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Physics, zooplankton, and the distribution of least auklets in the Bering Sea – a review

George L. Hunt Jr



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In the eastern Bering Sea, the overall distribution of least auklets (*Aethia pusilla*) reflects the distribution of different water masses and their associated plankton communities. Within these water masses, the foraging distribution of least auklets is influenced by physical processes that result in predictable aggregations of prey, most often because of property or flow gradients with which the plankton interact. Examples include the accumulation of zooplankton at, or above, the pycnocline and near-surface patches of plankton concentrated in downwellings formed at convergences. These small-scale processes influence avian use of the larger-scale features. Breeding colonies of least auklets are located within commuting distance of physical features in the ocean at which appropriate prey are concentrated; where large copepods or physical features to concentrate them are absent, auklets do not breed. Thus, control of the distribution of foraging seabirds and their breeding colonies in the eastern Bering Sea is a multi-scale process.

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Key words: *Aethia pusilla*, Bering Sea, biological–physical coupling, foraging ecology, least auklet, multi-scale analysis, seabird.

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Introduction

In this paper, I focus on the foraging ecology of least auklets (*Aethia pusilla*) in the Bering Sea as a means of understanding both their distribution at sea and the location of their colonies in the Bering region. The distribution and availability of planktonic prey result from interaction between plankton populations and physical processes that influence production, vertical distribution, and aggregation. Thus, the foraging distributions of planktivorous seabirds should reflect the locations of physical processes that play a major role in determining the distribution and abundance of planktonic prey. Nesting least auklets are constrained to visit their colonies two to three times daily, and colonies are thus limited to locations of appropriate nesting habitat within commuting distance of water masses where large copepods are abundant and concentrated near the surface.

In Alaska, the breeding distribution of least auklets is well documented (Sowls *et al.*, 1978), as is their at-sea distribution (Hunt *et al.*, 1981c; Gould *et al.*, 1982). Several generalizations explain these distribution patterns in terms of water-mass origins and the types of prey present in the water mass (Drury *et al.*, 1981; Hunt

et al. 1981b, c; Springer and Roseneau, 1985; Springer *et al.*, 1987; Piatt and Springer, 1992). Additionally, within the preferred foraging habitats, auklet densities are not uniform, and exploration of these smaller-scale patterns provides insight into the larger-scale patterns of their distribution. Finally, because the ability to relate the foraging distributions of seabirds to the distribution and abundance of their prey is critical in the process of interpreting their use of situations in which physical processes concentrate prey, I discuss some recent efforts to relate the abundance of foraging least auklets to the abundance of their prey, thus using a multi-scale approach in trying to understand the overall distributions of these seabirds in the eastern Bering Sea.

Oceanography of the eastern Bering Sea

The eastern Bering Sea covers a continental shelf that is up to 500 km wide (Fig. 1). The south-eastern Bering Sea is differentiated into four domains on the basis of hydrographic structure and currents, and these domains are associated with characteristic bottom depths (Kinder and Schumacher, 1981a, b; Coachman, 1986; Schumacher and Stabeno, in press). The Coastal Domain occurs shoreward of the 50 m isobath and is

