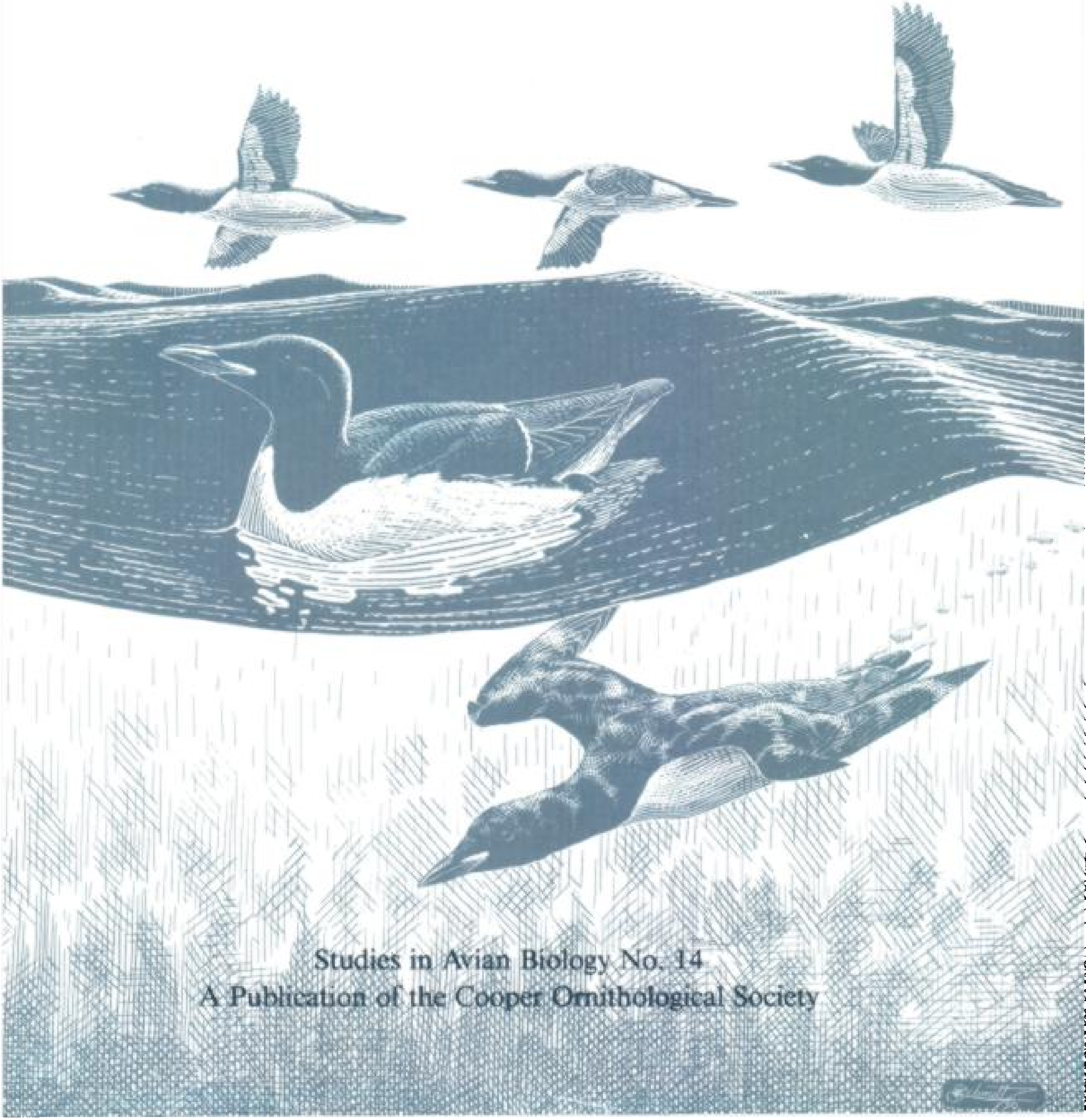
AUKS AT SEA

SPENCER G. SEALY, EDITOR



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Spencer G. Sealy, editor

Proceedings of an International Symposium of the
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Cover drawing of murres at sea by John Schmitt

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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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Patch Use

THE INFLUENCE OF HYDROGRAPHIC STRUCTURE AND PREY ABUNDANCE ON FORAGING OF LEAST AUKLETS

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Abstract. We investigated the foraging distribution of Least Auklets (*Aethia pusilla*) near their breeding colonies in the Chirikov Basin, northern Bering Sea, to determine the physical and biological aspects of the ocean important in their use of foraging areas. In this paper we report on a series of transects radiating out from colonies on St. Lawrence and King islands, along which we examined the importance to foraging Least Auklets of vertical structure in the water column. We counted birds, collected them for food samples, described the hydrography using conductivity-temperature-depth casts, and obtained data on the distribution and abundance of prey from net tows and high-frequency acoustic surveys. Copepods (*Neocalanus* spp.) were prominent in the diets, and auklets foraged in greatest numbers in waters where *Neocalanus* was present and where the water was strongly stratified. Auklet numbers were correlated more strongly with plankton biomass in the upper water column than with biomass in the water column as a whole. Within the upper water column, it appeared that these correlations were stronger at a scale of 9–22 km than at 1.8–4 km and that auklets select their foraging habitat in a coarse-grained fashion.

Key Words: Least Auklet; *Aethia pusilla*; foraging habitat; Bering Sea; predator-prey studies; stratified water.

The pattern of marine bird distribution at sea results from the selection and use of foraging areas. Ocean habitats vary in scale from major portions of ocean basins that may be occupied continuously for months or years, to tidal rips that are attended for, at most, hours at a time (Hunt and Schneider 1987). Descriptions of these marine foraging habitats have usually focused on the physical characteristics of the surface layer (sea surface temperature and salinity) (e.g., Pocklington 1979, Brown 1980, Ainley et al. 1984, Fraser and Ainley 1986). In the nearshore zone, features such as fronts separating stratified and well-mixed water (Pingree et al. 1974, Schumacher et al. 1979, Kinder et al. 1983), eddies at headlands and islands (Ashmole and Ashmole 1967, Pingree et al. 1978, Hamner and Hauri 1981), and sills that force currents to the surface (Vermeer et al. 1987, Brown and Gaskin 1988), are predictably attended by foraging seabirds. In the open ocean, physical features also act as foci to aggregate seabirds (Schneider 1982, Briggs et al. 1984, Schneider and Duffy 1985, Haney and McGillivary 1985, Briggs and Chu 1987). The strength of fronts in the Bering Sea is an important correlate of their attendance by seabirds (Schneider et al. 1987), and it is likely that topographically fixed inshore features, with steep gradients and high kinetic energy, are attractive for similar reasons (Roseneau et al. 1985, Schneider et al. 1986). Unfortunately, in many studies oceanographic and ornithological data have not been gathered simultaneously, and virtually no study has investigated how prey abundance or availability affects the linkage between physical features and birds.

Implicit in studies of seabird habitat preferences is the assumption that the birds aggregate where their preferred prey is most readily obtained. The rate of prey capture will depend not only on the number of prey present (abundance), but also on their degree of aggregation (density), and availability, which is a function of their accessibility (e.g., depth in the water column). Relatively few investigators, however, have been able to measure prey density or accessibility. Most investigators who have attempted to link bird abundance to prey availability have found either weak to moderate correlations (Schneider and Piatt 1986, Cairns and Schneider 1990, Safina and Burger 1988, Heinemann et al. 1989) or no correlation (Woodby 1984, Safina and Burger 1985, Obst 1985) at small and intermediate scales (but see Piatt [1987] and McClatchie et al. [1989]). At larger scales, from 100s of kilometers to whole ocean basins, strong positive correlations have emerged between bird numbers and the abundance of presumed prey or marine secondary productivity (Jesperson 1930, Heinemann et al. 1989, Erikstad et al. 1990). In studying seabird foraging, quantifying prey availability is even more difficult than measuring prey abundance. Foraging success is possibly the best indicator of prey availability, even though numerous factors other than prey availability may influence capture rates (Dunn 1973, Birkhead 1976, Searcy 1978, Morrison et al. 1978, Hunt et al. 1988).

The poor correlations often found between the abundance of marine birds (particularly subsurface foragers) and their prey may result from their inadequate knowledge of prey distributions. Surface cues may promote local, ephemeral corre-

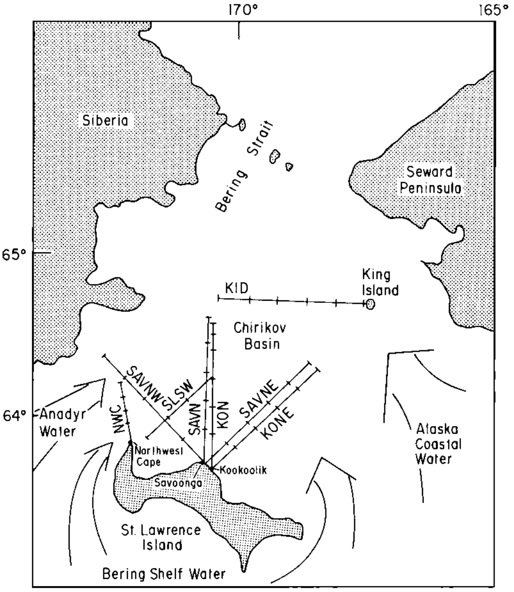

FIGURE 1. Study area and transect lines. Lines crossing transect lines indicate locations of stations. Stations were 18.5 km apart except on NWC where they were 9.8 km apart.

lations between birds and their prey. In some cases, prey are forced to the surface where they become apparent to flying birds. In other cases, surface characteristics, such as foam lines or narrow regions of choppy water, indicate the presence of subsurface processes that frequently concentrate prey (Hamner and Hauri 1981). However, subsurface foragers, such as alcids, may have few or no clues about the presence of prey many meters deep.

Although clues to the distribution of prey in the horizontal dimension may be lacking, prey distribution in the vertical dimension may be relatively predictable. Property gradients are often steep, resulting in stratification of the water column where marked changes in density (pycnoclines), due to rapid changes in salinity (haloclines) or temperature (thermoclines), impair vertical mixing. Plankton may be concentrated at or in these gradients (Harder 1968, Barroclough et al. 1969, Turner and Dagg 1983). As suggested by Briggs et al. (1987), when prey is concentrated at haloclines or thermoclines, particularly those near the surface, subsurface-foraging birds should be able to locate prey predictably and capture food more readily than when an equal abundance of prey is dispersed throughout an unstratified water column.

The Least Auklet (*Aethia pusilla*) is a small planktivorous alcid that specializes on various species of copepods during the summer breeding season (Bédard 1969, Springer and Roseneau 1985, Hunt and Harrison 1990). Auklets obtain these prey while diving beneath the surface, and frequently take the large oceanic copepods *Neocalanus cristatus* and *N. plumchrus* (Springer and Roseneau 1985, Bédard 1969, Hunt and Harrison 1990). *Neocalanus* spp. are known to form dense layers in the ocean and respond to steep property gradients in the laboratory, which could lead to dense concentrations of these prey in the vertical dimension in a stable water column (Harder 1968, Barroclough et al. 1969). Thus, Least Auklets might be expected to concentrate their foraging in well-stratified water.

In this study we examined the foraging distribution of Least Auklets in the Chirikov Basin between St. Lawrence Island and King Island with respect to hydrographic structure and prey distribution in the vertical and horizontal planes. Using observations from transects that radiated from Least Auklet colonies on the north side of St. Lawrence Island and from King Island in the northern Bering Sea, we quantified bird distribution, water column structure, and the horizontal and vertical distribution of acoustically-determined biomass, the composition of which was determined by net tows.

STUDY AREA AND METHODS

Study area

The Chirikov Basin averages less than 50 m in depth and is bounded by St. Lawrence Island to the south, Siberia to the west, the Seward Peninsula of continental Alaska to the east and Bering Strait to the north (Fig. 1). Water enters the basin in two major currents: the Anadyr Current along the west side, and the Alaska Coastal Current along the eastern edge. Between these, Bering Shelf Water enters the basin from the south, passing primarily around the east end of St. Lawrence Island. The Anadyr Current originates in the deep Bering Sea, mixes with cold saline water in the Gulf of Anadyr, and sweeps northeasterly between Siberia and St. Lawrence Island into the basin and then out through Bering Strait (Coachman et al. 1975). The Alaska Coastal Current originates in Norton Sound. Compared to the Anadyr Current, the Alaska Coastal Current is a relatively warm, low salinity water mass that is similar to the coastal domain water of the southeastern Bering Sea (Coachman et al. 1975, Kinder and Schumacher 1981). Water in these currents is usually unstratified.

Bering Shelf Water is of intermediate salinity, compared to Anadyr Current Water or Alaska Coastal Current Water, and is a mixture of water from the deep Bering Sea to the south and cold bottom water present on the seasonally frozen northern Bering Sea shelf. Bering Shelf Water forms a broad expanse of water that flows northward more slowly than the currents on either side, and it is usually strongly stratified in summer (Coachman et al. 1975, Hunt and Harrison 1990). Near the northern shore of St. Lawrence Island, Bering Shelf Water may be diluted by freshwater runoff, and may be unstratified due to a combination of tidal and wind mixing, as seen elsewhere in the Bering Sea (Kinder and Schumacher 1981, Kinder et al. 1983).

The boundaries of these three water masses in the Chirikov Basin are not static. The area occupied by the stratified Bering Shelf Water varies greatly over short periods depending on the positions of the Anadyr and Alaska Coastal currents. Both currents meander, and large horizontal excursions on the order of tens of kilometers have been observed over the period of 2–4 days, as well as from year to year (Hunt and Harrison 1990).

The copepod community of the Anadyr Current is dominated by the very large *Neocalanus cristatus* (10 mm), *N. plumchrus* (5 mm), and *Eucalanus bungii* (8 mm) (Brodskii 1950; Smith and Vidal 1984; Springer et al. 1987, 1989). In contrast, the Alaska Coastal Current lacks these large species and is dominated by the smaller *Calanus marshallae, Acartia* spp. and *Pseudocalanus* spp. (Motoda and Minoda 1974, Cooney and Coyle 1982, Smith and Vidal 1984). The Bering Shelf Water contains representatives of both copepod communities, but in our experience, the larger oceanic forms predominate (Table 1, but note 1986, and Hunt and Harrison 1990). These oceanic copepods originate in the Anadyr Water and are advected into the Bering Shelf Water in the Chirikov Basin; their presence in the stratified waters of the basin is an indication of the mixture of oceanic water and Bering Shelf Water there (Springer et al. 1987, 1989).

