homogeneity. Horizontally isothermal conditions in the surface layer probably derived from mixing due to storms and lack of upwelling (which otherwise would lend considerable cross-shelf structuring to surface temperature).

In an ongoing study of satellite image archives L. C. Breaker and J. C. Mueller (pers. comm.), found that thermal and color features having length scales of 30 to 60 km typically persist for many days (up to several weeks). Smaller features rotate, advect, or evolve into unrecognizable forms within shorter periods (for features of 5 to 15 km, the durations may be on the order of hours to a few days). Large features such as shelf-edge eddies and associated current "jets" (that are traced because they entrain cold water upwelled over the shelf) may persist for several weeks and frequently recur at known sites such as Point Reyes and Point Sur. Thus, with larger features at least, seabirds are exposed to patches of habitat that offer a degree of persistence and stability, and that recur seasonally at given locations.

DISCUSSION

These are the first data collected in such a way that the abundance, distribution, and selected habitat affinities of seabirds off California can be assessed synoptically. As a result of regular monthly sampling, quantitative aspects of seasonality have emerged, and we have described certain attributes of the fauna as a whole: species diversity, composition, biomass density, and relationships of these measures to certain physical habitat characteristics. We have also determined which species occur together over different spatial scales, how certain species respond to habitat gradients at different scales, and how the apparent scales of seabird aggregations compare to patch size of ocean surface thermal habitat. When this new information is added to information on seabird breeding biology at the Farallones and several of the Channel Islands (Ainley and Lewis 1974, Hunt et al. 1981, Ainley et al. ms), the result is a compendium that makes the seabird fauna of the California coast perhaps the best known in the world.

VARIATION IN BIOMASS AND ABUNDANCE

Concentrations of seabirds over shelf waters off California were quite dense, comparable to those reported for other upwelling regions in eastern boundary currents, and those seen in high latitudes. In offshore (California Current) waters, densities and biomass were similar to the much lower values reported for western boundary currents and central ocean basins. Off California we found densities averaging about 6 birds km^{-2} in

water deeper than 2000 m and more than 110 birds km^{-2} over the shelf. Densities reported by Wiens and Scott (1975) for a small number of numerically dominant species off Oregon are in this range (in fact, the two states share much the same fauna), and reports of bird densities off Washington and British Columbia are also similar (Wahl et al. 1981, Vermeer and Rankin 1984). For the Gulf of Alaska, Gould et al. (1982) reported aggregate densities ranging from 3.5 to 13.7 birds km^{-2} offshore and 44 to 158 birds km^{-2} over the shelf, whereas in the Bering Sea during the nonwinter months, densities were 6 to 24 birds km^{-2} in the oceanic zone and 9 to 240 birds km^{-2} over the shelfbreak. In all these studies much local variation is subsumed within the grand averages; for some areas of 10s to 100s of km^2 density may be on the order of 10^3 to 10^4 birds km^{-2}.

Fewer estimates have been reported for polar or subtropical regions. Based on ship sampling and estimates of breeding numbers, Ainley et al. (1983) calculated that density of adult birds peaked at about 16 birds km^{-2} throughout the Ross Sea, Antarctica, whereas in the Atlantic Haney (1986) computed densities of 0.6 to 10.9 birds km^{-2} in Gulf Stream cold-core eddies and 7 to 15 times less in oligotrophic shelf and Gulf Stream waters unaffected by the eddies. In oceanic areas of the South Pacific, Ainley and Boekelheide (1983) found densities ranging from 3.4 to 9.5 birds km^{-2}.

Estimates of biomass density or seabird standing stock have been made for a few of these same regions, albeit with a variety of approaches. Biomass varied regionally off California from 2.2 kg km^{-2} to 67.6 kg km^{-2}; off central California it ranged as high as 283 kg km^{-2} and as low as 0.2 kg km^{-2} in shelf and offshore waters, respectively. Matching monthly estimates from different years in the south and north, we arrive at maximum "instantaneous" populations of 5.5 to 6.0 million birds in late fall or early winter, representing a biomass of about 4.8 million kg. Turnover rates were not determined for migrants so total numbers of birds passing through the area are not known. For 43,000 km^2 of shelf waters off British Columbia (one-sixth of the area upon which we report), Vermeer and Rankin (1984) estimated a peak of 6.4 million birds, mainly shearwaters and alcids. Schneider and Hunt (1982) estimated numbers ranging from a few million to 20 to 40 million birds in shelf/slope waters of the Bering Sea (10^6 km^2), most of these being Short-tailed Shearwaters visiting during summer. Bird numbers in the Benguela Current system off Africa are reported to be similar to those we found off California (Abrams and Grif-

fiths 1981, Furness and Cooper 1982, Schneider and Duffy 1985), while numbers are lower in the upwelling region off Senegal (Brown 1979).