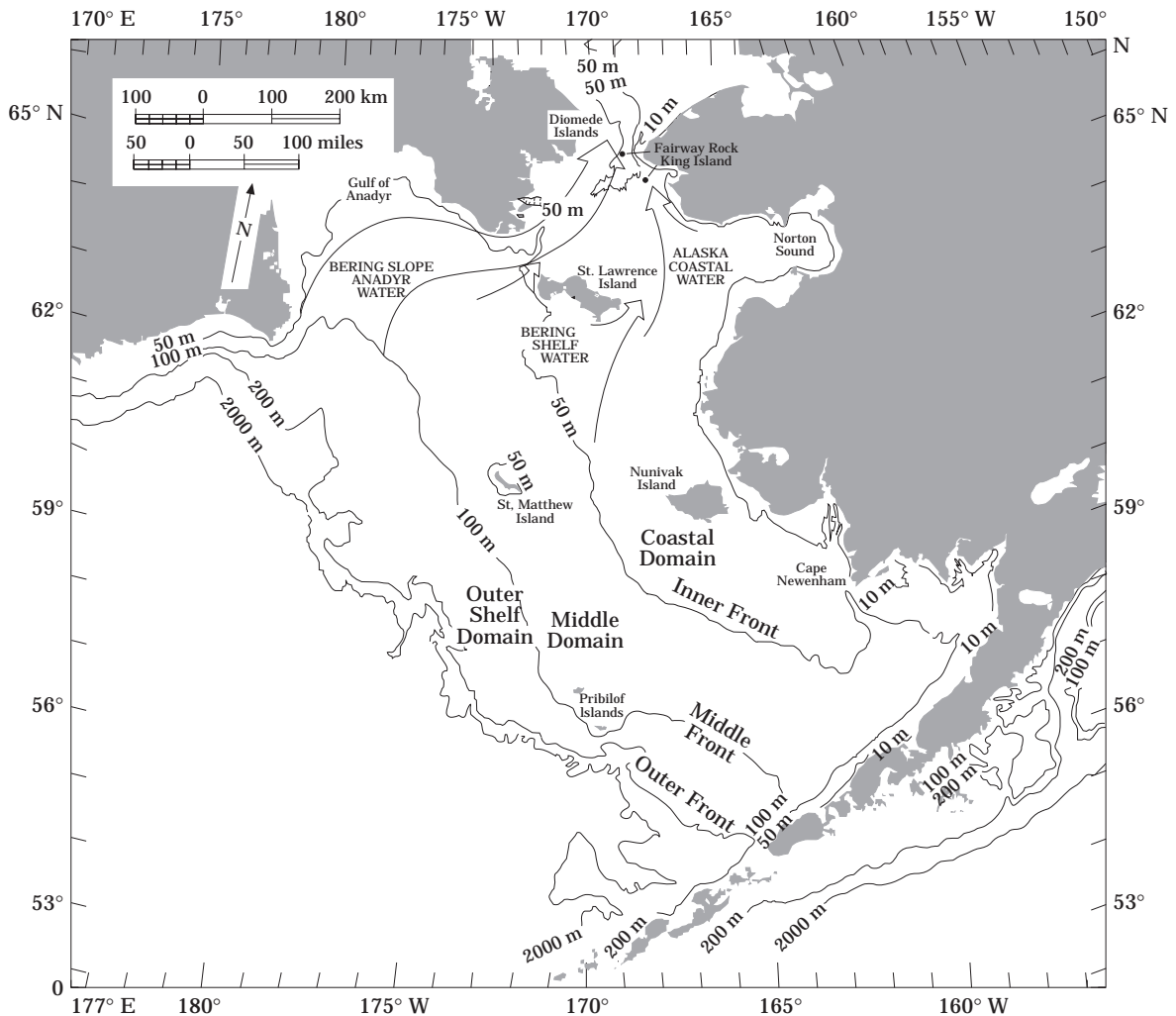


Figure 1. The eastern Bering Sea, showing the 50 m, 100 m, and 200 m contours with which the fronts between the Coastal and Middle Shelf Domains, the Middle Shelf and Outer Domains, and the Outer and Shelf-Slope Domains, respectively, are associated.

either weakly stratified or well mixed as a result of mixing by tidal currents and winds. In the Coastal Domain, primary production, plankton populations and energy pathways have received little study.

The Middle Shelf Domain, between 50 m and 100 m deep, varies seasonally in structure. In winter, storms and cold temperatures result in a well-mixed water column. However, in spring, with the warming of low salinity surface water derived from ice melt, a two-layered system develops and remains throughout the summer and early autumn. In the Middle Shelf Domain, mixing energy in summer is not sufficient to break down this stratification. The grazing community of the Middle Shelf Domain is unable to capture fully the production of the spring phytoplankton bloom, so much of the bloom settles to the bottom where it supports a rich benthic and epibenthic community (Walsh and McRoy, 1986).