Methods

We studied Least Auklets at St. Lawrence Island from 8 July to 10 July 1984, 4 August to 13 August 1985, and 11 August to 15 August 1986. In 1984, 1985, and 1986, one, seven and three transects, respectively, were run from the Savoonga-Kookoolik area. Of these 11 transects, nine had sufficient bird sightings on them to permit analysis and they are illustrated here, as are examples from the Northwest Cape area of St. Lawrence Island and from King Island. The proximal ends of transects at St. Lawrence Island were within 2–5 km of the nearest Least Auklet colonies. All transects but one (18 August 1986) were started no earlier than an hour after dawn and all were complete before dark. Times given are local time (GMT-10).

To determine the foraging distribution of Least Auklets, we counted birds from the bridge (eye height 7.7 m above the sea surface) of the R/V *Alpha Helix* while underway at speeds of 6–10 knots. All birds within an arc from 300 m ahead of the vessel to 90° off the beam were counted and data entered in a handheld microcomputer to the nearest 0.1 minute from time of entry for later processing. Time of entry was then used to correlate bird numbers with location and acoustic survey data. Distinction was made between birds on the water (assumed to be or have recently been foraging) and flying birds. Additionally, we recorded environmental conditions and the ship's position each half-hour, whenever we arrived at or departed an oceanographic station, or when significant changes were observed. For the analysis in this paper, for which changes along a transect line are more important than absolute numbers or density, we used only counts of birds on the water, reported as birds per five- or ten-minute time interval.

Prey use was ascertained by collecting birds on the water along the transects in August 1985 and August 1986, the period when auklets were raising chicks. We also mist-netted auklets returning to the Kookoolik colony on St. Lawrence Island in August 1985 and recovered the regurgitated contents of the gular pouches. All samples were preserved in 85% ETOH for examination in the laboratory. Percent occurrence was calculated as the percentage of all birds containing a particular class of prey. Percent composition of prey was calculated as the percentage of individuals of a particular prey type in each food sample collected, averaged over all samples.

We obtained vertical profiles of water column structure by lowering a conductivity-temperature-depth (CTD) probe to within 3–5 m of the bottom at stations usually spaced 18.5 km apart along transects (Fig. 1). Although salinity is a more conservative marker for the various water masses, we have presented temperature profiles for this study as they indicated where the sharpest property gradients were located. Density profiles were similar, but gradients were less steep and the depth of the pycnocline was less easily determined.

We used two methods to determine zooplankton distribution and abundance. The species composition of the copepod community was determined using vertical tows of a 1-m, 505 μm mesh plankton net at each CTD station, weather permitting. Plankton were identified to the lowest taxon possible in the laboratory. Identifications were complete prior to the description of *Neocalanus flemingeri* (Miller 1988, Miller and Clemons 1988) and therefore our taxon *N. plumchrus* includes an unknown number of *N. flemingeri.*

We investigated both the horizontal and vertical distribution of plankton biomass using a Biosonics® Model 101 echo-sounder (200 kHz) with the transducer towed in a V-fin depressor at about 6 knots. The calibrated system source level at maximum power was +224.8 dB re 1 μPa at 1 m. The receiver sensitivity under 20 log R time varied gain was −135.3 dBv re 1 μPa at 1 m.

A Biosonics Model 120 scientific echointegrator was used to integrate measures of volume scattering in vertical intervals of two meters from 5 m below the surface to the bottom. At ship speeds of 6–8 knots, each integration sequence of 60 pings covered 0.1 to 0.2 nautical miles (0.185 to 0.37 km) of transect line. Individual integrations were read immediately by a micro-computer, which applied corrections for water temperature, salinity, and previously determined system calibration (source level and gain, transducer directivity). Estimates of acoustically determined biomass were obtained by using the results of Richter (1985) to estimate target strengths for the commonest large zooplankters in the Chirikov Basin. At a wavelength of 7.5 mm, the largest copepodid stages of *Neocalanus* spp. and *Ecualanus bungii* were expected to contribute significantly to the sound-scattering. The resulting conversion, -80 dB g^{-1}, was used to estimate the wet weight of plankton beneath the transect line. This was derived from an empirical relationship for target strength as a function of body size and frequency (Richter 1985). This procedure would overestimate the

TABLE 1. PREY IDENTIFIED IN LEAST AUKLETS NEAR ST. LAWRENCE ISLAND AND COMPOSITION OF PLANKTON IN VERTICAL NET TOWS

	1985	1985 at sea		1985 colony		1986	1986 at sea	
Prey type	$\bar{X}$ % individuals in net tows	% occurrence in prey	$\bar{X}$ % individuals in prey	% occurrence in prey	$\bar{X}$ % individuals in prey	$\bar{X}$ % individuals in net tows	% occurrence in prey	$\bar{X}$ % individuals in prey
Sample size	12	37	37	25	25	9	25	24
All *Neocalanus*	36.3	78	33.7	100	89.5	28.3	92	78.2
N. cristatus	1.2	73	29.4	56	4.7	1.1	68	19.5
N. plumchrus	35.1	24	4.3	100	84.8	27.2	72	58.7
Eucalanus bungii	4.7	13	1.4	4	0.1	0.9	—	—
Calanus marshallae	7.8	—	—	—	—	64.7	—	—
Pseudocalanus spp.	12.8	—	—	—	—	1.6	—	—
Metridia	1.3	—	—	—	—	0.8	—	—
Pandalidae	0.3	78	33.5	80	4.8	—	—	—
Hippolytidae	0.1	16	3.0	40	0.5	—	—	—
Euphausiids	35.1	30	12.5	44	2.4	2.2	8	0.0
Hyperiids	1.9	35	12.1	32	1.5	0.4	28	10.1
Gamarids	—	—	—	4	0.3	0.4	8	3.0
Crab larvae and zoea	1.3	16	2.2	60	1.5	0.7	—	0.0
Limacina	1.1	—	—	4	0.0	—	—	0.0
Other	—	—	1.6	—	—	0.3	—	8.7

contribution to integrated biomass from the larger fishes in the area, but these fish were rarely encountered.

The major problem with the use of single frequency acoustic observations is associated with converting measures of volume scattering to estimates of biomass, due to the relationship between body size and characteristics and backscattering efficiency (i.e., target strength). The use of 200 kHz probably eliminated detectable acoustic returns from most organisms <2–3 mm long. Thus, although we present our data in terms of g of zooplankton, our results are primarily useful as relative estimates of large zooplankters beneath the transect line and not of absolute levels of total plankton biomass.

To quantify the use of stratified waters by foraging auklets near St. Lawrence Island, we used two approaches, one focusing on the location of peaks in the number of foraging auklets, the other on whether more auklets foraged over stratified water than expected by chance. Stratified water was defined as having a thermocline in which there was a change of $\geq$4°C in a five meter depth-interval. A peak was defined as a 10 min sampling period in which the number of foraging auklets exceeded the mean for the whole transect plus 1.96 times the standard deviation for the transect.

To examine the relationship between auklet numbers and the strength of the thermocline, we standardized data to allow combining of data from several transects. For auklets, the standardized number was computed by dividing the mean for the four ten-minute counts nearest a station by the maximum number for any ten-minute count on a particular transect; for the thermocline we divided the change in temperature per unit depth for the thermocline at the station by the maximum thermocline strength observed on the transect in question.

RESULTS

Data on prey obtained from Least Auklets at sea and at the Kookoolik colony are presented in Table 1, as are data from vertical plankton tows. For both 1985 and 1986, *Neocalanus* spp. were prominent in the diet. The occasional use of other prey, such as euphausiid larvae and shrimp larvae (Pandalidae), probably results from year-to-year changes in their relative abundance. Pandalid larvae were relatively large and were apparently a preferred prey of Least Auklets in 1985, as the larvae were relatively rare in our net samples of zooplankton (Table 1). Auklets took euphausiids in the year that they were abundant in net tows, but to a lesser extent than would have been expected based on their relative abundance. Evidently euphausiids were less preferred than *Neocalanus* spp. Least Auklets at King Island fed primarily on *Neocalanus* spp. (Hunt and Harrison 1990).

There were striking differences between 1985 estimates of auklet diets based on birds shot and birds mist-netted in the colonies. The prey collected in the colony was exclusively the regurgitated contents of gular pouch-loads destined for chicks. The at-sea collections, including many subadults in heavy primary moult that were unable to take flight, or did so only with great difficulty, usually yielded small numbers of items. The use of calanoid copepods would likely be underestimated in these birds, as many of these birds contained a large proportion of unidenti-

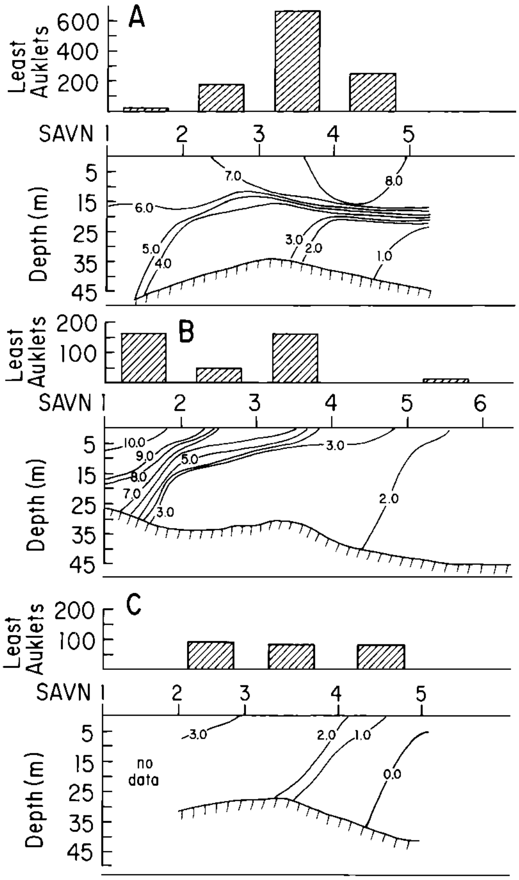

FIGURE 2. Temperature profiles and numbers of foraging Least Auklets on a series of lines north of Savoonga, St. Lawrence Island for (A) 13 August 1986, 11:45 to 16:30, (B) 4 August 1985, 05:00 to 12:00 and (C) 8 July 1984, 11:19 to 16:45. Variations in bottom profile represent soundings for each line or date run. Stations were 18.5 km apart.

fiable mush that was almost certainly derived from copepods. The difference in the species composition of the *Neocalanus* identified in the two sets of samples is of interest but we have no explanation for it.

We encountered three different classes of physical profiles on the transects at St. Lawrence Island (Fig. 2). The commonest pattern showed a relatively warm, well-mixed water inshore and stratified water with a strong thermocline between 18.5 and 37 km offshore (Fig. 2A). In these cases, the water inshore and on the surface was slightly fresher than the offshore, deeper water (32.2 vs. 32.6‰). Less commonly, we found poorly stratified water at the distal end of the transect (Figs. 2B and 3A), in areas where extensions of the Anadyr Current had intruded eastward close to the north side of St. Lawrence Island. In these cases, the long, sloping thermoclines indicate the breakdown (or setting up) of structure offshore. At times the thermocline was absent and the offshore region had cold water mixed top to bottom, with a thermal front marking the

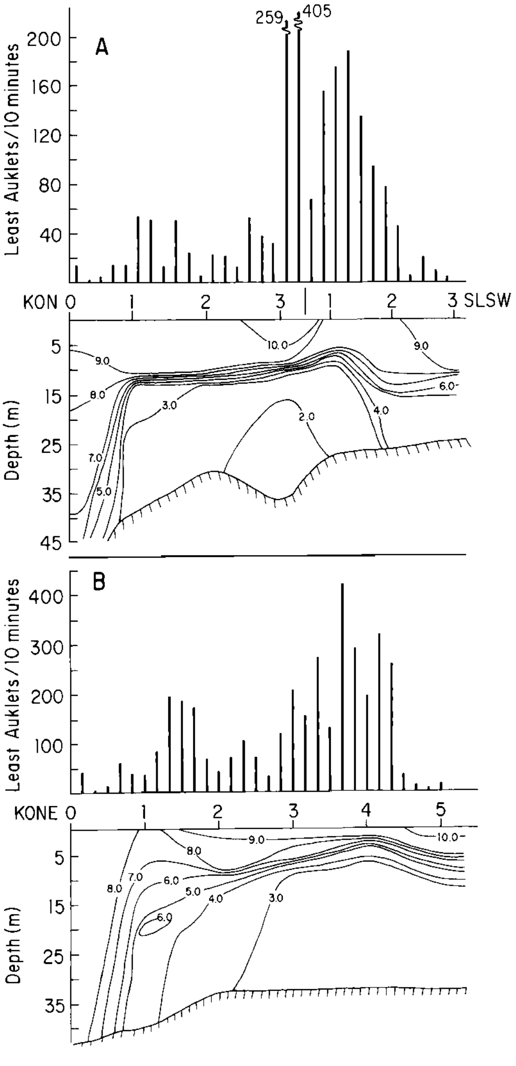

FIGURE 3. Temperature profiles and numbers of foraging Least Auklets per 10 min of counting north of St. Lawrence Island. A. A line due north from Kookoolik starting at 05:44 for 56 km in stormy weather, with a change in course at KON-3 (at 12:32) toward the southwest toward Northwest Cape on 7 August 1985. B. A line to Kookoolik from the northeast on 11 August 1985 between 05:00 and 10:43. On both lines auklet numbers reach their maximum where a strong thermocline is near the surface.

