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Symposium Overview

AUKS AT SEA: PROSPECTS FOR FUTURE RESEARCH

SPENCER G. SEALY

Like other birds, seabirds interact with environments that are variable. Ernst Haekel (1890) recognized this variability when he proposed his then-controversial notion that the plankton composition of oceans was irregular and its distribution unequal in time and space. Farther up the trophic scale, the relationships between fine-scale oceanographic events and fish aggregations became better known, in 1938, with the publication of Uda's important study. Thus, not surprisingly, the early surveys of birds over large areas of the sea (e.g., Jespersen 1929, Wynne-Edwards 1935, Murphy 1936), and studies of the interrelations of birds and the oceans (e.g., Kullenburg 1947, Hutchinson 1950), began to reveal that the numbers, species, and movements in a given region were influenced by physical and biological attributes of the surface waters. Although Murphy (1936) had showed that some seabirds have affinities for certain fine-scale features of the sea such as special current systems and gyres, the interactions between birds and the marine environment were still regarded generally simplistically, in part because ornithologists lacked ways of elucidating the complexities of the birds' behavior in the vastness of the oceans. Phillip Ashmole (1971:224) characterized this dilemma when he lamented that "... few marine biologists have given due weight to sea birds as components of marine ecosystems, and few ornithologists have also been oceanographers." This situation soon changed, however. It was Ashmole, and his wife, Myrtle, whose classic study (1967) of the feeding ecology of seabirds nesting on Christmas Island in the Pacific Ocean, caused oceanographers almost overnight to look once again at animals. The Ashmoles recorded seabirds feeding their young with midwater myctophids that existing knowledge suggested should be hundreds of meters below the surface, and out of reach of the surface-feeding birds! They discovered that plankton, concentrated near the surface by oceanic fronts, attracted schools of tuna whose foraging activities made available to birds prey that was otherwise out of their reach.

The oceanic study of birds soon became recognized as an important branch of ornithology. The timing was right because the early 1970s saw a world-wide, economic crisis arise over the availability and price of oil, and exploration for new reserves increased throughout the world's oceans. We urgently needed to learn quickly the extent of our seabird resources and to determine their vulnerability to disturbances and accidents considered by many to be inevitable. This meant, too, that we had to learn more about birds at sea. Seabird biologists had been largely land-based up to that time, but they responded swiftly to the availability of new funding, and marine ornithology matured rapidly. The disciplines and tools of oceanography and ornithology were merged, and the rapidly developing technology was used imaginatively. Bourne's (1963) concern about the dearth of knowledge of birds at sea began to dissipate. Marine ornithologists now publish regularly in journals of oceanography and marine science, and some oceanography departments have ornithologists on their staffs.

The family Alcidae dominates other groups within its range in terms of the number of species and biomass. It includes 22 living species of primarily wing-propelled diving birds confined mainly to the colder waters of the Northern Hemisphere. Sixteen of the species are restricted to the Pacific Ocean and adjacent waters, four are confined to the Arctic/Atlantic oceans, and two others occur in both oceans. Bédard (1969a: 189) noted that "the [Alcidae are] interesting among birds in being the only one that in the Northern Hemisphere has achieved adaptive radiation within a broad and diversified ecological zone, the subsurface waters of the ocean. Since no other sea-bird family occupies this ecological zone, the family ... gives us an opportunity to examine a group remarkably free of interactions with other groups, a condition seldom encountered in terrestrial situations."

Like other truly marine birds, auks cannot feed at their breeding stations. They must commute varying distances to find their prey, often out of sight of their colonies, and of observers. Having discovered food, they usually obtain it under the water's surface. Thus, the determinants of alcid foraging niches have remained largely speculative. This contrasts sharply with species in many terrestrial communities where we can often watch individuals forage.