The Outer Shelf Domain occurs in waters between 100 m and 200 m deep and is a three-layer system. It is influenced by both shelf water and deep, oceanic water that is transported onto the shelf by the tides. In contrast to the Middle Shelf Domain, oceanic copepods in the Outer Shelf Domain capture much of the spring production and provide the basis for a rich pelagic community (Walsh and McRoy, 1986). The Shelf Slope Domain occupies water deeper than 200 m along the shelf edge.

In the northern Bering Sea, the Chirikov Basin is a region of shallow water, on average less than 50 m deep, between St Lawrence Island and the Bering Strait and between Siberia and the Seward Peninsula of Alaska (Fig. 1). Two major currents enter the basin, the Anadyr Current along the west side, and the Alaska Coastal Water along the east side (for an overview, see Piatt and Springer, 1992). Between these, Bering Shelf Water

enters the basin from the south, around St Lawrence Island. The Anadyr Current originates along the shelf slope of the Bering Sea (Coachman *et al.*, 1975) and supports a copepod community dominated by *Neocalanus plumchrus*, *N. cristatus*, and *Eucalanus bungii* (Brodskii, 1950; Springer *et al.*, 1987, 1989; Hunt and Harrison, 1990). In contrast, Alaska Coastal Water originates in the Gulf of Alaska, flows northward in the Coastal Domain, and is influenced by inflows from the Kuskokwim and Yukon Rivers. Compared with the Anadyr Current, Alaska Coastal Water is relatively warm and has a lower salinity. The Alaska Coastal Water lacks the species of large copepods present in Anadyr Water, and supports primarily smaller, neritic species (Motoda and Minoda, 1974; Cooney and Coyle, 1982; Smith and Vidal, 1984; Springer *et al.*, 1989; Hunt and Harrison, 1990). Bering Shelf Water originates on the northern Bering Sea shelf and is usually strongly stratified (Coachman *et al.*, 1975). Along the northern shore of St Lawrence Island, Bering Shelf Water is diluted by freshwater run-off and is unstratified (Hunt and Harrison, 1990), presumably because of mixing by tidal and wind action (Kinder and Schumacher, 1981a; Kinder *et al.*, 1983). The copepod community of the Bering Shelf Water is dominated by *Calanus marshallae* south of St Lawrence Island. In the Chirikov Basin, Bering Shelf Water may also contain the large oceanic species, such as *Neocalanus* spp. and *E. bungii*, as a result of mixing with the Anadyr Current Water. In the Chirikov Basin, the fronts between the three water masses are narrow, have steep property gradients, and usually have a strong salinity signal at the sea surface (Harrison *et al.*, 1990; Hunt and Harrison, 1990).

Fronts are transition zones between water masses, and they vary in their width and whether they have a surface expression. The Inner or Structural Front separates the Coastal and Middle Domains (Schumacher *et al.*, 1979). This front is less than 10 km wide and is a region of marked transition in the vertical structure of the water column. A similar feature exists around each of the Pribilof Islands (Kinder *et al.*, 1983). The structural fronts around the Pribilof Islands vary in the extent of their surface expression (Coyle and Cooney, 1993). Structural fronts are regular, but unstudied, features around islands that occur in stratified water, such as St Lawrence and St Matthew Islands (Hunt *et al.*, 1990; Hunt, unpublished). The Middle Front, which separates the Middle Shelf and Outer Domains is broad (about 50 km), weak, and is expressed primarily by changes in subsurface features (Kinder and Schumacher, 1981a).

Least auklets

Breeding colonies of least auklets (Fig. 2) are located, with few exceptions, on islands in or near oceanic water containing *N. plumchrus* (Drury *et al.*, 1981; Hunt *et al.*,