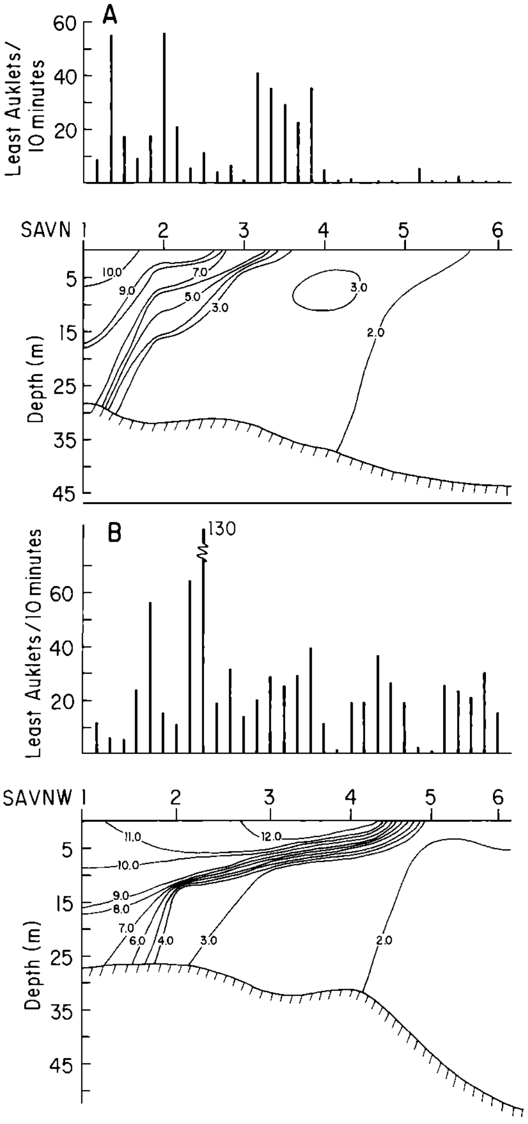

FIGURE 4. Temperature profiles and numbers of foraging Least Auklets per 10 min of counting along two lines on 4 August 1985 (A) to the south to Savoonga, run between 05:00 and 12:00 and (B) to the NW from Savoonga, run between 12:30 and 18:45. Stations were 18.5 km apart.

region where the thermocline surfaced (Figs. 2B, 3A, 3B). The offshore thermal front varied in its distance from the island and in its strength (Figs. 2B and 3A vs. 3B), presumably in response to the extent of the Anadyr Current intrusion. In one instance (Fig. 2C), cold unstratified water was found for the entire length of the transect and there was no evidence of a thermocline.

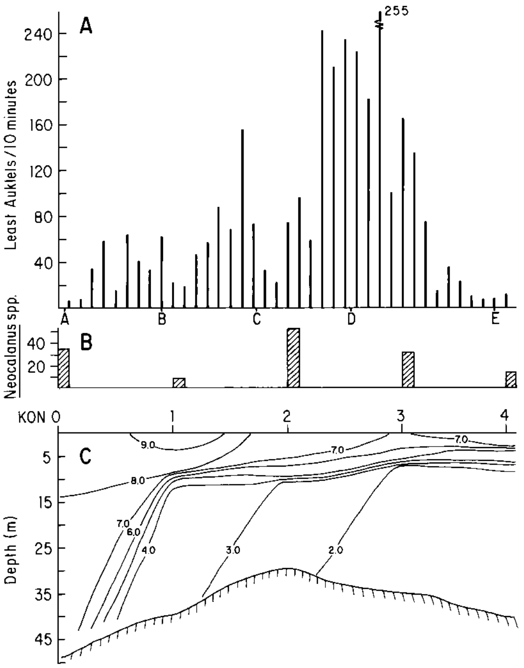

FIGURE 5. Temperature profiles, counts of *Neocalanus* spp. and Least Auklet numbers per 10 min of counting on a line north from Kookoolik, 10 August 1985 between 13:20 and 19:56, in calm weather. Stations were 18.5 km apart. Letters at the base of Figure 5A show location of profiles given in Figure 7B.

The distribution of Least Auklets varied with the type of temperature profile encountered (Fig. 2). When there was a strong thermocline offshore, peak numbers of auklets were found, although not necessarily where it was strongest (Fig. 2A). Concentrations above the thermocline, particularly where it bent toward the surface, were particularly striking on 7 and 11 August 1985 (Figs. 3A,B). In contrast, where the thermocline was closer inshore, with a front marking its offshore transition to unstratified water, we found two relatively small peaks in auklet numbers, one inshore near the commencement of the stratified layer, and one offshore at the outer end of the stratified layer (Figs. 2B, 4A, and for the inner end, 4B). On two of these three transects, numbers dropped immediately when auklets encountered the unstratified water offshore (Figs. 2B, 4A). Their distributions were relatively even over the unstratified water encountered in July 1984 (Fig. 2C).

Foraging auklets were most abundant in regions where *Neocalanus* spp. were present, and where the water was also strongly stratified. The transect north from Kookoolik on 10 August 1985,

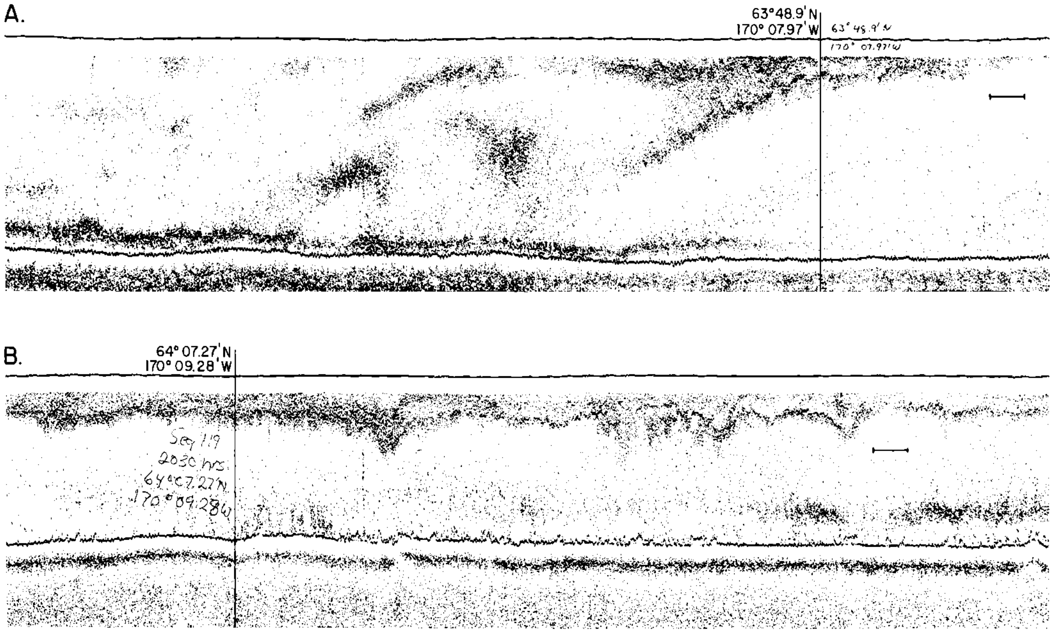

FIGURE 6. A. Echogram of acoustically determined biomass in the region of the inner front as seen in Figure 5 just inshore of station KON-1. The scale bar equals 1.85 km. B. Echogram of acoustically determined biomass between stations KON-2 and KON-3 where the plankton is in dense layers at and above the thermocline.

for example (Fig. 5A), revealed large concentrations of auklets between stations KON-2 and KON-3, approximately 40–65 km from shore. *Neocalanus* spp. were present in net tows at all stations (Fig. 5B). Acoustic estimates taken concurrently with the bird counts showed that total plankton biomass, inshore where few birds were present, was widely dispersed in the upper water column, with evidence of concentrations rising toward the surface in the vicinity of the inshore front (Fig. 6A). In contrast, beneath the offshore concentration of Least Auklets, plankton in the upper water column was concentrated above the thermocline (Fig. 6B). Plankton distribution along the transect was extremely patchy, with numerous biomass peaks in the upper 9–15 m of the water and in the water column as a whole (Fig. 7A). Acoustically determined biomass showed peak abundances near the bottom inshore, and at 7–10 m depth offshore, where the auklets were most abundant (Fig. 7B). A strong thermocline was present offshore starting near station KON-1, which appeared to rise from about 10 m depth at station KON-2 to 5–7 m depth at KON-3 (Fig. 5B). Thus, the birds were most concentrated where a strong, shallow thermocline coincided with an accumulation of plankton.

The transect on 14 August 1986, NE from Savoonga, provided a similar association. We saw virtually no auklets until just before we reached station SAVNE-3, approximately 40 km offshore (Fig. 8A). Between SAVNE-3 and SAVNE-4 numbers increased and then dropped off as we progressed toward SAVNE-5. Plankton hauls indicated that *Neocalanus* spp. were scarce or absent inshore (stations SAVNE-1 and 2), but were present at SAVNE-3, 4, and 5. The physical structure of the system also changed at SAVNE-3. Farther inshore the water column was relatively well mixed from top to bottom; offshore a strong thermocline developed. Again, the presence of *Neocalanus* spp. coincided with the presence of a stratified water column.

To examine in detail the relationship between the distribution of auklets and plankton we returned down the transect from station SAVNE-5 to SAVNE-3 with counts of birds and an acoustic survey of plankton (Fig. 9). The bird distribution had shifted somewhat inshore from the previous survey that day, but there was still a major peak near where we had taken station SAVNE-4 four hours earlier (Fig 9A). Biomass also showed a broad peak in the vicinity of station SAVNE-4 (sections C, D), with a large portion of the de-

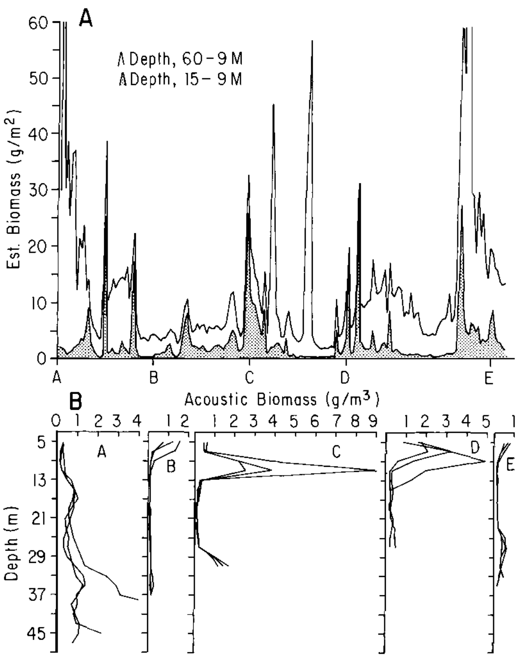

FIGURE 7. A. Horizontal profile of acoustically determined biomass obtained concurrently with bird counts reported in Figure 5 on 10 August 1985. B. Selected vertical profiles of acoustic biomass at the positions indicated. For each section, three adjacent profiles are presented to give a sense of the variation in vertical plankton distribution.

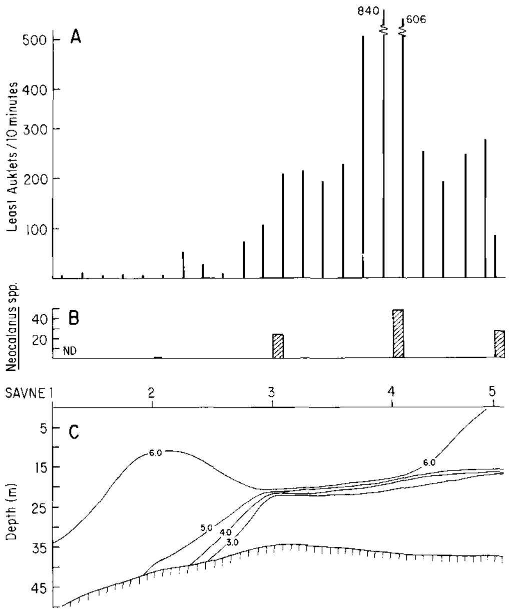

FIGURE 8. The distribution of Least Auklets, *Neocalanus* spp., and sea temperature along a transect NE from Savoonga, St. Lawrence Island, 14 August 1986 between 05:15 and 12:04. The stations are 18.5 km apart.

tected biomass above 24 meters (Figs. 9B,C). Although birds and plankton biomass were not well matched up over the smallest measurable scales, over larger scales (5.5–9.3 km) there was greater concordance.

We used two approaches to examine the small-scale distribution of plankton within the stratified zone offshore. First, we obtained acoustically determined vertical profiles of the prey distribution between SAVNE-5 and SAVNE-3 (Fig. 9). Peaks in biomass were found consistently 13 to 17 m below the surface in the area where foraging auklets were most abundant (C and D). Similar but smaller biomass peaks were present at A and B, where birds were less abundant. These patches of biomass were all apparently above the thermocline (See Fig. 8C). Second, we conducted net tows with single replicates at five stations, 3.7 km apart, between SAVNE-3 and -4 (Fig. 10). We found that tows taken at the same position, one immediately after another, often differed as much as those from stations 18.5 km apart. There were individual tows that sampled biomass peaks, and their results supported those from the acoustic survey that high plankton biomass occurred near SAVNE-4.

The 8 August 1985 transect northeast from Kookoolik also showed most auklets foraging over stratified water, but without a single strong peak (Fig. 11). All plankton tows along this line contained *Neocalanus* spp., including the inshore station where there was no thermocline. Thus, in this case most auklets overflew unstratified water containing appropriate prey to forage in more distant, stratified water, and missed the area of greatest prey concentration.