Early attempts to determine the foraging ranges of breeding auks were hampered by an inability to maintain or regain contact at sea with individuals known to be breeding, and a failure to recognize the short-term influences the surrounding physical features of the marine environment probably exerted on the foraging birds (e.g., Pearson 1968, Cody 1973). Bottom fish taken near shore by guillemots (*Cepphus* spp.) revealed the often shallow depths to which they dived (e.g., Drent 1965, Preston 1968), but at the same time obscured the true nature of the distances many individuals travelled. Using transects around colonies along which were recorded the positions of feeding and flying birds, marked with specially-designed streamers color-coded to reveal their colony of origin, Cairns (1987) measured foraging ranges that were greater than those suggested from previous, largely anecdotal observations (e.g., Slater and Slater 1972, Asbirk 1979). Although the birds foraged near shore, Cairns determined that maximum ranges were not normally attained, as was suggested when foraging distances were calculated from intervals between chick feedings (e.g., Pearson 1968, Wiens et al. 1984).

Conducting transects, however, is costly, time-consuming, and often impractical. Although a speed/distance meter has been used successfully with penguins (Wilson and Achleitner 1985), it remains to be tested on alcids. Conventional radio-telemetry has limited applications for determining the foraging movements of widely ranging animals (e.g., Wanless et al. 1985; but see Trivelpiece et al. 1987). Satellite tracking may be the way of the future for quantifying the flight speeds and foraging ranges of pelagic birds over large areas of the sea. Multiple locations can be obtained night and day, from a stationary base position. Using this technique, Jouventin and Weimerskirch (1990) found that Wandering Albatrosses (*Diomedea exulans*) travelled at speeds between 63 and 81 km per h and covered between 3664 and 15,200 km in a single foraging trip, while their partners incubated. Knowledge of species' foraging ranges, especially while breeding, also has important conservation implications. For example, commercial fishing limits may have to be established in the future around islands to safeguard colonies or known feeding areas from competition (e.g., Carter and Sealy 1984).

We know little about the depths to which alcids dive to capture prey. Incidental drownings in stationary gill nets set at known depths (Piatt and Nettleship 1985) and miniature gauges attached to free-living birds (Burger and Wilson 1988) have provided important data on maximum diving depths, which appear to be related directly to body size (Piatt and Nettleship 1985). However, we still know little about the amount of time auks forage at different depths (but see Wilson and Bain 1984), the habitat parameters that influence the nature of dives, and the clues birds use when deciding to give up and try somewhere else. Comparisons of dive and pause times, obtained relatively easily on the surface of the water, may provide important insight into how auks exploit prey patches (see Ydenberg and Forbes 1988).

Extremely important in their own right, diet studies have preoccupied many workers over the past 20 years or so. Prey removed from stomachs were often the closest we could get to "sampling" the prey at sea. Seasonal and year-to-year changes in prey choice, among other things, were identified and interpreted by synthesizing the often-scanty literature on the natural history of the prey species identified (e.g., Bédard 1969b, Sealy 1975). Many species taken had been largely ignored by fisheries biologists because they had no commercial value, and therefore little information existed on their natural history. Now, some of the common prey species are being exploited commercially, and seabirds presumably must compete against man for their food (reviewed by Evans and Nettleship 1985). Indeed, some auk populations have declined in recent years (this volume), and it is easy to blame the declines on overfishing and its presumed alteration of year-class stocks. But the associations, though facile, are often questionable. Sorting out the links between seabird numbers and their prey will require serious attention by physical oceanographers, meteorologists, and fisheries and seabird biologists working together.

Quantifying prey abundance, let alone prey availability and its accessibility, is difficult in all habitats (Johnson 1980), and demonstrations of the relationship between the abundance of foraging birds at sea and the availability of their prey remain elusive, especially over small spatial scales. The foraging success of the birds themselves still may be the best indicator of prey availability. More diet studies are needed, preferably conducted over several years at many points in the breeding and non-breeding ranges of species, and selected carefully in terms of surrounding hydrographic features of the marine environment. However, changing ethical values have forced biologists to justify the initiation of large-scale studies that require large numbers of birds to be collected and to seek other, nondestructive ways to obtain dietary information (see review in Duffy 1986).