1981b; Springer and Roseneau, 1985; Springer *et al.*, 1987). *Neocalanus plumchrus* is taken by least auklets in preference to most other types of zooplankton, particularly late in the breeding season when the auklets are provisioning chicks (Bédard, 1969; Springer and Roseneau, 1985; see Hunt *et al.*, 1993 for a review). At the Diomed Islands, least auklets forage on *N. plumchrus* and *N. cristatus* close to the islands in stratified Bering Shelf Water and appear to avoid the frontal area between Anadyr Current Water and Bering Shelf Water (Piatt *et al.*, 1992). At King Island in the Chirikov Basin, least auklets forage at, and west of, the front separating Alaska Coastal Water and Bering Shelf Water, despite the abundance of *C. marshallae* (a species taken at St Matthew Island) in the Alaska Coastal Water around King Island (Springer and Roseneau, 1985; Harrison, 1987; Springer *et al.*, 1987; Hunt and Harrison, 1990). In the western Aleutian Islands from Gareloi Island (178°W) to Buldir Island (178°E), *N. plumchrus* is the predominant prey with which least auklet chicks are fed (Day and Byrd, 1989; Hunt, unpublished).

For least auklets that breed at St Matthew and Hall Islands and at a colony on the south side of St Lawrence Island (Sowls *et al.*, 1978), *Neocalanus* copepods are for the most part unavailable and the primary prey is the neritic copepod *C. marshallae* (Hunt *et al.*, 1981a; Springer and Roseneau, 1985; Harrison, 1987). At the Pribilof Islands, least auklets provision their young in some years with *C. marshallae*, and in other years they take *N. plumchrus* and other species of oceanic copepods (Hunt *et al.*, 1993, 1996). Oceanic copepods may be transported to the vicinity of the Pribilofs by flow that originates in the north-westward flowing current along the shelf break of the eastern Bering Sea (Schumacher and Stabeno, 1994), thereby providing a source of oceanic zooplankton in a Middle Shelf Domain region (J. M. Schumacher, pers. comm.).

The distance that least auklets commute between their colonies and foraging sites differs with the species of copepod sought and the distribution of the copepods in the water column. In the Chirikov Basin, least auklets from King Island and St Lawrence Island fly 55 km to 75 km from their colonies to forage where *N. plumchrus* is concentrated in near-surface layers over shallow thermoclines (Hunt *et al.*, 1990; Piatt *et al.*, 1992), or in the vicinity of fronts, where convergences concentrate organisms attempting to maintain position near the surface (Hunt and Harrison, 1990; Harrison *et al.*, 1990). Despite evidence that sometimes least auklets will avoid strongly stratified water (Haney, 1991), least auklets usually do not forage where *N. plumchrus* is dispersed throughout the water column, such as occurs in the well-mixed water inshore of the structural front along the northern coast of St Lawrence Island (Hunt *et al.*, 1990). In contrast, at St Matthew Island, least auklets restrict their foraging to an average radius of 5 km from