We conducted an acoustic survey concurrently with the bird counts depicted in Figure 11 and found that the distribution of plankton differed strikingly from that of the birds (Fig. 12A). For the water column as a whole, biomass was extremely patchy. Plankton was scarce in the upper layers for most of the transect of the offshore stratified water. In contrast, in the unstratified water inshore, there were dense small patches of plankton in the upper layers. However, vertical profiles showed that most of the biomass was near the bottom throughout the transect (Fig. 12B). Inshore, biomass in the upper water column was widely dispersed in depth, with great km-to-km variability (A); offshore the small amount of biomass present in the upper water

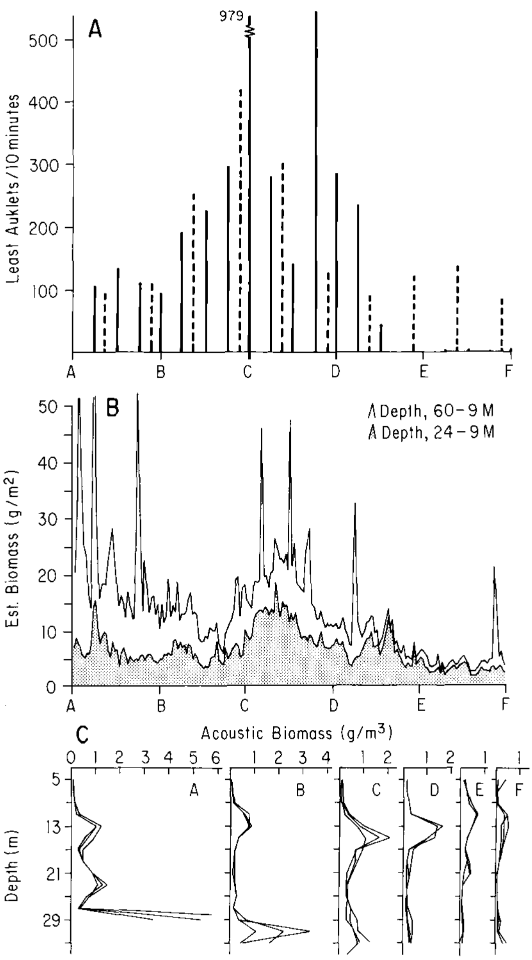

FIGURE 9. Comparison of the distribution of (A) Least Auklets over 10 min of counting and (B) acoustically determined biomass between stations SAVNE-5 and SAVNE-3, 14 August 1986 immediately after completing the run in Figure 8 (10:30 to 13:45). Dotted lines in (A) represent numbers of auklets seen on the first run, with stations; the solid lines represent auklet numbers on the repeat run. C. Vertical profiles of acoustically determined biomass. Three adjacent profiles are presented for each section. Acoustic profiles (A–F) are each 9.3 km apart.

column was concentrated at or above 9 m, with less small-scale variability (B, C, D, E and F).

Two transects at King Island on 16 and 18 August 1986 also illustrated the importance of the vertical position of plankton concentrations. On 16 August, auklets foraged 55–75 km from their colony, in a region where acoustic data indicated the plankton was more abundant above 20 m than it was in surface waters closer to the island (Fig. 13). Due to rough weather, we obtained no CTD profiles or net tows along this transect. However, past experience (Hunt and Harrison 1990) would suggest that the large copepods would have been absent within 18 km of King Island but common 18–55 km to the west. Vertical profiles along this line showed peaks

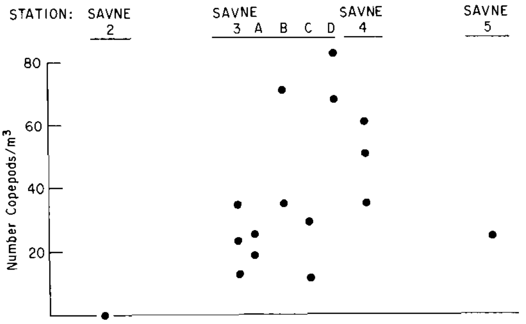

FIGURE 10. Number of *Neocalanus plumchrus* per m³ in vertical net hauls along SAVNE transect, 14 August 1986. Stations were at 3.7 km intervals between SAVNE-3 and SAVNE-4.

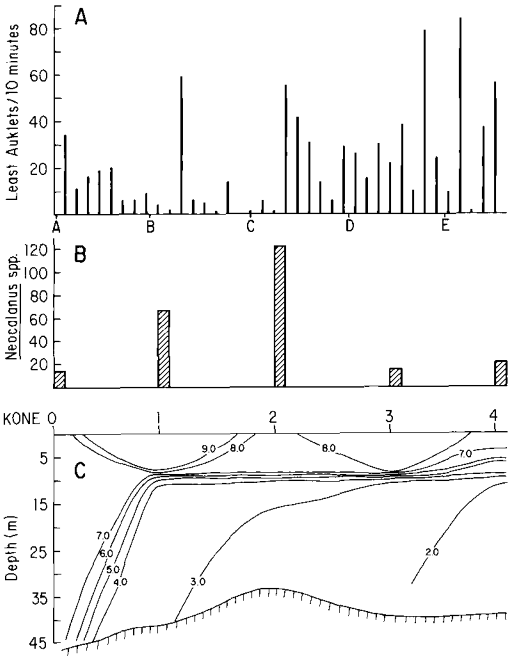

FIGURE 11. The distribution of (A) Least Auklets over 10 min of counting, (B) their *Neocalanus* spp. prey and (C) sea temperatures along a transect NE from Kookoolik, St. Lawrence Island, 8 August 1985 between 05:40 and 13:15, the day after a major storm. Stations were 18.5 km apart. Letters at the base of Figure 11A show the location of profiles given in Figure 12B.

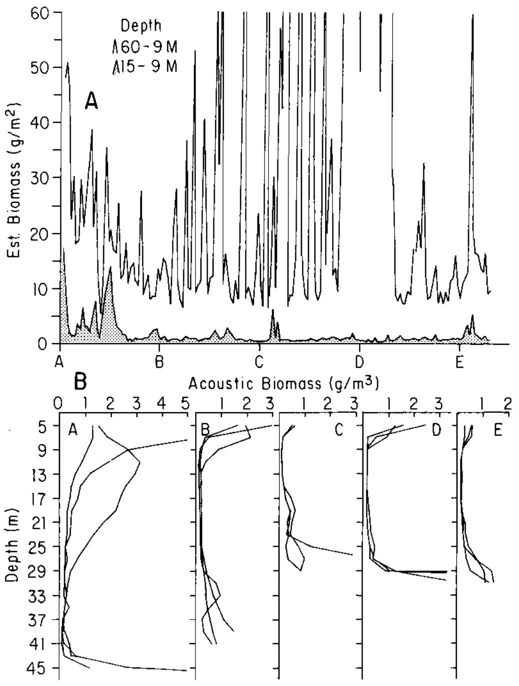

FIGURE 12. A. Horizontal profile of acoustically determined biomass along the same transect as depicted in Figure 11. B. Vertical profiles of the distribution of acoustically determined biomass at the positions indicated. Three adjacent profiles are presented for each station.

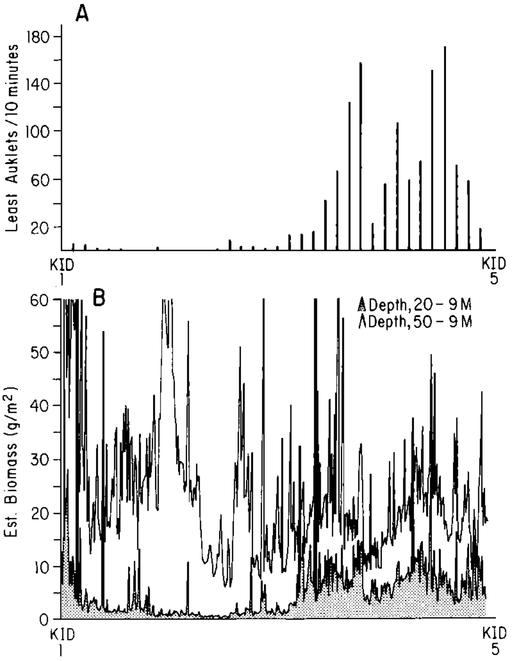

FIGURE 13. Distribution of Least Auklets (A) and acoustically determined biomass (B) along a transect west of King Island on 16 August 1986, 05:45–11:35, during stormy weather. The distance between KID-1 and KID-5 is 74 km.

in plankton biomass between 9 and 13 m depth (interference from entrained bubbles obliterated the record above 7–9 m). Two days later, most foraging auklets were near KID-4, well within the region with a strong thermocline (Fig. 14). Biomass was patchily distributed along the whole transect, but concentrated near the bottom. Several broad areas of concentration were evident in the upper water column, one of which coincided with the concentration of auklets near KID-4. Vertical plankton tows showed *Neocalanus* spp. at all stations, but more abundant west of KID-2 (Table 2). Vertical profiles from the acoustic measurements showed that in the region where the thermocline was strong (KID-3 to KID-5), most biomass in the upper water column was concentrated at 11–16 m (Fig. 15), above the top of the thermocline at 16–20 m (Fig. 14).

Structures, such as thermoclines, that rise toward the surface sometimes (Figs. 4, 5 and 11), but not always (Fig. 3), had foraging auklets above them. This relationship can be particularly striking in the vicinity of fronts where prey may become available near the surface (Fig. 16). A transect run 12 August 1986, from Northwest Cape to the boundary between United States and Soviet-controlled waters, encountered a remarkable peak in foraging auklets as we approached a front between Bering Shelf Water and the Anadyr Current. In the region of the front, the isohalines bent toward the surface (between NWC-4 and NWC-5), and Least Auklet numbers increased from ≤ 10 to over 2500 in 5-min counts (Fig. 16).

Least Auklets occurred more frequently over stratified water than was expected by chance. Of the 24 transect segments between stations over stratified water, 42% contained peaks in auklet numbers, as contrasted with only 7% over unstratified water ($\chi^2 = 5.60$, $P < 0.05$). Data from interstation observations provided similar results (unpubl.). When we compared total counts of auklets over stratified and unstratified water near St. Lawrence Island, we found that although only 50% of the transects were over stratified water, 82% of all foraging auklets were seen over this habitat (unstratified $\bar{X} = 139.75 \pm$ SD 154.23; stratified $\bar{X} = 649.79 \pm 642.58$, N = 24 for both).

The number of foraging auklets in the vicinity of a station was positively correlated with the

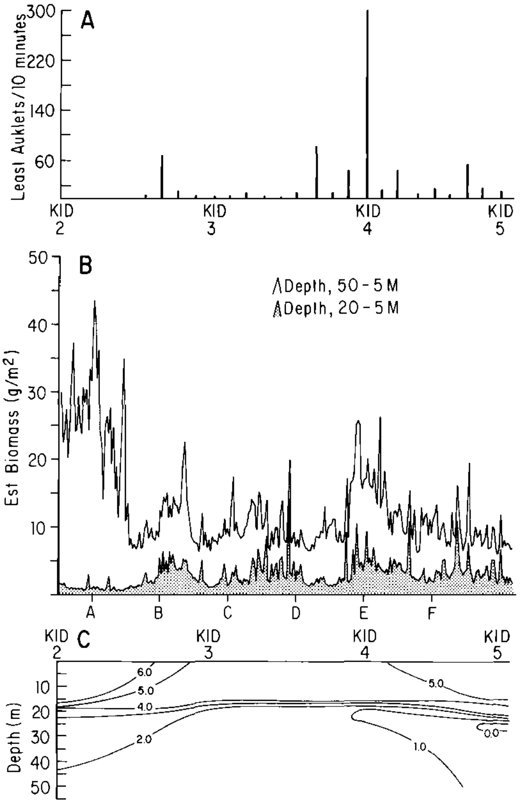

FIGURE 14. Distribution of (A) Least Auklets over 10 min of counting, (B) acoustically determined biomass and (C) sea temperatures along a line from 18.5 km west of King Island to 74 km west of the island, 18 August 1986, 04:18 to 12:08. Letters along the bottom of (B) refer to the patterns of vertical profiles in Figure 15.

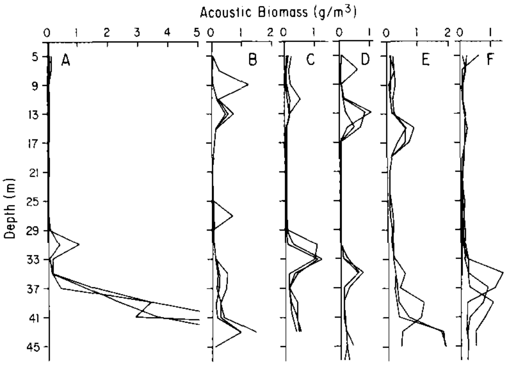

FIGURE 15. Vertical profiles of the distribution of acoustically determined biomass at the positions indicated along the transect of 18 August 1986 in Figure 14. Three adjacent profiles are presented for each section.

steepness of the thermocline at that station, when both auklet numbers and thermocline strength were standardized (Fig. 17, Spearman Rank Correlation $r_s = 0.34$, $P < 0.05$). The lack of auklets in the upper left hand and lower right hand portions of the figure shows that the correlation is driven by both the auklets' avoidance of weakly stratified water and their use of the most stratified water available on a given transect. A similar examination revealed no significant negative correlation of auklet numbers with thermocline depth.

We examined the extent to which the correlation of numbers of foraging Least Auklets with acoustic estimates of biomass depended on the depth interval over which biomass was estimated, and on the horizontal scale at which correlations were sought. At horizontal scales of 1.9–3.7 km and 9.4–22.2 km, we found that auklets may be better correlated with estimates of prey biomass at and above the thermocline than within the whole water column (Tables 3A,B). For the upper water column, there is also some evidence that correlations were stronger at 9.3–22.2 km (4 of 5 cases). Since at the small measurement scales (1.9–3.7 km) autocorrelation is a problem, effective sample sizes are smaller than the number of segments compared. Therefore, acceptance of the null hypothesis is conservative, and apparently significant P values can lead to a false rejection of H_0. When auklet numbers were compared with plankton biomass over 1.9–3.7 km intervals for the 9.3–22.2 km runs between stations, values of r_s were consistently low (Table 4).

Although small sample sizes and autocorrelations make establishing the statistical significance of differences in the strength of correlations at different spatial scales difficult, our data suggest that Least Auklets show their strongest correlations with presumed prey when correlations are based on biomass estimates for the upper water column over relatively long distances. We can assert with considerable certainty that cor-

TABLE 2. PRESENCE OF CALANOID PREY OF LEAST AUKLETS AS SAMPLED BY VERTICAL PLANKTON TOWS ALONG A LINE WEST OF KING ISLAND, 18 AUGUST 1986. DATA ARE EXPRESSED AS INDIVIDUALS/M³

	Station			
Species	KID-2	KID-3	KID-4	KID-5
Calanus marshallae	11.9	6.1	41.1	21.3
Neocalanus plumchrus	1.5	36.6	86.8	42.7
N. cristatus	—	0.9	4.9	0.7
Eucalanus bungii	3.0	0.8	0.6	—

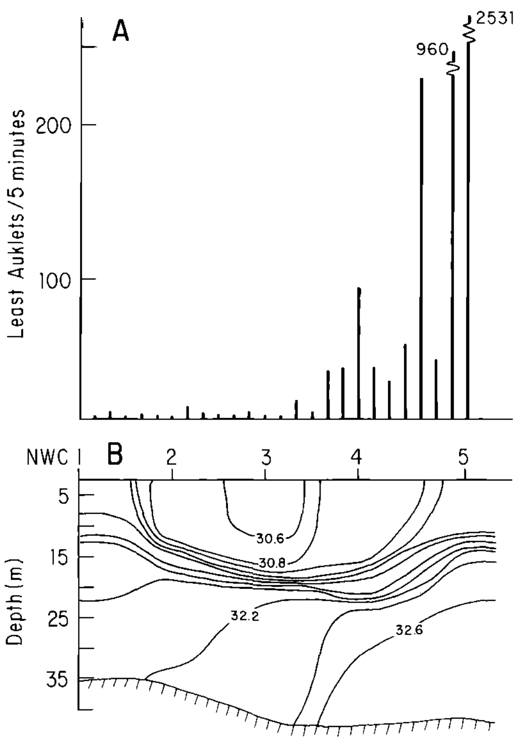

FIGURE 16. Distribution of (A) Least Auklets per 10 min of counting and (B) salinity along a line northward from Northwest Cape to the International Dateline, 12 August 1986 between 05:00 and 08:10. At station NWC-5 we were close to, but not yet in, Anadyr Current Water. Stations are 9.8 km apart.

relations between Least Auklets and acoustically estimated biomass are weak when estimates of biomass are based on the whole water column.