Bird biomass in the Peru Current has not been estimated from direct surveys at sea. The best estimates for the region are based on guano production figures, which do not include the fraction of total biomass attributable to species nesting outside the region (Duffy and Sigfried 1987). Idyll (1973) and Duffy (1980) have shown that collapse of the Peruvian anchovetta (*Engraulis ringens*) stock due to recurrent ENSO episodes and sustained overfishing led to a five-fold decline in the abundance of the Guanay Cormorant (*Phalacrocorax bougainvillii*) from the former level of around 20 million birds. At present, this and the Peruvian Booby (*Sula variegata*) remain the most numerous of birds within 20 or so km of the coast near Lima, followed by Sooty Shearwaters. It is reasonable to assume that seabird biomass density in the Peru Current is at least as high as that seen off California, perhaps a good deal higher. Interestingly, the bulk of seabirds off California are seasonal visitors, whereas off Peru breeding species make up a much larger proportion of the total fauna (at least historically). The pelagic wetfish fauna of the two current systems are very similar in structure and species composition (R. H. Parrish, pers. comm.). In the interest of understanding why only one region supports a large component of breeding species, it would, therefore, be very instructive to make a quantitative comparison of the community structure and feeding preferences of the two bird faunas.

Ainley et al. (1983) calculated that approximately 12 million birds inhabiting the Ross Sea in late summer represented a biomass of about 44 kg km^{-2}. In contrast to these high figures for cold water and upwelling areas, Haney (1986) estimated that in cold-core eddies of the Gulf Stream, bird biomass ranged from 0.1 to 7.9 kg km^{-2}, while in less fertile adjoining areas, biomass was 7 to 15 times lower. In the oceanic South Pacific, biomass averages 0.9 to 10.2 kg km^{-2} (Ainley and Boekelheide 1983).

How do these figures compare with those from terrestrial systems? Estimates of bird biomass have ranged from 2 to 78 kg km^{-2} for a variety of terrestrial ecosystems (Szaro and Balda 1979), roughly the same range seen in seabird communities studied to date. Because metabolic rate varies inversely with bird size, smaller, terrestrial birds have a higher mass-specific rate of energy consumption, placing seabirds at the lower end of estimates of energy flow per unit area. Model estimation of seabird trophic requirements remains a controversial and active area of research.

At one end of the spectrum of estimates, Furness and Cooper (1982) note that several models of energy use agree that seabirds may consume 17 to 29% of the small, schooling fish produced annually in four different temperate (cool-water) areas (Schaefer 1970, Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982). At the other end of the spectrum, Schneider and Hunt (1982) estimated that seabirds took only 0.03 to 0.05% of summer primary production in the Bering Sea (3 to 5% of tertiary production if we assume 10% efficiency in transfer of energy between trophic levels). Similarly, Briggs and Chu (1987) calculated that seabirds consumed about 500 to 600 metric tons of fish, squid, and plankton per day off California, representing 4 to 7% of estimated tertiary production. Sport and commercial fisheries in the same area represented landings 200% to 400% higher than the figures for seabird predation in general (albeit with several substitutions of age classes and species exploited by fisheries).

California seabirds probably consume no more than 10% of annual production of small schooling fish (Briggs and Chu 1987). However, several seabird populations nesting in California are well below historical sizes, whereas others may be somewhat larger (Ainley and Lewis 1974, Hunt et al. 1981). For example, Common Murres are probably an order of magnitude less abundant now at the Farallones than in the past century. Given the large proportion of total nesting birds represented by the murres, impact on California Current fish stocks (by nesting seabirds at least) may have been greater in the past than at present.