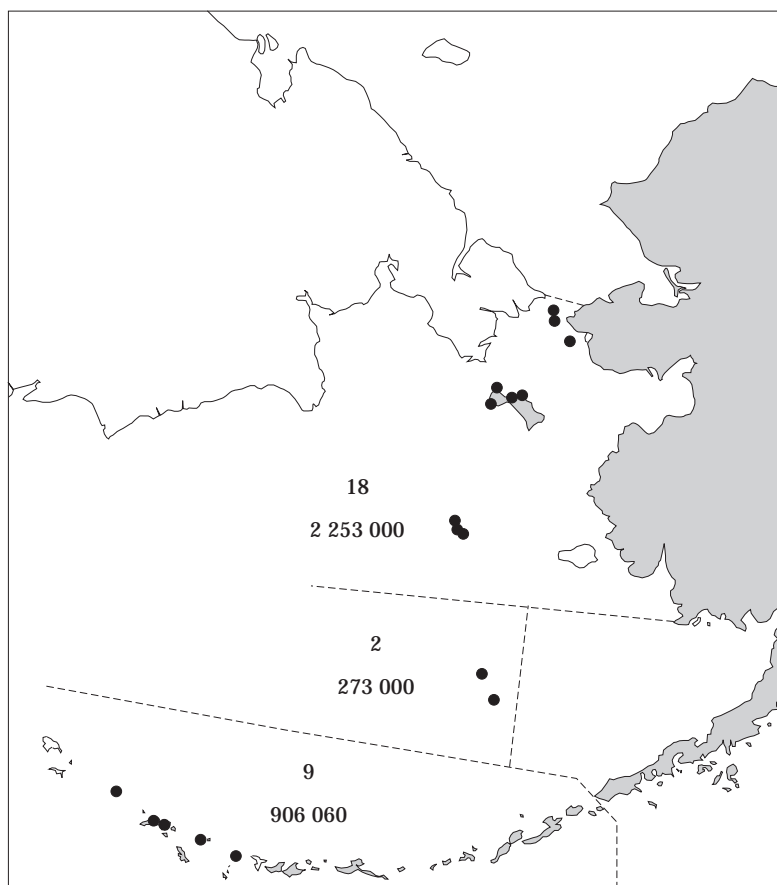


Figure 2. The distribution of breeding colonies of least auklets in the eastern Bering Sea and Aleutian Islands. The upper numbers indicate the number of colonies in each region, and the lower, the estimated population size of least auklets in those regions. From Sowls *et al.* (1978).

their colonies and take *C. marshallae* in the shallow, tidally mixed water in the strait between St Matthew and Hall Islands (Fig. 3), where tide rips are hypothesized to concentrate prey. Foraging least auklets are scarce over the strongly stratified Middle Shelf Domain water farther offshore, despite the presence there of concentrations of biomass at the pycnocline (Harrison, 1987; Obst *et al.*, 1995; Hunt *et al.*, unpublished data). Similarly, at the Pribilof Islands, least auklets forage, on average, within 12 km of the islands, but mechanisms that may influence the concentration of their prey have not been studied there (Obst *et al.*, 1995). *Calanus marshallae* has a lower energy content than *N. plumchrus* (S. Smith, cited in Hunt and Harrison, 1990), and it is possible that it is not profitable for least auklets to fly as far in search of *C. marshallae* as they do for *N. plumchrus*.

Discussion

Two prominent themes in biological oceanography are the scale-dependence of processes in the ocean (e.g.

Haury *et al.*, 1978; Steele, 1978; Dayton and Tegner, 1984; Hunt and Schneider, 1987; Schneider, 1994), and the importance of the coupling of biological and physical processes for production and its fate (e.g. Mann and Lazier, 1991). One approach to the issue of scale has focused on identifying characteristic spatial and temporal scales at which ecological patterns and processes occur. An alternative approach is to examine the dynamics of spatial variability. For example, in a fluid environment, it may be possible to relate changes in the structure of a population to the propagation of events in the fluid medium from large spatial and temporal scales to events at smaller scales (Schneider, 1994). In these processes, the role of coupling between physical and biological processes becomes the key to understanding the mechanisms responsible for the observed biological patterns (Mann and Lazier, 1991). Coupling between biological populations and physical processes occurs over a continuum of spatial and temporal scales, and may result in biological processes occurring along shifting spatial and temporal scales, rather than at a “characteristic” scale (Schneider, 1994).