Auks do not find their prey at sea by randomly flying over the surface of the water. Large-scale transects have provided evidence (this volume) that they track their food resources, as some terrestrial birds apparently do (e.g., Cody 1981). The "information-center" hypothesis focuses on the discovery of patchily distributed prey, and circumstantial evidence from alcid studies supports it. Indeed, the nesting dispersion in the Alcidae ranges from solitary through large colonies, which should facilitate the testing of this and other related hypotheses. Birkhead (1985) noted that nonrandom departures of Thick-billed Murres (*Uria lomvia*) could be correlated with colony size and the location of food patches. However, individuals must be followed or encountered again at sea, and food predictability must be measured accurately, before support for this hypothesis is more than just correlative.

We know almost nothing about the behavior of auks once they have discovered prey. Decisions they make while hunting probably are affected by the complexity of the visual field and the dispersion of the prey, as Fitzpatrick (1981) noted in tyrant flycatchers. Fitzpatrick argued that these variables are intimately associated with overall foraging-mode differences and combine to determine the minute-by-minute movement pattern within each species. Although birds in general are highly visual animals, the optical aspects of their foraging remain virtually unexplored. In 1972, MacArthur commented on some predictable effects of visual field characteristics of two species of kingfishers in Panama, the smaller (38 g), Green Kingfisher (*Chloroceryle americana*) and the larger (300 g), Ringed Kingfisher (*Ceryle torquata*). MacArthur stated (p. 68):

> "The green kingfisher must eat small fish and hence must perch near the water, where the small fish are close enough to be visible. The ringed should perch where the greatest number of grams of fish per day can be captured, so it perches high enough to search a wide area for big fish. But notice how this restricts its diet: by perching so high that it can survey a large area, it can no longer see the very small fish, or if they are visible, the energy it would get by eating one would not compensate for the energy expended in the long dive. Hence the ringed kingfisher is largely confined to eating big fish, and its feeding position has affected its diet."

Characteristics of surface waters, such as clarity and light intensity, possibly influence the searching strategies of seabirds. Ainley (1977) hypothesized that turbidity may limit species' distributions, and noted that the pursuit-diving alcids, as well as other species, are found primarily in the more turbid waters of polar regions, while plunge-divers are more common in clear, tropical oceans (but see Haney and Stone 1988). Implicitly, foraging alcids operate under conditions of lowered light where the detection of prey probably involves contrast discrimination (see Lythgoe 1979). Concomitant retinal oil droplet constitutions should be expected, and preliminary information from diving birds suggests this is the case (Begin and Handford 1987). Furthermore, auks foraging over shallow bottoms, especially with pale substrates, will be faced with different light environments (see Munz and McFarland 1977). Interestingly, plumage coloration of pursuit-diving seabirds seems to be related to the depths at which different species forage (Cairns 1986). The visibility and behavior of prey under different lighting regimes may influence their prey choice. This is a wide-open area of research, ideally suited for experimental manipulations under controlled conditions in aquaria.

Research on the oceanic biology of birds has lagged behind that of terrestrial communities with regard to long-term and manipulative studies. Seabird biologists must move beyond the correlational approach and experimentally manipulate habitat variables, because quantitative and manipulative studies are needed to test such basic questions as which sets of variables are critical for habitat selection (Morse 1985). It may never be realistic to do this at sea, and hence the development of suitable research aquaria seems to be necessary. These facilities already exist (see Everett and Todd 1988), and seabird biologists may be able to answer important questions using captive birds. For example, Duffy et al. (1987) determined that larger auks dived longer and beat their wings more frequently. Six of the seven captive species studied propelled themselves under water with only their wings, while Pigeon Guillemots (*C. columba*) used both their feet and wings, and hung their heads down while they probed the bottom. Among the species observed, behavioral differences in foraging also were apparent.