As a group, seabirds often have figured in conceptual debates about the role of food limitation of populations. The upper limits of bird biomass density consistently appear to be 50–100 kg km^{-2} in the most densely inhabited upwelling and polar regions, worldwide. This suggests that a practical limit to sustainable bird concentrations is reached at about 10% of tertiary production (perhaps representing 30% of biomass available at the level of schooling fish and squid; e.g., Wiens and Scott 1975, Furness 1978, Briggs and Chu 1987). Beyond this, Brown (1980) has argued that if mixed uniformly, background concentrations of bird prey in the ocean typically would be insufficient for the needs of these metabolically active predators; seabirds are thus selected to recognize and exploit physical and biological processes that concentrate prey above ambient levels. Brown (1980), Schneider and Hunt (1982), Ainley and Jacobs (1981), Haney (1985), and others have described situations in which birds concentrate at sites where physical processes truncate the usual diffusion of oceanic produc-

tion (by trapping of plankton). From the perspective of the California Current, total food biomass probably does limit the size of the fauna: It is known that nesting species exhibit interannual variations in numbers of breeding attempts and various measures of reproductive output related in general to food abundance and specifically to food availability (Hunt and Butler 1980, Hunt et al. 1981, Anderson et al. 1983, Anderson and Gress 1984, Hodder and Graybill 1985, Ainley et al. ms), and some migrant and seasonal resident populations change dramatically in years of low prey abundance (Ainley 1976; this study). In certain, well-documented cases, many of the links between food abundance, predation rates, feeding of the young, and overall reproductive success of California seabirds are known. And, even for feeding generalists like Western Gulls, reproductive success and breeding numbers track the yearly and seasonal changes in prey abundance (e.g., Hunt and Butler 1980, Ainley and Boekelheide in press). These are exclusively colony data, however, and the details of foraging behavior at sea during times of food abundance and shortage are poorly known.

Interestingly, in early to mid-summer, when energy requirements of nesting species are maximal (due to provisioning of the young), waters off California harbor the largest numbers of shearwaters (10^5 to 10^6 birds)—the species described by Hoffman et al. (1981) as the primary "suppressors" of mixed-species feeding flocks in Alaska. Although there is known to be broad overlap in diets between shearwaters and several of the breeding species, our data show that flocks containing many shearwaters seldom contained many gulls, murres or auklets. It would be informative to observe bird behavior in flocks of breeders in the presence and absence of shearwaters. This might increase our understanding of whether the presence of shearwaters in years of food shortage poses additional problems to species attempting to raise young at nearby colonies.

COMMUNITY COMPOSITION AND DIVERSITY

The California seabird fauna is dominated in numbers and biomass by species that reach greatest abundance in cool waters of the upwelling zone. Many of these nest at high latitudes. Further, in warm waters seaward of the upwelling zone and in the eastern half of the Southern California Bight (east of the main influence of the Point Conception upwelling system and cool California Current), bird numbers are greatest in winter when visitors from arctic and subarctic regions predominate.

The fauna is quite similar in composition to that off Oregon, Washington, and British Columbia (Wahl 1975, Wiens and Scott 1975, Sanger 1973, Vermeer and Rankin 1984). Ainley (1976) pointed out the gradual decline in abundance of subtropical species as one passes northward along the Pacific Coast. At the latitude of Washington, a number of species common in warm waters off California are relatively rare (e.g., Brown Pelicans, Black-vented Shearwaters, Heermann's Gulls, Elegant Terns, Ashy Storm-Petrels, and Xantus' Murrelets). Several more species characteristic of cool waters in central California do not reach as far as Alaska (Western/Clark's Grebe, Western Gull, California Gull).

For the Common Murre, Cassin's Auklet, Sooty Shearwater, and the two phalaropes, abundance peaks where water clarity is relatively low. Ainley (1977) noted the predominance of diving species (in this case, alcids) in regions where upwelling and other processes maintain high standing stocks of phytoplankton, and thus relatively turbid waters. Sooty Shearwaters also obtain some prey by underwater pursuit (Brown et al. 1978), although surface-seizing certainly is the method of prey capture emphasized off California. Additional diving species are numerous: Pacific Loons, Western/Clark's Grebes, Brandt's Cormorants, scoters, and Rhinoceros Auklets. Gulls, which obtain most prey at sea by seizing organisms at the surface (Ashmole 1971, Ainley 1977), also reach high abundance in turbid waters of the upwelling zone. Only the phalaropes among the extremely abundant species feed exclusively at the surface and these birds occur primarily at the seaward edges of upwellings (Briggs et al. 1984).

Leach's Storm-Petrel is the only species reaching anything approaching high abundance in the clear, blue waters offshore, a habitat type exploited by this species throughout the Pacific Basin (Gould 1971, Crossin 1974, Ainley 1977).