Quantification of the relationship between the numbers of Least Auklets and *Neocalanus* spp. is limited by the paucity of net hauls in unstratified water. However, for the 10 suitable stations at St. Lawrence Island we obtained *Neocalanus* spp. at eight. On at least two dates, 8 and 10 August 1985, *Neocalanus* spp. were present in unstratified water but there were no concentrations of Least Auklets nearby (Figs. 4, 5). We do not know whether *Neocalanus* spp. were less abundant in the unstructured water because we are unable to partition acoustically-measured biomass among the various species of plankton in the water column. However, distinct layers of biomass in the unstructured water were unusual (Fig. 7B, section A, but see Fig. 12), and concentration of biomass (g/m^3) may be more important to the auklets than overall abundance in the water column as a whole (g/m^2).

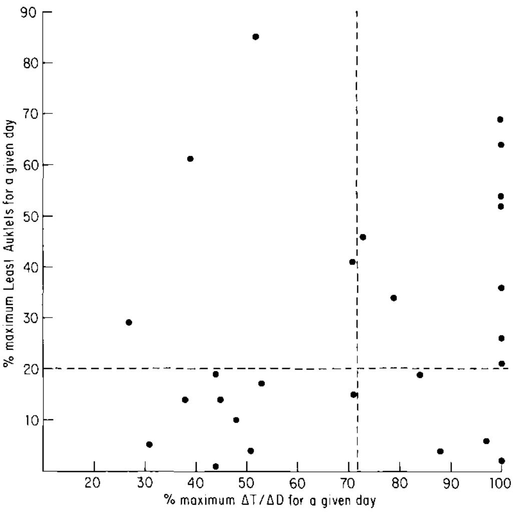

FIGURE 17. The relationship between the percent of the maximum number of Least Auklets seen on a given transect and the strength of the thermocline as defined by the percent of the maximum change in temperature per change in depth for a given transect. Dotted lines represent position of median values.

DISCUSSION

We think three aspects of the marine environment operate simultaneously to influence selection of foraging areas by Least Auklets in the Chirikov Basin: the presence of preferred types of prey (e.g., *Neocalanus* spp. copepods), their abundance in the water column, and their availability as determined by their vertical distribution in the water column. The relative contribution of the three elements is difficult to assess.

At King Island, Least Auklets overfly Alaska Coastal Water to forage in Bering Shelf Water (Hunt and Harrison 1990, this study). Two variables, water stratification and the prey community present, vary in parallel. Near King Island, Alaska Coastal Water is unstratified and lacks *Neocalanus* spp., and farther offshore the Bering Shelf Water is stratified and contains *Neocalanus*. Still farther from King Island, where Bering Shelf Water abuts the Anadyr Current, there is a change from stratified shelf water to unstratified Anadyr Current Water, with both water masses containing *Neocalanus* spp. Auklets foraged more commonly in the stratified water (Hunt and Harrison 1990), suggesting that they prefer foraging areas with a stable vertical structure.

Our work near St. Lawrence Island provided the opportunity to test the importance of vertical structure. There we found Least Auklets overflying nearshore unstratified water containing *Neocalanus* spp. to forage in stratified water offshore.

TABLE 3. RESULTS OF SPEARMAN RANK CORRELATIONS BETWEEN FORAGING LEAST AUKLETS AND ACOUSTICALLY DETERMINED BIOMASS OVER TWO DEPTH RANGES AT A, A HORIZONTAL SCALE OF 1.85–3.7 KM AND B, A HORIZONTAL SCALE OF 9.3–22.2 KM

Transect	Date	km over which biomass integrated	N	r_s bottom to 5 m	r_s thermocline to 5 m
A.					
KONE	8 Aug 85	3.7	17	0.24	−0.24
KON	10 Aug 85	3.7	18	−0.12	−0.07
SAVNE	14 Aug 86	1.85	20	0.47*	0.46*
KID	16 Aug 86	3.7	35	−0.20	0.77***
KID	18 Aug 86	1.85	26	−0.07	0.64***
B.					
KONE	8 Aug 85	18.5	4	0.40	−0.60
KON	10 Aug 85	18.5	4	−0.80	0.80
SAVNE	14 Aug 86	9.3	4	0.40	1.00*
KID	16 Aug 86	18.5	4	−0.54	0.77
KID	18 Aug 86	18.5	5	−0.40	0.90*

* $P < 0.05$.
*** $P < 0.001$.

And, as at King Island, relatively few Least Auklets foraged over unstratified Anadyr Current Water. Along transects, the large feeding flocks nearest shore usually occurred when we first encountered stratified water. Frequently additional feeding flocks were encountered up to 90 km offshore in areas where the thermocline was strong and shallow. In virtually all cases, Least Auklets were the only species present on the water. Although the occasional Parakeet Auklet (*Cyclorrhynchus psittacula*) or small numbers of Crested Auklets (*A. cristatella*) were encountered, we rarely observed mixed-species foraging aggregations.

We have too few samples of prey biomass in unstructured water in which *Neocalanus* spp. occurred to determine whether the abundance of Least Auklets foraging in stratified water was due to differences in food availability (density and accessibility) or differences in food abundance in the two habitats. Therefore, we cannot rule out the possibility that the auklets were responding to differences in prey biomass. However, two types of evidence suggest that Least Auklets selected their foraging areas in a coarse-grained fashion on the basis of vertical stratification (and prey availability) and only secondarily on the basis of local prey abundance. First, correlations between the presence of foraging Least Auklets and presence of stratified water were stronger than correlations between auklet numbers and estimates of local prey abundance. Second, within the stratified water Least Auklet numbers tended to be greatest where the stratification was strongest. The vertical profiles of acoustically-estimated prey biomass revealed consistent peaks in the concentration of biomass at or above the thermocline, and *Neocalanus* spp. are known to form dense layers 20–40 m below the surface in the open ocean (Barroclough et al. 1969); *N. plumchrus* occurs mostly above the seasonal thermocline (C. Miller, pers. comm.), while *N. cristatus* occurs mostly below the thermocline (see also R. Le Brasseur in Vermeer 1981). Thus, stratification partitions the water column vertically and sets up the potential for "vertical compression" and increased density of plankton biomass. Data from our net tows indicate that the biomass in the surface waters was dominated by *Neocalanus* spp. Our replicate net tows showed a consistent species composition in the plankton over scales of up to 19 km, despite considerable local patchiness. Thus, we tentatively conclude that auklets are foraging in the stratified water because prey is more likely to be concentrated at or above the thermocline there. Auklet use of fronts or areas where the thermocline approaches the surface is the extreme expression of this pattern.

TABLE 4. SPEARMAN RANK CORRELATIONS BETWEEN FORAGING LEAST AUKLETS AND ACOUSTICALLY DETERMINED BIOMASS AT A SCALE OF 1.85–3.7 KM WITHIN INTERSTATION SEGMENTS (9.3–22.2 KM)

Transect	Date	No. inter-station segments	Mean r_s bottom to 5 m	Mean r_s thermo-cline to 5 m
KONE	8 Aug 86	4	0.43	0.08
KON	10 Aug 86	4	−0.15	−0.28
SAVNE	14 Aug 86	5	0.00	0.18
KID	16 Aug 86	5	0.54	0.48
KID	18 Aug 86	4	0.25	0.30

In the Southern California Bight, vertical stratification of the water column has been shown to be important to Xantus' Murrelets (*Synthliboramphus hypoleuca*). Murrelets delayed reproduction in a year when storms increased the depth of the mixed surface layer of the water column (Lasker 1979, Hunt and Butler 1980). The murrelets' apparent dependence on a stable water column involves a different, though related, phenomenon to that found in Least Auklets. Xantus' Murrelets prey extensively on larval northern anchovies (*Engraulis mordax*) (Hunt et al. 1979). The anchovies in turn depend upon high concentrations of phytoplankton if they are to survive the first-feeding stage; if turbulence in the upper water column disperses their prey, they fail to survive (Lasker 1979, Peterman and Bradford 1987). Thus, in the murrelet-anchovy system, the importance of a stable upper water column is mediated through an additional link in the food chain.

These instances in which a stable vertical structure enhances food availability differ from those in which more dynamic physical processes are involved. In the case of vertically stable systems, prey are aggregating in a narrow zone to enhance their own energy intake and growth. In systems with high kinetic energy, currents may cause the passive accumulation of prey in eddies (Alldredge and Hamner 1980, Hamner and Hauri 1981) or the active accumulation of organisms resisting either upwelling or downwelling (Pingree et al. 1974, Brown 1980, Barstow 1983).

The relatively poor correlation between Least Auklets on the water and the distribution of acoustically determined plankton biomass at scales of 2–5 km may be the result of the methods we used, or an important aspect of the foraging biology of these birds. Three aspects of our methods could have contributed to an apparently weaker correlation between the auklets and their prey than actually existed. First, we could not obtain data on plankton distributions in the top 5–7 m of the water, and we do not know if it held significant prey populations that were not correlated with deeper, measured prey populations. However, the four (of a possible five) strong positive correlations between auklets and biomass in the upper water column at a scale of 9–22 km suggest that acoustically-estimated biomass in the upper water column was a reasonable indicator of potential prey abundance. Second, the transect width over which we counted birds was considerably wider than the cone-shaped area beneath the ship that was scanned by the echosounder. Given our evidence for patchiness in the plankton at very small scales, the birds may have been responding to different distributions of prey than we could detect. Third, we assumed that birds on the water were foraging or had been foraging in the recent past. If long periods elapsed since their foraging, auklets could have drifted away from the food patch, especially since the water mass below the thermocline may have been moving with respect to the surface waters. At present, we cannot eliminate or even estimate the magnitude of these sources of error.

There exist, however, at least two related reasons why auklets might not be well correlated with small-scale variations in the abundance of their prey. First, overall prey abundance may be sufficiently high that it would not pay auklets to search out the peak concentrations, as suggested by Woodby (1984) for murres (*Uria* spp.) in the southeastern Bering Sea. An alternative, though not mutually exclusive, hypothesis is that seabirds are not particularly good at locating the best prey patches, and instead of searching for such patches, they join birds already foraging (Hoffman et al. 1981, Obst 1985). In this scenario, the first bird to find an adequate, "threshold" concentration of prey would have a disproportionate effect on the distribution of foraging birds with respect to prey. Piatt (1990) has found evidence for threshold densities of prey necessary to attract foraging Common Murres (*U. aalge*) and Atlantic Puffins (*Fratercula arctica*), and observations of seabirds joining others already on the water are commonplace.

We suggest that Least Auklets locate suitable foraging areas by using a combination of physical and biological cues. Sea surface temperature in some instances is indicative of water column structure in the Bering Sea (Schumacher et al. 1979, Kinder et al. 1983). Near St. Lawrence Island, cool surface temperatures offshore indicate unstratified water, as is also frequently the case close to the island. We suggest that Least Auklets may seek areas with the warmer surface temperatures that can indicate subsurface stratification. The auklets commence foraging either when they encounter some minimum "threshold" concentration of plankton by chance, or by joining other birds already engaged in foraging. We interpret the stronger correlation of predators and presumed prey at larger scales as due to the auklets' being better at locating generally rich foraging areas than at locating specific prey patches.

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ALCID PATCHINESS AND FLIGHT DIRECTION NEAR A COLONY IN EASTERN NEWFOUNDLAND

DAVID C. SCHNEIDER, RAYMOND PIEROTTI, AND WILLIAM THRELFALL

Abstract. Topographic features, including shape of the coastline and shape of the bottom, generate spatially predictable flow gradients that can concentrate seabird prey. We hypothesize that bathymetrically induced flow gradients influence the distribution, flight orientation, and patch scale of foraging alcids around colonies. Two potentially important sites were identified from hydrographic charts of the waters around the colony at Witless Bay, in eastern Newfoundland. One site was a bank 70 km southeast of the colony. The second was a strip of high topographic relief running along the western margin of the Avalon Channel, which carries the inshore branch of the Labrador Current southward past the colony. Surveys in 1985 showed that murres (primarily Common Murres, *Uria aalge*) and Atlantic Puffins (*Fratercula arctica*) were present in abundance at the offshore bank. Both species brought fish to the colony from this bank. Surveys also showed that the abundance of murres and puffins was greater along the coastal strip south and north of the colony than at similar distances east of the colony. Surveys in 1987 showed that murres and puffins on the water were aggregated at the scale of the first internal Rossby radius, which is the characteristic scale of flow gradients at water mass boundaries (fronts). Our results suggest that multiple rather than single focus spatial models are required to describe the foraging behavior of colonial alcids.

Key Words: Alcids; habitat selection; oceanography; upwelling; Newfoundland.

Habitat selection by birds has been investigated in many terrestrial environments (Cody 1985); little work has been done in marine environments. Preliminary models of foraging distribution and energetics of marine birds have assumed that rate of encounter with prey is either spatially uniform or unpredictable in oceanic (Diamond 1978) and continental shelf ecosystems (Cody 1973, Furness 1978). A growing body of evidence indicates that, at least in shelf ecosystems, rates of encounter with prey are likely to be predictable in space (Brown 1980a) and time (Schneider et al. 1987). One important source of spatially predictable variability in shelf ecosystems is topography, including shape of the coastline and shape of the bottom. Bathymetric features generate spatially predictable flow gradients in shelf ecosystems (Csanady 1982, Allen et al. 1983), with important effects on the production and local distribution of marine organisms (Holligan 1981, Owen 1981, Richards 1981).