An important natural manipulation occurs every so often at sea. This is the meteorological and physical oceanographic results of El Niño-Southern Oscillation events (ENSOs) that affect prey resources and thus their seabird predators (Schreiber and Schreiber 1984). Here, long-term monitoring of seabird numbers and distribution at sea, and studies of population parameters at the colonies, are vital if we are to identify changes that occur during and after ENSOs. Unfortunately, long-term studies of pelagic bird communities are generally lacking. One exception is Briggs et al.'s (1987) study, which is the first to examine comprehensively and exclusively the pelagic biology of seabirds occupying a specific coastal region. This study sets a standard that future workers should strive to achieve.

Seabirds often feed in large, conspicuous mixed-species flocks. Recent evidence reveals that auks contribute importantly to the dynamics of these flocks in northern waters. Perplexed to find euphausiids, known to migrate to deeper water during daylight hours, in the stomachs of surface-feeding species, Hunt et al. (1988) put SCUBA divers in the water near a feeding flock off St. Matthew Island. They discovered that murres routinely dived more than 30 m to capture euphausiids hovering above the shelf, but in doing so stunned or injured many of the invertebrates, forcing them to the surface where they were picked off easily by gulls and other surface-feeding species. Schneider et al. (this volume) confirmed hydrographically that the feeding sites were at confluences of different water masses, or fronts, areas long-recognized as important sources of food for seabirds (e.g., Martin and Myres 1969). These observations suggest that seabird communities may sometimes partition resources by access to prey rather than by diet.

The Alcidae is unique among families of birds because of the diverse behaviors found shortly after hatching (e.g., Sealy 1973, Gaston 1985). The precocial murrelets (*Synthliboramphus* spp.) spend only a couple of days in the nest, and then are reared at sea. The intermediate species (*Uria* spp. and *Alca*) complete the first part of their development in the nest, and finish it up at sea. The other (semi-precocial) species are reared in the nest sites until fully grown. We know little about diets, feeding and growth rates, and at-sea parental care of the precocial and intermediate species, although much information exists for many of the semi-precocial species (see Gaston 1985). Scott (this volume) determined that family groups of Common Murres (*U. aalge*) at sea consisted of single young accompanied by only one parent, usually the male. Opportunistic observations of family groups of Ancient Murrelets (*S. antiquus*) provided incomplete information on movement patterns (Sealy and Campbell 1979), but parallel transects near colonies showed that the groups moved to the continental shelf, apparently the rearing area (Vermeer et al. 1985). Using radio-telemetry, Duncan and Gaston (this volume) determined that murrelet families moved rapidly and steadily away from the colony during the first 24 hours after departure, and that the groups became scattered at sea. Because they followed only a handful of families, more information is needed, despite the difficulty and expense in obtaining it.

The founders of the Pacific Seabird Group (PSG) emphasized cold and temperate water systems and, not surprisingly, the auks have been popular subjects among group members over the years. Up to and including 1987, four symposia have been held at PSG meetings that dealt specifically with aspects of alcid biology, but the present one is the first to examine auks exclusively at sea. Most of the studies in this volume were centered in the Bering Sea and western Atlantic Ocean, and were conducted by North Americans. Although this has cast a somewhat parochial air on the proceedings, it reveals a reality to be overcome, and challenges us to recognize the differences between the faunas of these oceans, and to be careful not to generalize from the narrow data bases. Furthermore, and not surprising considering that fewer species of auks occur in the north Atlantic, the Common and Thick-billed murres received most of the attention; only five of the 17 papers did not deal directly with one or both of these species, while 12 species received little or no attention at all. Five major subject areas emerged from the topics discussed in this volume. Six papers identified hydographic cues auks use to locate food, which is often distributed patchily in time and space. Once food is located, in often-distant prey patches, its efficient utilization is examined in three papers. The precocial auks reduce commuting distances and travelling times during chick-rearing by taking their portable young to the food source at sea. Two papers deal with this challenging and little-studied aspect of alcid biology. Diets are examined in three papers. Croll's and Elliot et al.'s studies point out the need for more cross-seasonal studies in the breeding and non-breeding seasons. In my remarks above, I have anticipated some of the topics that will be discussed in this volume, and have attempted to identify some of the areas where research by seabird biologists is likely to be concentrated in the future.

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