At a finer scale avifaunal composition in shelf waters of central and northern California is somewhat distinct from that in southern California. In fact, the southern California fauna is similar to the offshore fauna of central and northern California. The disparity between shelf faunas is due largely to differences in abundance of birds that concentrate in the coastal upwelling zone (Common Murres, Cassin's Auklets, Sooty Shearwaters) versus those inhabiting thermally stratified, translucent waters of the California Current (especially storm-petrels). In essence, there seems to be a fauna of the coastal upwelling zone that disperses offshore into the California Current during winter, versus a fauna found everywhere else. Among the latter are included many gulls, storm-petrels, pelicans, cormorants, and migrant terns.

A similar disparity exists within the Southern California Bight. A changeover from cool-tem-

perate to warm temperate and subtropical species occurs in the vicinity of Point Conception (Hubbs 1963, Ainley 1976). This change corresponds to diminution in the influence of sub-Arctic waters carried in the California Current (Bernal and McGowan 1981). As traced by the subsurface 32.4‰ isohaline, the tongue of sub-Arctic water penetrates about as far south as the latitude of San Diego (mean position), but only at distances of 200 to 300 km from shore (Chelton 1980). Warmer, saltier water of the Southern California Countercurrent lies closer to the coast. Our general impression from winter data is that high latitude breeders such as kittiwakes and fulmars mostly remain in the waters of the California Current, moving in large numbers eastward, toward the southern California coast, only when the warmer countercurrent is less well developed, or storminess thoroughly mixes the upper ocean (especially winter 1976).

Species diversity is much higher over the shelf and slope off California than in oceanic regions of the South Pacific, where Ainley and Boekelheide (1983) reported values of H' from 0.54 to 0.88. Compared to species diversity of terrestrial bird faunas, the fauna of the California continental shelf is similar to that found in physiographically diverse forests (Noon et al. 1980), whereas oceanic faunas have low species numbers and diversity, comparable to those seen in grassland (Willson 1974, Szaro and Balda 1979). Almost certainly this difference in species diversity between ocean habitats is related to greater horizontal and vertical variability of shelf habitats. Particularly important are topographic (seabed) influences on currents, shallow thermocline structures (within diving range from the surface), and access to the bottom itself. Indeed, we found species diversity to be much higher where habitat heterogeneity was highest: over the shelf and slope.

SPECIES ASSOCIATIONS

Association between species and between a species and a type of habitat is a function of the scale at which a pattern is analyzed; i.e., species sharing similar patterns of seasonal occurrence over large regions (10^4 km^2) may or may not associate over smaller spatial scales. Obviously, it is among birds that co-occur at all scales that we should look for interactions that might shape communities in terms of mutualism, interference, competition, predation, parasitism, etc. Along these lines we found several groups wherein the species co-varied in density through space and time, generally occupied similar positions relative to the simplified gradients in PC space, and frequently associated in flocks. The most prominent of these were: (1) a nearshore fauna

including Pacific Loons, Western/Clark's Grebes and Surf/White-winged Scoters in winter together with Brown Pelicans and Brandt's Cormorants (and other cormorant species) at other times of the year; (2) Common Murres and Brandt's Cormorants, the most numerous piscivores among the nesting species; to which also might be added Western Gulls, which frequently formed mixed-species flocks with the cormorants and which are neither avoided nor actively attracted to murres; (3) the four species of shearwaters and Northern Fulmar, which associated with each other but appeared to be avoided by almost all other birds; (4) a gull fauna that intermingled freely at sea but was avoided by alcids, several of the inshore species, and the phalaropes [Gulls frequently associated with pelicans and cormorants; this was especially true of Heermann's Gulls. This group does not include the kittiwake, probably because of limited overlap between offshore range of the kittiwake and the neritic ranges of most other species.]; (5) (Red) phalaropes and Northern Fulmar, species that co-occurred spatially and associated frequently in flocks over the outer shelf during winter. As a group, the alcids avoided flocks containing gulls, shearwaters and all the inshore species. Leach's Storm-Petrel associated consistently with no other species and was quite distinct in regional distribution and occurrence in PC space.

Our flock data corroborate some of the finding of Hoffman et al. (1981), Porter and Sealy (1981) and Grover and Olla (1983). These authors show that one or more seabird species such as kittiwakes and murres act to locate concentrations of fish, squid or plankton. These are joined by diving species, gulls and shearwaters that appear to recognize which individuals of the 'nuclear' or 'catalyst' species have discovered aggregations of prey. The behavior of the 'joiners' may serve to further concentrate the prey (e.g., murres, auklets and puffins promoting tight schooling behavior in fish by approaching from below or the sides of a school) or, if joiners are numerous (especially shearwaters), may disrupt cohesive schooling behaviors of the prey, contributing to termination of feeding opportunities for all but the deepest divers.