Flow gradients, which are defined as changes in water velocity in horizontal or vertical directions, can concentrate the prey of marine birds in at least four different ways. Convergent flow (downwelling) can increase the patchiness of vertically migrating prey such as myctophids (Olson and Backus 1985) and gelatinous zooplankton (Hamner and Schneider 1986). Divergent flow (upwelling) can bring prey to the sea surface, where it can be captured by non-diving species (Brown 1980a). Coastal upwelling can increase subsurface concentrations of negatively phototactic prey such as euphausiids (Simard et al. 1986). Flow gradients can also maintain temperature gradients to which nekton can respond directly (Laurs et al. 1977, Magnuson et al. 1981, Olla et al. 1985).

Several recent studies indicate that bathymetrically induced flow gradients influence the distribution of alcids around breeding colonies. In the Bering Sea, murres (*Uria* spp.) occurred at greater densities near the shelf break southwest of the Pribilof Islands than at similar distances to the northwest of the Pribilof Islands (Schneider and Hunt 1984). Nearer to the islands Kinder et al. (1983) reported an increase in the number of murres at a shallow sea front associated with a change in bottom slope. In Hudson Bay Cairns and Schneider (this volume) showed that the abundance of Thick-billed Murres (*U. lomvia*) was related to depth gradient as well as to water depth.

If areas of bathymetrically induced flow gradients are important to foraging seabirds, then several predictions can be made about the distribution and behavior of alcids foraging near colonies. First, alcids should be more abundant in areas of high topographic relief than in areas of less relief. Second, alcids should be observed commuting to areas of high topographic relief. Third, patchiness of alcids on the water should be observed at the scale of the first internal Rossby radius, which is the characteristic scale of flow gradients at water mass boundaries (fronts) in the ocean (Gill 1982:207). To test these predictions we measured the distribution and flight orientation of murres and Atlantic Puffins (*Fra-*

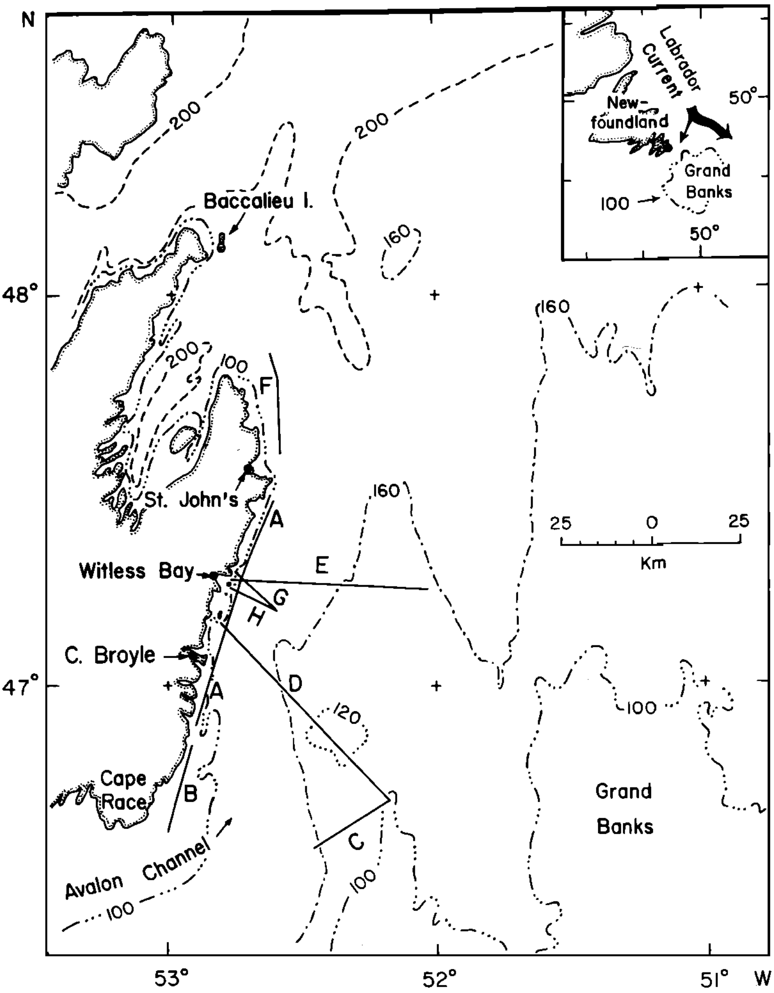

FIGURE 1. Seabird colonies, topographic features, and experimental transects in the Avalon Channel.

tercula arctica) in relation to bathymetric gradients in the Avalon Channel, which carries the inshore branch of the Labrador Current southward past the breeding colony at Witless Bay (Fig. 1).

A variety of standard statistical methods has been used to test hypotheses about the distribution and abundance of marine birds. Confirmatory analyses have been carried out using F-distributions (Abrams and Griffiths 1981, Schneider 1982, Kinder et al. 1983, Briggs et al. 1984), chi-square distributions (Haney 1986), and non-parametric methods based on ranks (Woodby 1984, Schneider and Duffy 1985) or on randomizations (Schneider and Piatt 1986). Counts of marine birds rarely conform to the assumptions underlying parametric methods based on F or chi-square distributions; yet, attempts to identify an appropriate statistical model (Schneider and Duffy 1985) have been rare. Non-parametric tests based on ranks are relatively insensitive, and can fail to detect a true effect. Diggle (1983) has recommended the use of Monte Carlo randomizations to evaluate Type I error (erroneous rejection of a null hypothesis) in the analysis of spatial data. This non-parametric method makes no assumptions about the error structure of the data, and has greater sensitivity (lower Type II error) than rank-based tests.

PHYSICAL AND BIOLOGICAL SETTING

The study area is strongly influenced by the Labrador Current, which brings cold (<0°C) water of relatively low salinity (28–30‰) southward to the Grand Banks. The main branch of the Labrador Current flows around the east side of the Grand Banks, while a secondary branch flows through the Avalon Channel between the Grand

Banks and the Avalon Peninsula (Fig. 1). Stratification of the water column is delayed until June, when a thermocline forms above the cold core of the Labrador Current. Figure 2 shows the typical depth of the upper layer that forms above the cold core of the Labrador Current in the Avalon Channel. Upward deflections of the thermocline, which indicate strong local flow gradients, are associated with shoaling water on the eastern side of the Avalon Channel (Hollibaugh and Booth 1981). A temperature profile along the 47th parallel (Fig. 2) shows an upward doming of isotherms approximately 50 to 100 km east of the Avalon Peninsula; the forces responsible are not known. Upward doming of the thermocline also occurs along the coast of the Avalon Peninsula during the summer (Piatt and Methven 1986). The thermocline can rise to the surface during a single day; rises are associated with southwest winds, which favor upwelling (Schneider and Methven 1988).

Two major alcid colonies occur in the Avalon Channel—one at Witless Bay and one on Baccalieu Island (Fig. 1). Alcids at Witless Bay nest on Great Island, which is located at the western end of transect D (Fig. 1), on PeePee Island, which is just northwest of Grand Island, on Gull Island, which is located at the western end of transect E, and on Green Island, which is located just south of Gull Island. Recent estimates of breeding populations at Witless Bay are listed in Table 1.

Capelin (*Mallotus villosus*) is the predominant prey species in the diet of alcids at these colonies during the nesting period (Brown and Nettleship 1984, Burger and Piatt 1990). Capelin appear along the coast when the water temperature rises to ca. 5°C (Templeman 1948). Near the Witless Bay colony schools concentrate in the warm upper layer (Piatt and Methven 1986). During early July the upper layer varies in thickness from 10 m in a cold year such as 1984 to 30 m in a warm year such as 1987. At the time scale of days, episodic rises of the thermocline concentrate capelin near the sea surface (Piatt and Methven 1986). The horizontal scale of the rise in the thermocline is the first internal Rossby radius, which was calculated as 4.7 km in late July in the Avalon Channel (Appendix I).

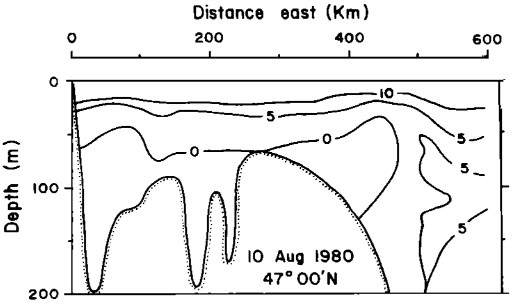

FIGURE 2. Thermal profile across the Avalon Channel and Grand Banks during the summer. Redrawn from Hollibaugh and Booth (1981).

METHODS

Nautical charts were used to identify regions of high bathymetric gradient within 100 km of the Witless Bay colonies. Salinity and temperature profiles from Hollibaugh and Booth (1981) and Lively (1983) were used to identify hydrographic gradients associated with bathymetric features. Two areas of bathymetrically-associated hydrographic gradients were identified. The first was an offshore bank 70 km southeast of Witless Bay (Fig. 1), where hydrographic profiles showed upward doming of the thermocline on the western side (Fig. 2). The second area was the coastal strip on the west side of the Channel, where episodic upwelling occurs in response to winds from the southwest.

To test for enhanced abundance and foraging activity along the coast, we ran transects in July of 1985 along the coast (transects A, B, and F, Fig. 1) for comparison with those running away from the coast (transect E and the central third of transect D). To test for enhanced abundance and feeding activity at the offshore bank we compared a transect across the bank (transect D) to a

TABLE 1. APPROXIMATE NUMBER OF BREEDING PAIRS OF SEABIRDS NESTING ON ISLANDS AT WITLESS BAY (FROM CAIRNS ET AL. 1986)

	Gull	Green	Pee Pee	Great
Fulmarus glacialis				20
Oceanodroma leucorhoa	530,000	present		250,000
Larus argentatus	3850	300	75	2700
Larus marinus	113	50	3	80
Rissa tridactyla	10,140	10,000		23,230
Uria aalge	687	74,000		2800
Uria lomvia		600		
Alca torda	60	170		120
Cepphus grylle	present	present	present	present
Fratercula arctica	60,000	17,000	1200	148,000

TABLE 2. NUMBER OF BIRDS ENCOUNTERED ALONG 6 TRANSECTS IN THE AVALON CHANNEL IN 1985. TIMES ARE LOCAL (GMT + 3.5 HR)

	A	B	C	D	D	E	F
Date	24 Jul	24 Jul	5 Aug	5 Aug	25 Jul	25 Jul	26 Jul
Start	07:35	15:58	06:39	09:00	05:35	12:35	05:45
Duration (min)	360	120	113	191	345	275	195
Distance (km)	76.28	25.53	46.51	79.90	71.08	56.64	29.85
Area (ha)	763	255			711	566	299
Species							
Fulmarus glacialis	0	3	25	20	28	26	0
Puffinus spp.	1	0	0	0	0	250	0
Puffinus gravis	0	11	20	32	15	32	1
P. griseus	2	6	4	7	17	11	0
P. puffinus	3	0	0	0	1	1	1
Hydrobatidae	0	0	95	45	59	2	0
Sula bassanus	9	4	1	4	2	0	5
Phalaropus fulicarius	7	0	0	0	1	0	0
Sterocorarius spp.	1	0	0	1	0	0	0
Catharacta skua	0	0	0	3	0	0	2
Larus spp.	0	0	1	3	0	0	0
Larus marinus	2	0	0	0	3	2	0
Larus argentatus	48	2	2	0	12	5	85
Rissa tridactyla	174	0	19	12	58	7	23
Alca torda	22	0	2	0	4	0	1
Uria spp.	1404	245	11	32	188	334	171
Fratercula arctica	1457	62	33	138	492	303	27

control transect through a nearby area of low bathymetric gradient (transect E). To test whether murres and puffins on the water aggregate at the scale of the first internal Rossby radius, we first calculated the radius for typical summer conditions in the Avalon Channel, then compared variability at this scale to variability at the scale of the count resolution, which was 300 m in 1985. The analysis was repeated using higher resolution data obtained in 1987 (transects G and H).

Bird abundance and behavior were recorded during 1985 in a 100-m wide strip on one side of a 30-m sailing vessel moving at speeds greater than 9 km/hr. All birds were identified to the lowest possible taxonomic level, usually species. Behavior of each bird was recorded in two categories: on the water or flying. The presence of fish in the bill was noted in flying birds. Flight directions were recorded in 45° sectors.

To determine whether spatial patterns observed in July were repeatable, transect D was re-surveyed in early August. Counts were made from the R/V *Dawson*, using a strip transect out to the horizon. The difference in method does not preclude comparison of spatial patterns in August to those in July because pattern was measured as a dimensionless number, the ratio of two variances. The difference in method does preclude comparison of average abundance in August to average abundance in July.

Temperature measurements were not made during the 1985 surveys, so a theoretical model was used to calculate the approximate scale of the first internal Rossby radius for conditions typical of the Avalon Channel in summer (Appendix I). Variability in abundance at the scale of the calculated Rossby radius (R_2 = 4.7 km) was compared to variability at the scale of minimum resolution, which was the product of temporal resolution (2 minutes) and vessel speed along each transect. Pattern at the scale of $L = R_2$ was measured as:

$$F(L) = [n_L - 1][\mathrm{Var}(N_L)][\mathrm{Var}(N_0) - \mathrm{Var}(N_L)]^{-1},$$

where n_L denotes the number of segments of length L along a transect of total length $T = Ln_L$, $\mathrm{Var}(N_L)$ denotes variance among counts within contiguous segments of length L, and $\mathrm{Var}(N_0)$ denotes variance among counts within segments of length equal to the minimum spatial resolution. The null hypothesis, no increase in variability at the scale of the first internal Rossby radius, was accepted if the observed F-ratio F(L) was not significant at the 5% level. Significance was evaluated by comparing each observed F-ratio to 500 ratios computed from random permutations of the vector of counts N_0. Randomizations were obtained by assigning a sequential number to each section of a transect, e.g., 258 sections of length 300 m on transect A. Counts were then shuffled by location, using random permutations of the sequence of numbers (GGPER routine, International Mathematics and Statistics Library, Houston, Texas, U.S.A.). Each call to this routine generated a random number that was used as the seed in the next call to the routine. The frequency of identical permutations due to identical seeds was found to be less than 10^{-7}. Type I error was computed as p_M, the proportion of randomized F-ratios exceeding the observed ratio. Aggregation at scale $L = R_2$ was declared significant if p_M was less than the criterion level, 5%. Sokal and Rohlf (1981) describe a similar randomization test.