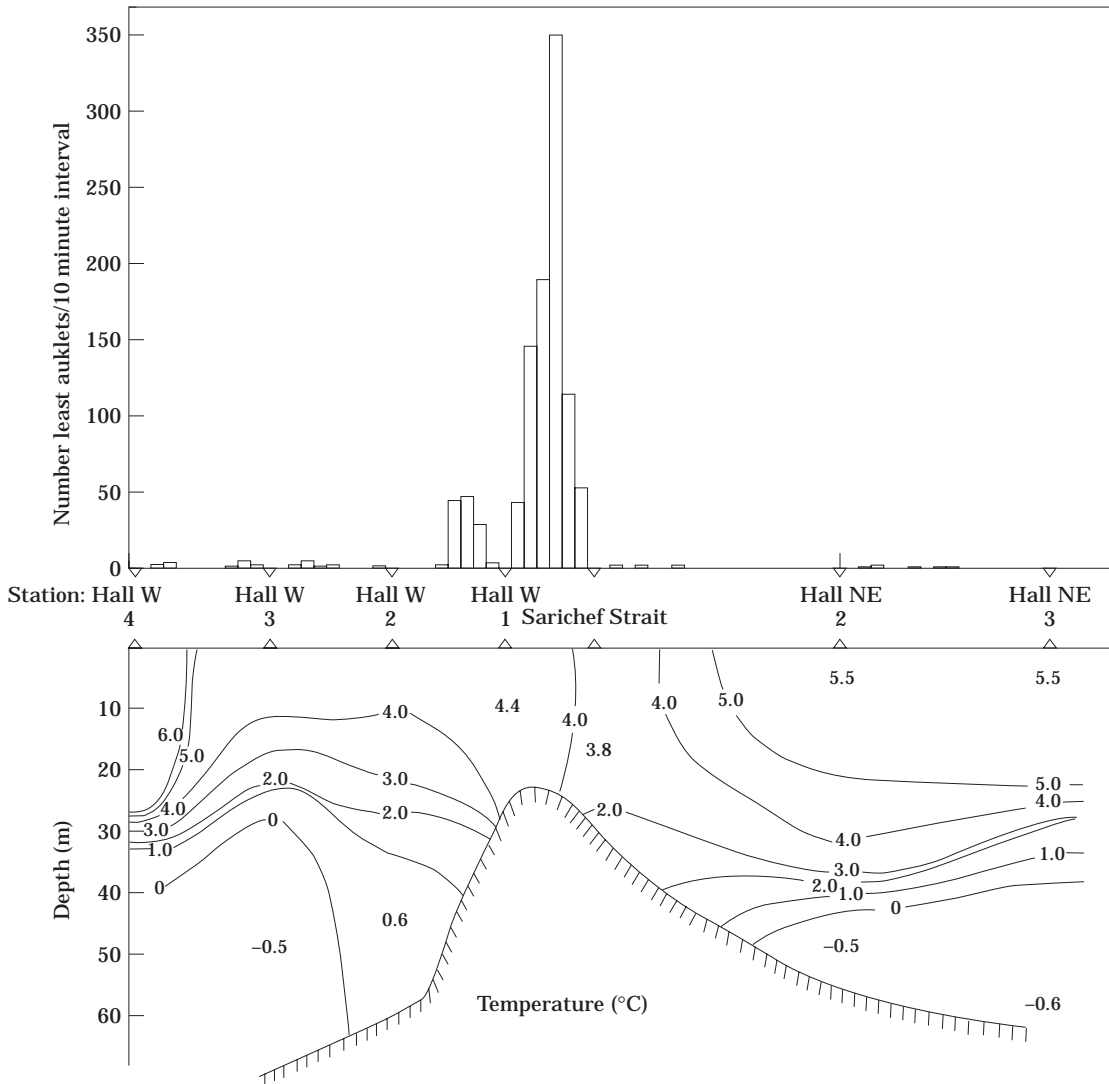


Figure 3. *Top*: The distribution of least auklets on the water (per 10 min counting interval) across Sarichef Strait between St Matthew and Hall Islands, Bering Sea. *Bottom*: The thermal structure of the water column in deg C, showing the transition from stratified water offshore of the pass, to well mixed water over the shallowest portion of the pass. Tidal mixing was responsible for the breakdown of the stratification. Station locations indicate where CTD casts were made for determination of hydrographic structure.

Hunt and Schneider (1987) used a series of temporal and spatial scales to organize data on the distribution and abundance of marine birds with respect to physical oceanographic features and processes. Implicit in their approach was the assumption that there were characteristic spatial scales at which community composition would be expected to change, or at which seabird abundances would respond to variability in prey biomass. They did not investigate the possibility of shifting scales of response, or have access to seabird studies that had relied on multi-scale analyses.