Off California the most numerous catalysts are murres, Brandt's Cormorants, Western Gulls, kittiwakes and Brown Pelicans; porpoises, sea lions and large predatory fish also frequently serve to concentrate seabird food fishes near the surface. Bird species that might be classified as 'joiners' include all above-mentioned catalysts, as well as other cormorants, jaegers, Rhinoceros Auklets and shearwaters. As is seen elsewhere, the primary suppressors are the shearwaters, whose aggressiveness and splashing, shallow dives were

described by Hoffman et al. (1981). The plunging behavior of feeding pelicans is of the sort reported to disrupt dense schools of fish (Hoffman et al. 1981), so the importance of pelicans as catalysts probably lies in the fact that fish must already be concentrated and visible to pelicans before feeding begins for these large and visible birds.

Because they do not penetrate below about one meter when feeding, gulls probably do not disrupt concentrated schools of prey like shearwaters do, but they certainly steal the foods brought to the surface by other species. This aggressiveness may be at the root of the many significant negative flock association indices between gulls and other species (Tables 3–5).

The basis for co-occurrence among the nearshore species may be shared food (e.g., loons, grebes, gulls, and cormorants feeding on fish schools in shallow waters) but in other cases is probably simple partitioning of shared habitat according to food specialization (e.g., cormorants feeding on fish while nearby scoters take benthic invertebrates).

Among congeners that might potentially compete for foods we noted much mixed-species flocking among shearwaters and fulmars and much overlap among the two phalaropes (within ship counts where species could be distinguished). The shearwater species are sufficiently distinct in geographic/temporal abundance that competition for food may not be important: Buller's Shearwaters concentrate over the continental slope in central and northern California in late summer; the Sooty is most numerous over the shelf in late spring; the Pink-footed reaches greatest abundance in the south in late summer. Shearwater diets and foraging techniques may also be somewhat dissimilar (Baltz and Morejohn 1977, Briggs et al. 1981, Chu 1984).

In contrast, gulls, especially the larger species, are aggressive towards each other when they occur in interspecific flocks (Briggs 1977). We saw Western and Glaucous-winged gulls (the largest-bodied and socially dominant species) inhabiting seal rookeries in winter (where competition for defensible food sources is intense), while Herring and California gulls mainly frequented refuse dumps, estuaries and shelf waters. Kittiwakes, Bonaparte's Gulls, Sabine's Gulls, and Heermann's Gulls do not compete with the larger gulls on seal rookeries and specialize instead in fishing nearshore (Bonaparte's), far offshore (Kittiwake, Sabine's), or with pelicans (Heermann's).

Large, mixed-species flocks of storm-petrels are quite exceptional (notwithstanding the repeated occurrence of these flocks in Monterey Bay; Stallcup 1976). Mostly, these birds occur in different habitats and reach peak abundance at different times.

SEABIRD HABITATS AND HABITAT CHOICE

Several studies of the last decade have quantified habitat characteristics of birds at sea. As in terrestrial studies, variations in bird occurrence and density "fit" best to environmental conditions when evaluated over large scales. The finer the scale, the less evidence there is for close tracking of habitat characteristics: i.e., birds appear not to "fine-tune" their preferences to local habitat conditions (Rotenberry and Wiens 1980).

Unfortunately, we cannot ignore the problem of scale, or we are met with one or the other of two pitfalls noted by Wiens (1985): ignorance of mechanisms whereby individuals choose among habitats and thus produce discernable patterns at large scale; or, ignorance of environmental events outside the scope of a study but that nevertheless affect the results. Wiens (1985) advocates approaching studies of habitat selection through a hierarchy of scales.

For seabirds, virtually all the detail and process of ocean habitat choice remains to be discovered. Thus, we have chosen to use broad-scale studies to allow the birds themselves to indicate responses to habitat variation. We can then proceed toward studies of habitat selection, focusing on times, areas, and conditions where such choices produce readily discernible patterns.