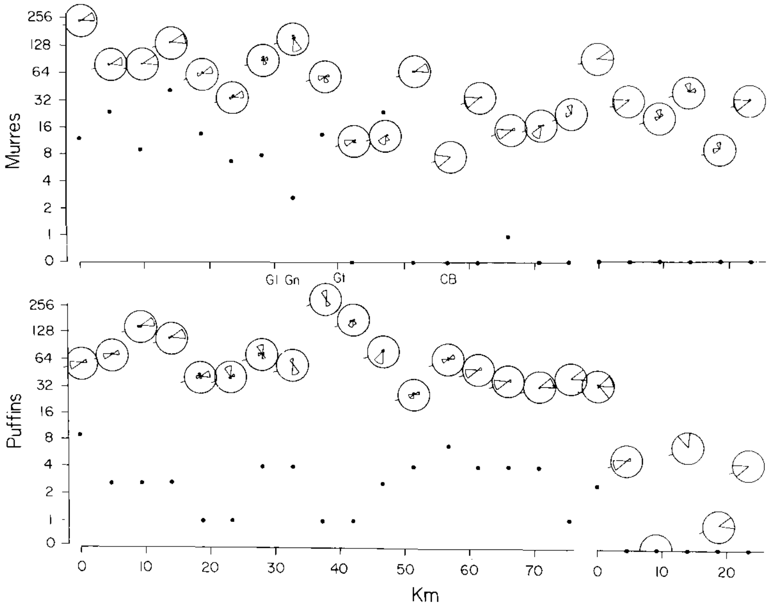

FIGURE 3. Distribution of murres and puffins along transects A (left) and B (right), 24 July 1985. Solid dots indicate density on water in contiguous 4.7 km sections of the transect. Height of circles above the abcissa indicates number of flying birds. Filled areas within each circle indicate percent flying in a given direction. Flight directions are relative to ship direction, which is the same as the abcissa (left to right). North is shown as a tic mark on the circumference of each circle. Gl = Gull Island, at base of transect E. Gn = Green Island. Gt = Great Island, at base of transect D. CB = Cape Broyle.

RESULTS

ABUNDANCE AND FLIGHT ORIENTATION OF MURRES AND PUFFINS

Murres and puffins were the most abundant birds along coastal transects A and B on 24 July 1985 (Table 2). Procellariids (Northern Fulmar *Fulmarus glacialis,* Greater Shearwater *Puffinus gravis,* and storm-petrels) were more abundant along offshore transects than along coastal transects (Table 2).

A more detailed analysis of murre and puffin distribution was obtained by mapping numbers seen per 4.7 km segment of each transect. Murres were abundant on the water along the coast north of the Witless Bay colony on 24 July 1985 (Fig. 3). The number of murres on the water did not decrease with distance out to 30 km north of Gull Island. Murres were less abundant along the coast south of the colony than to the north. Puffins were abundant on the water to the north and south of the colony. The number of puffins on the water did not decrease monotonically with distance from the colony. A sudden decrease along the coast was observed south of Cape Broyle, approximately 40 km from Great Island. Few puffins were observed on the water along the coast 40 km north of Gull Island (Transect F, Table 2).

Similar patterns were observed along the coast on 22 July 1985 while in transit from Cape Race (06:30 local time) to St. John's (15:00 hr). Few alcids were observed on the water from Renews to Cape Broyle (ca. 20 km); many alcids were observed on the water from Cape Broyle to Great Island (ca. 20 km). Many murres and puffins were observed on the water between Gull Island and St. John's (12:00–15:00), the same pattern observed during the morning of 25 July.

Murres and puffins were less abundant on the water along the offshore transects (D and E, Figs. 4–5) than along the coastal transects (A, B, and F, Fig. 3 and Table 2). Few puffins or murres were observed on the water beyond 20 km from the colony (Fig. 5). However, the transect data do not include the large number of murres and puffins observed on the water just before dawn at the southeastern end (beginning) of transect D (George Nichols, pers. comm.).

Flight direction of murres and puffins on coastal transects was generally either toward or away from the colony at ranges of 10 km or more (Fig. 3). Orientation was more variable within 10 km of the colony. Along transect D murres and puf-

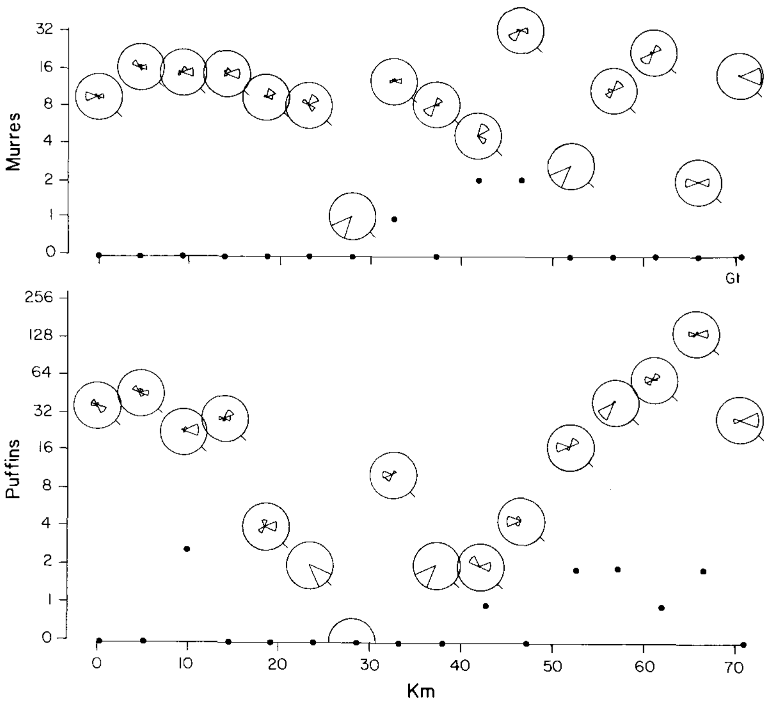

FIGURE 4. Distribution of murres and puffins along transect D, 25 July 1985. Symbols as in Figure 3.

fins were observed flying either toward or away from the colony at ranges of 40 km or more (Fig. 4), while on transect E (Fig. 5) orientation was less consistent. Consistent flight orientation indicates that birds were commuting either along the coast or directly to the offshore bank at the beginning of transect D. Fish of undetermined species were observed in the bills of murres and puffins flying toward the colony along transects A, B, and D.

The repeatability of the results in July was investigated by surveying transect D on the first available occasion, which was in early August. Murres and puffins were associated with the bank during the second traverse (transects C and D, 5 August, Table 2). The pattern of abundance of birds along transect D differed from that observed during the earlier traverse of this transect. Murres (primarily flying birds) were more abundant at the beginning and end of the transect during the second traverse (Fig. 6), compared to similar abundances of flying murres throughout the transect during the first traverse (Fig. 4). Puffins (primarily flying birds) increased near the colony on the second traverse, a pattern that differed from the large number of flying birds observed at the beginning of the transect on the first traverse (Fig. 4). These observations were consistent with our hypotheses. Alcids were more abundant on the water along the coast than in the Avalon Channel. Alcids were found on the water at the change in bathymetry on the eastern side of the Avalon Channel. Alcid flight direction (at distances of 40 km or more from the colony) was generally toward areas of strong bathymetric gradient. However, these patterns were variable. In particular, distribution along transect D varied between the two traverses, and flight orientation within 40 km of the colony was more variable than beyond 40 km. Also, alcids were observed on the water along transect F at distances greater than one internal Rossby radius from the coast.

PATCHINESS OF MURRES AND PUFFINS ON THE WATER

If flow gradients influence alcid patchiness, then significant spatial variability should be observed at the scale of the first internal Rossby radius, which was calculated at 4.7 km. During 1985 variability of murre counts at this scale was greater than variability at the scale of count resolution, 300 m (Table 3). However, the difference was significant in only one case, transect D. Variability in the abundance of puffins at the scale

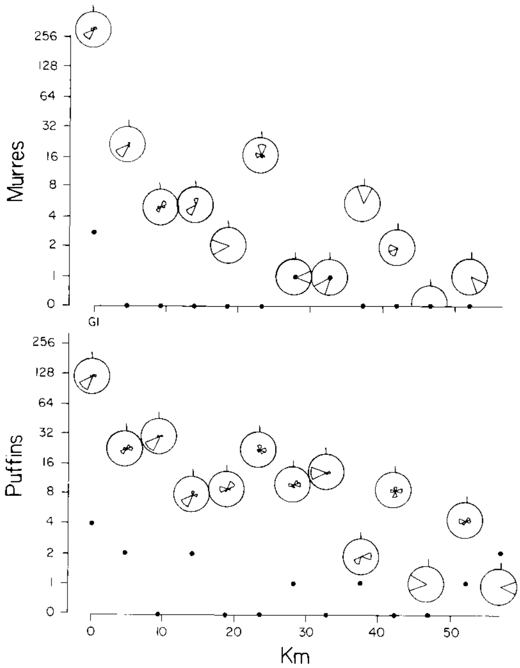

FIGURE 5. Distribution of murres and puffins along transect E, 25 July 1985. Symbols as in Figure 3.

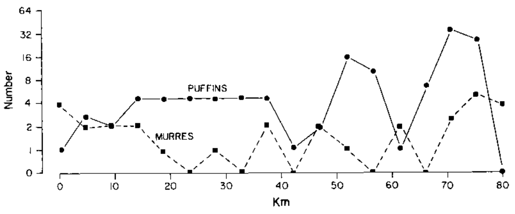

FIGURE 6. Distribution of murres and puffins along transect D, 5 August 1985.

of 4.7 km was not greater than variability at the scale of count resolution, 300 m.

The null hypothesis, no significant aggregation at the scale of the first internal Rossby radius, could be rejected in only 1 of 6 cases (Table 3). Type II error, erroneous acceptance of a null hypothesis, could have resulted from several problems with the 1985 data. The first was the lateness of the counts, which were made after murres had begun to fledge; the resulting low abundances around the colony certainly reduced the sensitivity of the analysis. Second, the scale of upwelling may have deviated from the theoretical value, contributing to a null result. Third, spatial resolution was 300 m, which may have reduced the ability to detect a real difference. Fourth, feeding activity appeared to be greater during the morning, so that counts made later in the day may not have reflected feeding conditions.

These problems were resolved by conducting experimental transects in late June 1987, when murres and puffins were incubating. The Rossby radius was estimated from sea-surface temperatures measured concomitantly with bird counts along two transects (G and H, Fig. 1). Spatial resolution was increased by using a microcomputer to record data to the nearest 5 seconds. Ship speed was 4 m/s, so spatial resolution was 20 m. Counts were made early during the day (07:00 to 09:00).

The scale of upwelling (frontal width) was estimated at 5.5 km, using the rate of change in sea surface temperature measured at 1 minute (240 m) intervals along transect G (Fig. 7). Most murres on the water were observed inside the front, i.e., less than 5.5 km from shore. A few were observed in the frontal area, which ran from 5.5 to 11 km offshore. Variability at the scale of 5.5 km was significantly greater than smaller scale variability (Table 4). Puffins on the water were most abundant nearshore or at the front (Fig. 7). Variability at the scale of 5.5 km was significant in 3 out of 3 cases (Table 4). We concluded that significant aggregation did occur at the scale of the Rossby radius.

Temperature and bird distributions along transect H were similar to those along transect G. Murres on the water were more abundant in upwelled water than at the front, whereas puffins were more abundant at the front, defined as the region of strongest horizontal gradient in sea-surface temperature (Fig. 8). Variability in murre abundance at the scale of 5.5 km was significantly greater than smaller scale variability (Table 4). The number of puffins encountered on the water along this transect was too small to permit an adequately sensitive test for aggregation at the scale of 5.5 km.

DISCUSSION

Coarse scale (1–100 km) aggregations of birds were first reported along a 500 km transect across the Bering Sea shelf (Schneider 1982). Extended aggregations have been reported along transects normal to hydrographic features in the California Current (Briggs et al. 1984), the Bering Sea (Kinder et al. 1983), the Benguela Current (Schneider and Duffy 1985), and the Labrador Current (Schneider and Piatt 1986). In the latter study, coarse scale aggregations of alcids near Witless Bay were associated with coarse scale aggregations of schooling fish, primarily capelin. The scale of bird-fish correlation was in the range of 2 to 6 km. Based on these findings, we hypothesized that coarse scale aggregations of marine birds result from concentrating mechanisms

TABLE 3. Variance in Alcid Abundance on Water in 1985 at the Length Scale of Count Resolution (0.3 km) and at the Length Scale of the Internal Rossby Radius (4.7 km). N is Total Number Seen. Type I Error Estimates are for the Null Hypothesis that $\tilde{N}^2(0.3\ \text{km}) = \tilde{N}^2(4.7\ \text{km})$, where $\tilde{N}^2(L)$ Denotes Count Variance at Scale L. Degrees of Freedom Shown in Parentheses after Each Variance. Type I Error Estimates (p_M) are Based on 500 Monte Carlo Runs. p_F is Type I Error Assuming an F-Distribution

Transect	Species	N	$\tilde{N}^2(0.3)$	$\tilde{N}^2(4.7)$	F	p_M	p_F
A	Murres	167	6.20 (257)	8.64 (15)	1.43	0.10	0.13
B		0					
D		5	0.029 (237)	0.068 (14)	2.57	0.01	0.002
E		5	0.035 (194)	0.051 (11)	1.46	0.07	0.15
F		0					
A	Puffins	58	0.393 (257)	0.359 (15)	0.91	0.56	0.55
B		3					
D		11	0.061 (237)	0.072 (14)	1.20	0.23	0.28
E		13	0.104 (194)	0.104 (11)	1.00	0.43	0.45
F		1					

at the scale of the first internal (baroclinic) Rossby radius, which is the characteristic scale of flow gradients at water mass boundaries (fronts). Our analysis of murre and puffin abundance supports that prediction.

