffaelli, D.G. (eds) *Aquatic Ecology; scale, pattern and process*. Oxford; Blackwell Scientific publications: 441-467.
- Schneider, D.C. & Duffy, D.C.** 1985. Scale-dependent variability in seabird abundance. *Marine Ecology Progress Series* 25: 211-218.
- Schneider, D.C., Harrison, N.M. & Hunt, G.L., Jr.** 1987. Variation in the occurrence of marine birds at fronts in the Bering Sea. *Continental Shelf Research* 5: 241-258.
- Schneider, D.C., Harrison, N.M. & Hunt, G.L., Jr.** 1990a. Seabird diet at a front near the Pribilof Islands, Alaska. *Studies in Avian Biology* 14: 61-66.
- Schneider, D.C. & Methven, D.A.** 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. *Journal of Marine Research* 46: 105-118.
- Schneider, D.C. & Piatt, J.F.** 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Marine Ecology Progress Series* 32: 237-246.
- Schneider, D.C., Pierotti, C.R. & Threlfall, W.** 1990b. Alcids patchiness and flight direction near a colony in eastern Newfoundland. *Studies in Avian Biology* 14: 23-35.
- Schneider, D.C. & Shuntov, V.P.** 1993. The trophic organization of the marine bird community in the Bering Sea. *Reviews of Fisheries Science* 1: 311-335.
- Schumacher, J.D., Kinder, T.H., Pashinski, D.J. & Charnell, R.L.** 1979. A structural front over the continental shelf of the eastern Bering Sea. *Journal of Physical Oceanography* 9: 79-87.
- Simard, Y., de Ladurantaye, R. & Therriault, J.** 1986. Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Marine Ecology Progress Series* 32: 203-215.
- Simpson, J.H. & Pingree, R.D.** 1978. Shallow fronts produced by tidal stirring. In: Bowman, M.J. & Esias, W.E. (eds) *Oceanic fronts in coastal processes*. Berlin; Springer: 29-42.

- Smith, J. & Sweatman, H.P.A.** 1974. Food-searching behavior of titmice in patchy environments. *Ecology* 55: 1216-1232.
- Springer, A.M. & Roseman, D.G.** (1985) Copepod-based food webs: auklets and oceanography in the Bering Sea. *Marine Ecology Progress Series* 21: 229-237.
- Swartzman, G., Brodeur, R., Napp, J., Walsh, D., Hewitt, R., Demer, D., Hunt, G. & Logerwell, E.** 1998. Relating spatial distributions of acoustically determined patches of fish and plankton: Image analysis, data viewing, and spatial proximity. *Canadian Journal of Fisheries and Aquatic Science*: In Press.
- Thetmeyer, H. & Kils, U.** 1995. To see and not be seen: the visibility of predator and prey with respect to feeding behaviour. *Marine Ecology Progress Series* 126: 1-8.
- Troy, D.M. & Johnson, S.R.** 1989. Marine Birds, Section 6 In: Truett, J. C. (ed.) Environmental characterization and biological utilization of the North Aleutian Shelf nearshore zone. Washington, D.C.; NOAA, Outer Continental Shelf Environmental Assessment Program, Final Reports of Principal Investigators 60: 453.355-453.
- Tsuda, A.** 1995. Fractal distribution of an oceanic copepod *Neocalanus cristatus* in the subarctic Pacific. *Journal of Oceanography* 51: 261-266.
- Van Eerden, M.R. & Voslamber, B.** 1995. Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at Lake IJsselmeer, The Netherlands: a recent and successful adaptation to a turbid environment. *Ardea* 83: 199-212.
- Vermeer, K., Szabo, I. & Greisman, P.** 1987. The relationship between plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. *Journal of Plankton Research* 9: 483-501.
- Veit, R.R. & Hunt, G.L., Jr.** 1991. BROADSCALE DENSITY AND AGGREGATION OF PELAGIC BIRDS FROM A CIRCUMNAVIGATIONAL SURVEY OF THE ANTARCTIC OCEAN. *Auk* 108: 790-800.
- Veit, R.R. & Hunt, G.L., Jr.** 1992. The spatial dispersion of seabirds near the South Orkney Islands and the Weddell-Scotia confluence. *Polar Biology* 11: 637-641
- Veit, R.R., Silverman, E.D. & Everson, I.** 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *Journal of Animal Ecology* 62: 551-564.
- Wanless, S., Harris, M.P. & Morris, J.A.** 1990. A comparison of feeding areas used by individual Common Murres (*Uria aalge*) Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the breeding season. *Colonial Waterbirds* 13: 16-24.
- Wanless, S., Harris, M.P. & Morris, J.A.** 1991. Foraging range and feeding locations of Shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* 133: 30-36.
- Ward, P. & Zahavi, A.** 1973. The importance of certain assemblages of birds as 'information centres' for food-finding. *Ibis* 115: 517-534.
- Weimerskirch, H., Bartle, J.A., Jouventin, P., Stahl, J.C.** 1988. Foraging ranges and partitioning of feeding zones in three species of southern Albatrosses. *Condor* 90: 214-219.
- Weimerskirch, H., Mougey, T. & Hindermeier, X.** 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to requirements of the chick: natural variation and experimental study. *Behavioural Ecology* 8: 635-643.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110: 325-342.

Wendeln, H., Mickstein, S. & Becker, P.H. 1994. Auswirkungen individueller Ernährungsstrategien von Flussseseschwalben (*Sterna hirundo*) auf die Anwesenheit am Koloniestandort. *Vogelwarte* 37: 290-303.

Whitledge, T.E., Reeburgh, W.S. & Walsh, J.J. 1986. Seasonal inorganic nitrogen distribution and dynamics in the southeastern Bering Sea. *Continental Shelf Research* 5: 109-132.

Whitledge, T.E. & Walsh, J.J. 1986. Biological processes associated with the pycnocline and surface fronts in the southeastern Bering Sea. In: Nihoul, J.C.J. (ed) *Ecohydrodynamics, Proceedings of the 17th International Liege Colloquium on Ocean Hydrodynamics*: 655-670.

Wilson, R.P. & Bain, C.R. 1984. An inexpensive depth gauge for penguins. *Journal of Wildlife Management* 48: 1077-1084.

Wilson, R.P., Culik, B., Coria, N.R., Adelung, D. & Spairani, H.J. 1989. Foraging rhythms in Adélie Penguins (*Pygoscelis adeliae*) at Hope Bay, Antarctica; Determination and control. *Polar Biology* 10: 161-165.

Wolanski, E. & Hamner, W.M. 1988. Topographically controlled fronts in the ocean and their biological influences. *Science* 241: 177-181.

Woodby, D. 1984. The April distribution of murre and prey patches in the southeastern Bering Sea. *Limnology and Oceanography* 29: 181-188.

Wright, P.J. & Bailey, M.C. 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Fisheries Research Services Report 14/93. Marine Laboratory Aberdeen.