A growing body of evidence now shows that seabirds are distributed in ways implying the importance of subdivisions of the ocean environment. Murphy (1936) and Ashmole (1971) documented affinity of some seabirds for specific current systems, gyres, and coastal regions. Later workers have explored relations of bird numbers to surface thermal and salinity conditions (e.g., Ainley 1976, Pocklington 1979, Ainley and Boekelheide 1983), nutrients, chlorophyll, and plankton stocks (Ainley 1977, Bradstreet 1979, Brown 1980, Ainley and Jacobs 1981, Briggs et al. 1984). For our studies off California we examined habitat primarily on the basis of various distance and depth functions and surface temperature. Three important axes of shared variation emerged from principal components analyses: PCI was a distance-depth gradient often correlated with temperature; PCII (which, of the three main components, included coarse-scale environmental variation; i.e., that occurring over of hundreds of km) reflected the latitudinal variation in temperature (and surely also included general trends in chemical properties in the California Current); PCIII comprised mainly the variation in thermal gradients. We did not di-

rectly measure salinity, but ignored this variable for two reasons: First, surface thermal conditions vary much more widely than does salinity (about 14°C versus about 2‰); birds thus may select along a broader thermal gradient. Second, temperature is the most important factor driving surface density variations (reviewed in Hickey 1979, Huyer 1983). Since surface circulation, and thus potential convergence/divergence mechanisms affecting surface concentrations of seabird prey, depends mostly on winds and density gradients, the importance of temperature probably overshadows that of salinity to California seabirds.

We recognized four main groupings of species in PC space. Density within the group including Common Murres, Cassin's Auklets, Western Gulls, and Sooty Shearwaters varied inversely with Component I (depth, distance from shore, and often temperature), and usually varied positively with gradients in temperature (Component III). The group including Rhinoceros Auklets, Black-legged Kittiwakes, and sometimes Northern Fulmars and Black-footed Albatross loaded strongly on the latitude-temperature component (II) and usually on Component III as well. Leach's Storm-Petrel, phalaropes, and in some cases Common/Arctic terns and Buller's Shearwaters varied in density as distance from shore and depth increased (Component I). Finally, density of Pink-footed Shearwaters, sometimes pelicans, and sometimes California Gulls varied as the inverse of Component II, indicating affinity for warmer, southern waters. The data presented above are representative of recurrent patterns; bird occupancy of these PC gradients was conservative through time and was usually similar between years.

In California, upwelling fronts (represented in PC space by short distances to the shelfbreak [PC I] and high temperature gradients [PC III]) appear to be the most important factor segregating different elements of the seabird fauna. There is good reason to believe that concentration of birds at upwelling fronts is biologically meaningful. At upwelling boundaries, circulation is very complex and may be convergent or have much vertical shear (Flament et al. 1985). Convergent fronts are thought to concentrate mobile zooplankton to levels above those found in surrounding waters, thus enhancing feeding opportunities for fish and birds (Brown 1980, Bourne 1981, Briggs et al. 1984, Haney 1985).

Timing is one aspect of scale-dependent variation; the other is patchiness in space. Our analyses of aggregation indicated that much important variation in abundance of murres, auklets, and phalaropes takes place over cross-shelf (spatial) scales of 8 to 16 km. On average, temperature was autocorrelated over broader scales than these (roughly 30 to 50 km in the analyses we presented). A variety of processes affecting temperature could lead to variation over 30- to 50-km scales. Among them are the eddies and current jets studied by Mooers and Robinson (1984) and Flament et al. (1985), which are prominent features of the California Current offshore environment. Processes that might generate the 8- to 16-km patterns seen in the bird data include behavioral aggregation (i.e., feeding flocks attracting birds from distances of 4 to 8 km), formation and maintenance of thermohaline or color fronts bordering upwellings; estuarine outflow from the Golden Gate; shear instabilities along surface density fronts; Langmuir circulation (three-dimensional wind-driven circulation in the upper few meters under low turbulence conditions); and internal wave propagation. We have seen phalaropes and auklets, as well as a variety of other species, aggregating on one side or the other of each of these kinds of features (e.g., Briggs et al. 1984), and these features are often embedded within larger structures, such as discrete upwellings. Haney (1985, 1987) and his co-workers have looked at seabird numbers as functions of each of these processes in the Gulf Stream/shelf/Sargasso Sea region off the southeastern United States. In that generally oligotrophic environment, each process appears to dramatically affect the distribution of one or more species, but not the whole fauna. Compared to the area studied by Haney, California Current waters typically are much more productive and support higher bird numbers, and the environment is cooler and windier. Nevertheless, physical features correlate with important structure of the bird communities in both areas. Ultimately, it is most important to discover how these processes affect prey abundance and availability and how well seabirds are able to detect and associate these features with enhanced feeding opportunities.