The distributions of planktivores in the eastern Bering Sea illustrate the difficulty in trying to assign specific

spatial scales to patterns of community change. In the south-eastern Bering Sea shelf, seabird communities are differentiated at the meso-scale by domains spread over a 570 km wide shelf (Hunt *et al.*, 1981b, c), and at the coarse-scale in the Chirikov Basin where the seabird communities are differentiated over a distance of less than 100 km (Drury *et al.*, 1978; Springer and Roseneau, 1985; Schauer, 1991; Elphick and Hunt, 1993). In Bering Strait, a distance of only a few tens of kilometres is all that is required for the support of two well-differentiated seabird communities (Piatt *et al.*, 1992). In each instance, changes in the seabird communities reflect changes in water mass, zooplankton

communities, trophic pathways, and the fate of carbon (Springer and Roseaneau, 1985; Springer *et al.*, 1987; Walsh and McRoy, 1986; Piatt and Springer, 1992). In the Bering Sea, as the spatial scale of the water masses required for the support of distinct seabird communities decreased, the sharpness of the boundaries between the water masses increased (Elphick and Hunt, 1993). Based on this experience, it does not seem instructive to define characteristic scales at which changes in community structure would be expected to occur.

Events at scales smaller than the water mass, as defined by its zooplankton community, may influence whether that water mass will support a particular species of planktivorous seabird. The distribution of planktivore breeding colonies depends upon several aspects of the environment. There must be appropriate nesting habitat (nest sites), an appropriate water mass with acceptable prey within commuting distance of the colony, and, within that water mass, appropriate hydrographic structure and/or physical processes to make the prey economically harvestable.

Interaction between physical processes and biological processes within water masses is often a critical feature that determines the availability of prey to planktivorous seabirds. Pycnoclines can result in the passive accumulation of prey as organisms settle to water of density equal to, or greater than, their own. The presence of internal waves can concentrate prey accumulated along the pycnocline and lift prey toward the surface (Haney, 1987). Convergences concentrate near-surface dwelling prey, whereas upwelling and divergences concentrate and increase the availability of prey resident deeper in the water column (Franks, 1992). These and other processes accentuate the heterogeneity of prey abundance within water masses and in so doing create foraging opportunities for planktivores. When prey is dispersed throughout the water column, it may be at a density too low to be economically harvested (Wishner *et al.*, 1988; Hunt *et al.*, 1990; Piatt and Methven, 1992; Piatt *et al.*, 1992). Thus, a complete understanding of the biogeography of breeding seabirds in the eastern Bering Sea (Hunt *et al.*, 1981b; Springer and Roseaneau, 1985) requires consideration of more than just the plankton community present in a water mass.

Since many of the physical processes that affect plankton distributions are multi-scale phenomena in which energy cascades from features at large spatial and temporal scales to features at smaller scales, it would seem promising to apply multi-scale analysis to the interactions between planktivores and their prey. Several studies of predator–prey relationships in seabirds have shown that correlations between predator numbers and prey biomass are stronger at larger scales of measurement. In part, this may be caused by statistical artifact resulting from smoothing across small-scale variability.

However, there also appears to be some validity in the notion of scale-dependence in predator–prey correlations. Mehlum *et al.* (unpublished data) show a leveling off and, eventually, an apparent decline in the degree of correlation between predators and prey as the scale of measurement increases. This supports the hypothesis of scale-dependence. In addition Piatt *et al.* (1992) found evidence for scale-dependence in a threshold response by least auklets to prey density. Using a different approach, Russell *et al.* (1992) compared fractal dimensions of least auklet foraging distributions and the fractal dimensions of plankton biomass in the Chirikov Basin and found strong correlations for most pairings indicating that the birds were responding to the spatial distribution of their prey in a spatially complex fashion. Recent data from the western Aleutians (Russell *et al.*, unpublished) show that the strength of correlation between least auklets and their prey is inversely correlated with the fractal dimension of prey biomass along the survey lines. This indicates that complex prey distributions are harder for auklets to exploit than prey distributions having strong autocorrelation across a range of spatial scales.

These multiscale approaches to understanding the foraging distributions of seabirds show that the characteristics used by seabirds to select foraging habitat change with spatial scale, and that features at the scale of water masses, physical features within water masses, and small-scale prey distributions all play important roles. Thus, the use of multi-scale approaches to studies of seabird foraging ecology may eventually permit evaluation of the importance of processes at different spatial and temporal scales for the evolution of seabird foraging strategies.

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