Consideration of scales of habitat features and of bird aggregations leads us toward certain questions about habitat choice. Habitat choice by individuals is the primary process leading to observed patterns of bird distribution and must also have important consequences in the life histories of the individuals themselves. In this regard it is interesting that among coastal plankton communities, species composition tends to be coherent over much larger scales than does abundance (Haury and Wiebe 1982, Mackas 1984). The practical implication is that seabirds or other predators can employ a strategy of first finding a habitat patch having suitable prey composition, then hunting within the patch for prey abundance maxima (*sensu* Haury and Wiebe

1982). Three aspects of this process for which we have no current information are (a) the role of individual experience and behavioral interaction (e.g., following) in truncating search time, (b) the relative sensory capabilities of different species, and (c) the role of "patience" in finding prey abundance maxima. In contrast to protocols (such as ours) of sampling a parcel of water "instantaneously," then moving on, a seabird can choose to wait at a spot for prey to aggregate. This process, coupled with monitoring of success of near neighbors is probably employed by gulls and other birds when they prey on ephemeral surface swarms of euphausiids (S. E. Smith pers. comm., D. G. Ainley and K.T.B. unpubl. data).

Obviously, very different strategies might be employed by storm-petrels, whose "patchiness" extends over scales greater than 64 km, and who might spend much time commuting between ephemeral abundance peaks of their prey (in fact, it seems certain that many records of solitary petrels reflect the protracted 'search' phase), versus Cassin's Auklets, whose aggregations are fairly similar in duration (days to weeks) and extent (~15 km across the shelf and 30+ km along the shelf) to patches of euphausiid prey (Briggs et al. in press). The alcids' morphological trade-off of excellent flight in water versus poor flight in air is related to exploitation of dense, predictable patches of prey (Ainley 1977). However, we do not yet have a clear understanding of the degree of correspondence of bird patches and those of their prey. Woodby (1984) found poor correspondence between patches of murres and their prey in the Bering Sea, whereas Obst (1985) and Schneider and Piatt (in press) found close juxtaposition of predators and their prey. Much work remains to be done in this area.

How do seabirds locate prey patches? Considering the nature of birds' sensory apparatus and the supporting media (air and water), we believe that for most birds the primary cues must be optical. Hutchinson and Wenzel (1980) and Hutchinson et al. (1984) have demonstrated use by procellariiforms of olfactory cues for food-finding, but most seabirds seem to lack this ability. In all cases, however, the amount of phytoplankton and other suspended particles in surface waters must directly influence the ability of seabirds to locate prey and the ability of prey to avoid being eaten (Ainley 1977). Optical properties, including sharp boundaries between waters of different color or clarity, may present seabirds with visual cues for locating current shears or frontal zones that support prey in elevated concentrations (abundance maxima within larger compositional patches). Preliminary results from a study of satellite-measured ocean optical properties and some of these seabird data suggest that

Cassin's Auklets preferentially occupy recently upwelled waters of intermediate clarity (5–8 m optical depths) while murres select murky water (1–3 m optical depths) without regard to temperature and salinity characteristics (Briggs et al. in press). For murres, murky water may influence the effectiveness of predation on (relatively) mobile fish, while for auklets, water clarity may influence prey capture or may only be a "tracer" for habitat having the largest stocks of euphausiid prey.

The number of variables included in our analyses is but a fraction of those that might affect bird distribution. Data do not yet exist to investigate some possible habitat characteristics, but it is tempting to wonder about the importance to (particularly) diving seabirds of the depth of the thermocline. The scales of variation in thermocline topography have not been resolved for much of the coastal zone. However, this is an important aspect of the environment of diving species. For instance, Haury (1976) points out that off California, as much variation in environmental conditions is encountered in 50 to 100 meters in the vertical dimension as in 50 to 100 km in the horizontal dimension at the surface. Off California, the mixed layer (that above the thermocline) generally is thinnest near the coast and deepens progressively offshore (Hickey 1979). Many authors have shown that a variety of mobile zooplankton and micronekton (e.g., euphausiids and copepods) remain at or below the thermocline by day and migrate toward the surface at night. Thus, we would expect birds such as auklets to forage near the thermocline during the day. This proposition is simple and testable in the field, and we wonder if patterns of horizontal distribution of these birds reflect something of the thermal (or density) structure at depth. Do diving seabirds base their habitat selections in part on variations in vertical structure of the coastal ocean in a manner analogous to the ways in which terrestrial birds react to vertical structure of vegetation (reviewed in Cody 1985)? Do variations in thermocline topography have surface correlates (optical?) that could be sensed by foraging seabirds? Supposing a relatively high energetic cost of underwater feeding (and other factors being equal), birds would harvest more net energy per dive where the thermocline is shallow than where it is deep. Are Cassin's Auklets, for instance, limited in their offshore distribution by the deepening thermocline? Do murres, cormorants, and shearwaters obtain schooling fish and squid by feeding at shallow thermoclines where the prey are themselves feeding on abundant plankton?

As might be expected, a major result of work such as ours is the generation of many new ques-

tions. With the appreciation that to find prey, seabirds probably depend on a suite of environmental cues, past experience, and behavioral interactions, we should now focus on determining how physical processes affect concentrations of prey, how well seabirds are able to recognize habitats having enhanced feeding opportunities and how such choices might affect bird life history parameters. This should involve not only behavioral and physiologic studies of foraging individuals but also simultaneous, integrated measurement of the foraging environment. We need to know much more about factors that make prey available to birds, and we need to determine the consequences of different habitat choices (mortality, reproductive output, etc.). These challenges will be technologically difficult, but the answers will provide a striking counterpoint to studies now proceeding in terrestrial environments.

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LITERATURE CITED

ABRAMS, R. W., AND A. M. GRIFFITHS. 1981. Ecological structure of the pelagic seabird community in the Benguela Current region. Marine Ecol. Progr. Ser. 5:269–277.

AINLEY, D. G. 1976. The occurrence of seabirds in the coastal region of California. West. Birds 7:33–68.

AINLEY, D. G. 1977. Feeding methods of seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. Pp. 669–686 in G. A. Llano (ed.), Adaptations within Antarctic ecosystems. Gulf Publ. Co., Houston, Tex.

AINLEY, D. G., AND R. J. BOEKELHEIDE. 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. Studies Avian Biol. 8:1–23.

AINLEY, D. G., AND R. J. BOEKELHEIDE (eds.). In press. The Farallon Island seabird community: dynamics and structure in an upwelling system. Stanford Univ. Press, Palo Alto, Calif.

AINLEY, D. G., AND S. S. JACOBS. 1981. Seabird affinities for ocean and ice boundaries in the Antarctic. Deep-Sea Res. 28:1173–1185.

AINLEY, D. G., AND T. J. LEWIS. 1974. The history of Farallon Island marine bird populations, 1854–1972. Condor 76:432–466.

AINLEY, D. G., E. F. O'CONNOR, AND R. J. BOEKELHEIDE. 1983. The marine ecology of birds in the Ross Sea, Antarctica. Ornith. Monogr. No. 32.

ANDERSON, D. W., AND F. GRESS. 1983. Status of a northern population of California Brown Pelicans. Condor 85:79–88.

ANDERSON, D. W., F. GRESS, K. F. MAIS, AND P. R. KELLY. 1980. Brown Pelicans as anchovy stock indicators and their relationships to commercial fishing. Calif. Coop. Oceanic Fish. Invest., Rep. 21:54–61.

ASHMOLE, N. P. 1971. Seabird ecology and the marine environment. Pp. 224–271 in D. S. Farner and J. A. King (eds.), Avian biology, vol. 1. Academic Press, New York.

AU, D. W. K., AND R. L. PITMAN. 1986. Seabird interactions with dolphins and tuna in the Eastern Tropical Pacific. Condor 88:304–317.

AUER, S. (ED.). 1980, 1981, 1982, 1983. Oceanographic monthly summary. U.S. Dept. Commerce, NOAA, Washington, D.C.

BALTZ, D. M., AND G. V. MOREJOHN. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay. Auk 94:526–543.

BECK, R. H. 1910. Water birds in the vicinity of Point Pinos, California. Proc. Calif. Acad. Sci. 4:57–72.

BELLROSE, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA.

BERNAL, P. A., AND J. A. McGOWAN. 1981. Advection and upwelling in the California Current. Pp. 381–399 in F. A. Richards (ed.), Coastal upwelling. Amer. Geophys. Union, Washington, D.C.

BOLIN, R. L., AND D. P. ABBOTT. 1963. Studies on the marine climate and phytoplankton of the central coastal area of California 1954–1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23–45.

BOURNE, W. R. P. 1981. Some factors underlying the distribution of seabirds. Pp. 119–134 in J. Cooper (ed.), Proceedings of the Symposium on birds of the sea and shore, 1979. African Seabird Group, Cape Town, South Africa.

BRADSTREET, M. S. W. 1979. Thick-billed Murres and Black Guillemots in the Barrow Strait area,