We did not identify the mechanism responsible for aggregation at this scale in the Avalon Channel. We speculate that along the coastal strip, wind-induced upwelling concentrates capelin, which avoid cold water just before spawning during the summer. Avoidance of a rising thermocline at the coast would tend to concentrate them vertically, whereas wind-induced surfacing of the thermocline, followed by offshore propagation of a cold water front, would tend to concentrate them horizontally. This is consistent with what is known of capelin behavior (Templeman 1948), but needs to be tested.

Upwelling on the coastal (right) side of the Labrador Current is somewhat unexpected, because the effects of the earth's rotation (Coriolis force) will tend to drive this current toward, rather than away from the coast. However, in the zone of prevailing westerly winds (ca. 40°N to 50°N) meteorological forcing would tend to cause upwelling on the coastal (i.e., right) side of the Labrador Current. Calculations (Hay and Kinsella 1985, Schneider and Methven 1988) show that winds prevailing on the Grand Banks are strong enough to reduce the thickness of the surface layer near a coastal (wall-like) boundary. Measurements in the Avalon Channel in 1984 (Schneider and Methven 1988) show that substantial thinning of the warmer surface layer does occur in response to upwelling favorable (south or southwesterly) winds. We speculate that the energy of the winds, via upwelling, contributes to the productivity of the large alcid colonies found along the coast of eastern Canada between 47°N and 54°N latitude (Brown et al. 1975).

Water depth on the eastern (Grand Banks) side of the Avalon Channel may be too great for simple coastal upwelling, such as that envisioned along the coast strip, to be important. Bathymetric contours diverge considerably in a downstream direction on the eastern side of the Channel, a circumstance that can cause persistent upwelling in a boundary current (Janowitz and Pietrafesa 1982). Temperature and density profiles across the bank (Hollibaugh and Booth 1981) suggest that upwelling does occur on the left side of the inshore branch of the Labrador Current. The observed property gradients, or their affiliated flow gradients, may affect either the density or availability of prey taken by the alcids that were observed feeding on the eastern side of the Avalon Channel. Wynne-Edwards (1935) reported alcids in this area over 50 years earlier.

TABLE 4. Variance in Alcid Abundance on the Water in 1987 at the Length Scale of Count Resolution (20 m) and at the Length Scale of the First Internal Rossby Radius (5.5 km). Symbols (N, $\tilde{N}^2(L)$, p_F, p_M) as in Table 3

Transect	Species	N	$\tilde{N}^2(0.02)$	$\tilde{N}^2(5.5)$	F	p_M	p_F
G	Murre	10	0.013 (788)	0.038 (2)	3.08	0.02	0.05
	Puffin	35	0.093 (788)	0.295 (2)	3.18	0.05	0.04
H	Murre	65	0.282 (810)	3.64 (2)	13.34	<0.002	0.0001
	Puffin	4	0.0049 (810)				

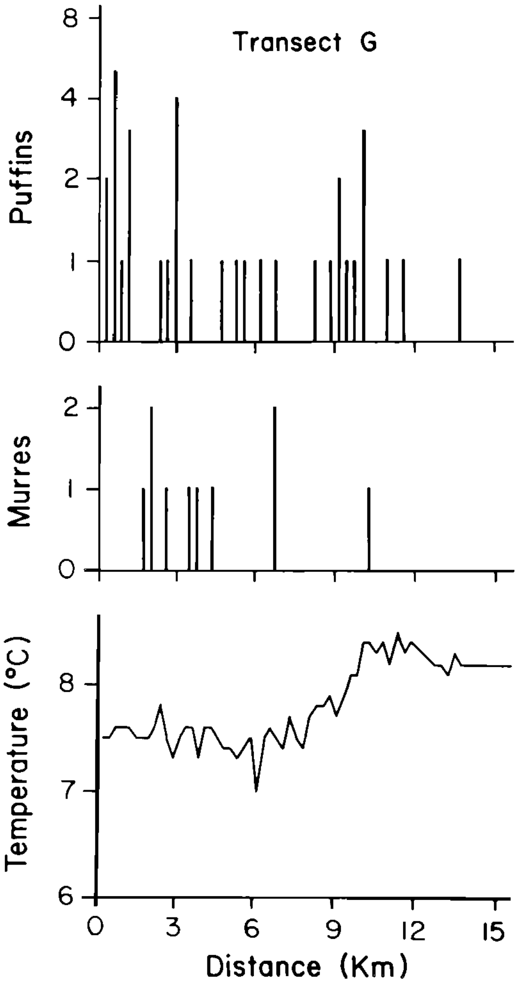

FIGURE 7. Sea surface temperature and distribution of murres and puffins on the water along transect G, 25 June 1987. Transect runs from coast to deep water.

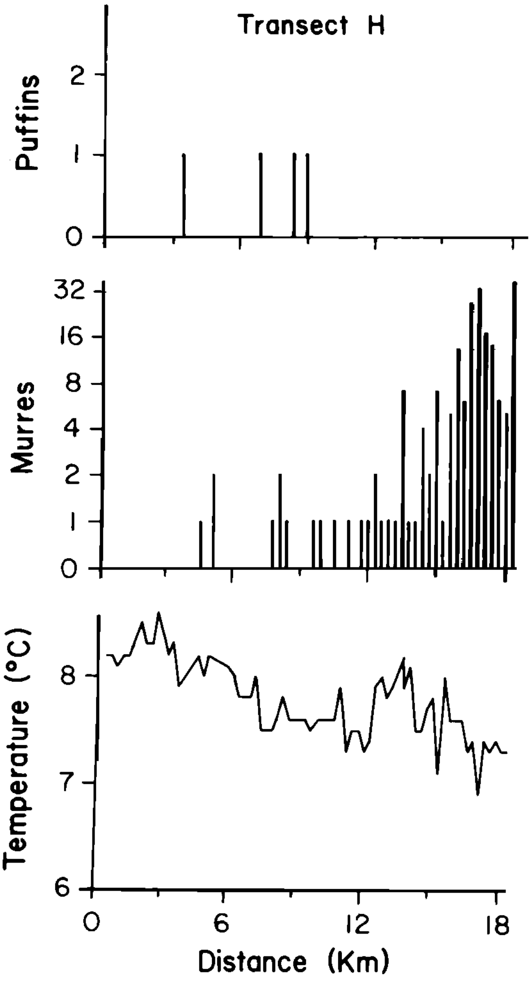

FIGURE 8. Sea surface temperature and distribution of murres and puffins on the water along transect H, 25 June 1987. Transect runs from deep water toward the coast.

The hypothesis that bathymetrically induced flow gradients increase the foraging success of alcids was proposed to explain the distribution of murres away from colonies in the southeastern Bering Sea (Schneider et al. 1986). We suggest that this hypothesis pertains to alcids foraging around colonies because: (1) abundance along radial transects is not uniform in all directions from large colonies (Hunt et al. 1981, Schneider and Hunt 1984, Schneider and Piatt 1986); (2) consistent flight directions have been observed at considerable distances from large colonies of alcids (Brown 1980b, Gaston 1982), and orientation is toward areas of strong hydrographic gradients (Brown 1980b); and (3) areas with high abundance of alcids on the water can be identified around colonies (Schneider and Hunt 1984, Cairns and Schneider 1990).

Our results, as well as reports on flight directions at other colonies, are consistent with the hypothesis that breeding alcids commute to selected areas. Organized streams of seabirds moving outward from colonies have been reported from the north Pacific (Bédard 1969, Bent 1912, Myres 1962) and the north Atlantic (Kay 1936, Sergeant 1951). In Hudson Bay Brown (1980b) reported that Thick-billed Murres from the large colony at Digges Island flew north of Mansel Island, where temperature and salinity gradients were strong. In 1981 Gaston (1982) found high abundances of murres at the location described by Brown (1980b). Gaston (1982) also reported high rates of movement to the south of Mansel Island over a period of a month. Farther north, Gaston and Nettleship (1981) reported that Thick-billed Murres leaving a resting area at Prince Leopold Island tended to fly west into Barrow Strait, rather than south into Prince Regent Inlet. These authors found that dense concentrations of murres were confined to coastal transects, but they emphasized that variation in counts was considerable at the time scale of days and months.

Considerable variability in abundance occurs in high usage areas near other colonies. Near the Pribilof Islands Kinder et al. (1983) reported dense concentrations of murres at a front associated with a bathymetric gradient over a 5-day period in August 1977, and again during August 1978. However, the presence of the front explained less than 10% of the total variance in numbers of murres observed on the water. In Hudson Bay Cairns and Schneider (1990) found that variance explained by location was small compared to daily variability. As a result, bathymetric gradients cannot be used to predict the distribution of foraging alcids on any given day.

Our results show that suitable foraging habitat may be much less extensive than the area within a typical foraging radius estimated from time away from a nest (Pearson 1968, Furness 1978). If foraging occurs primarily in restricted areas around colonies then area-specific rates of prey extraction based on foraging radii (e.g., Furness 1978) may underestimate the local impact of seabirds. At Witless Bay, the scale of interaction of alcids with their prey depends on recent upwelling (Schneider 1989) rather than simply on the average foraging radius.

The degree to which large alcids depend on fronts for food cannot be evaluated from our data. The variance in abundance explained by grouping can be calculated as

$$r^2 = [1 + (n_R - 1)(n_0 n_R^{-1} - 1)^{-1}(F)]^{-1}$$

The r^2 values for Tables 3 and 4 are all under 15%, a result that is consistent with previous analysis (e.g., Kinder et al. 1983). Our purpose was not, however, to explain variation in abundance of alcids, but rather to move toward some understanding of habitat selection by marine birds, beginning with an informal or verbal model, viz, that alcids feed on prey aggregated at flow gradients, then testing some simple predictions.

Statistical tests were made at a spatial scale appropriate to the model. This resolves several problems associated with exploratory analyses of spatial variability in marine birds. One problem is that repeating an analysis over a range of spatial scales can, if carried far enough, result in correlation of abundance with another variable. To take an extreme case the abundance of Atlantic Puffins becomes perfectly correlated with Sargasso weed at the scale of the Atlantic Ocean. Prior specification of scale eliminates Type I errors due to analysis at an inappropriate scale. Another problem is that repeated analyses over a range of scales result in a large number of tests, increasing the number of Type I errors. Reducing the number of tests, by specifying the spatial scale of the analysis, reduces this problem.

In our analysis of alcid abundance we have coupled statistical and graphical presentation of results as closely as possible so as to allow the reader to judge the relation of variables (James and McCulloch 1985) and to judge the "biological significance" (Tacha et al. 1982) of our results. Statistical analyses can close off inspection of the data, because of their powerful summarizing capacity. The analyses in Tables 3 and 4 are based on data displayed in Figures 3 through 8. Figures 3 through 8 were constructed with the idea of opening the original data to inspection by minimizing summary, and by concomitant presentation of variables (e.g., temperature and abundance in Figs. 7 and 8).

Data for this study were collected in the framework of an "observational experiment," (Stommel 1963). This usage is tenable on three counts for the Avalon Channel study: manipulation of a measurement variable relative to an extrinsic hypothesis, local control, and repeatability of results. The extrinsic hypothesis was that alcids aggregate in areas of strong topographic gradient near colonies. The hypothesis arose from work in the Bering Sea, not at the study site. The manipulated variable was transect location and direction. The response variable was number of birds seen per unit effort (transect distance or area scanned). The design consisted of transects run across areas of strong topographic relief. Control transects were run in nearby areas of weak topographic relief. Repeatability was assessed by re-surveying one of the 1987 transects as soon as practical, ten days after the first traverse. Repeatability was also assessed by performing the experiment with a slightly different protocol in 1987. One can argue that lack of intervention to change a variable weakens an experiment by reducing the chances of controlling for correlated effects. However, one can also argue that in any field situation, intervention will create correlated effects. In the absence of any logical grounds for preference, the strength of the experiment would then rest more on the use of comprehensive controls than on whether the experiment was manipulative or observational.

Uncontrolled variables limit interpretation of the results from the Avalon Channel. The experiments were carried out during limited periods in 1985 and 1987, so longer term variability, at the scale of weeks, seasons, or years, was not controlled. The experiment was carried out in a limited area in the Avalon Channel, so larger scale variability, at horizontal scales greater than one transect length from the colony, was not controlled.

Given these limitations, what can we conclude? First we can be sure that flow gradients were associated with topographic gradients in the Avalon Channel. This conclusion rests on our knowledge of fluids in motion, rather than on results from the Avalon Channel. Second, we can be sure that alcids were associated with topograhic gradients, and therefore with flow gradients, on the two occasions when transects were run. We cannot conclude that this will occur at other times or locations, nor can we conclude that flow gradients caused seabird aggregations, through the mechanism of change in prey abundance or availability due to flow gradients. However, the concept that flow gradients determine seabird distribution was derived from work in the Bering Sea (Ford et al. 1982). It has now been verified for murres in Hudson Bay (Cairns and Schneider 1990), and so it provides a reasonable working hypothesis at other colonies. The mechanisms that link alcids to flow gradients remain to be determined.

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APPENDIX I.

The Rossby radius of deformation is a length scale that is of fundamental importance in atmosphere-ocean dynamics (Gill 1982). It is the horizontal scale at which rotation effects become as important as inertial effects. The first internal (baroclinic) Rossby radius is the characteristic scale of boundary phenomena such as fronts and eddies. The Rossby radius (R_n) is calculated as:

$$R_n = c_n f^{-1}, \qquad (1)$$

where n is mode number, c_n is the phase speed (m s^{-1}) of the nth mode perturbation, and f is the Coriolis parameter (s^{-1}). The Coriolis parameter depends on latitude and has a value of 1.07×10^{-4} s^{-1} at 47°N.

An equation from Csanady (1982, Eq. 3.96) was used to calculate the phase speed of the first baroclinic mode in a two layer stratified fluid along a straight coast:

$$c_2 = (agh_t h_b/(h_t + h_b))^{1/2}. \qquad (2)$$

Parameter values for the Avalon Channel are density anomaly ($a = 0.001$), gravitational acceleration ($g = 9.8$ m s^{-2}), Coriolis frequency at 47°N ($f = 1.07 \times 10^{-4}$ s^{-1}), upper layer ($h_t = 30$ m), and lower layer ($h_b = 160$ m). Using these values, c_2 is 0.50 m s^{-1}, and R_2 is 4.7 km.

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THE AGGREGATIVE RESPONSE OF COMMON MURRES AND ATLANTIC PUFFINS TO SCHOOLS OF CAPELIN

JOHN F. PIATT

Abstract. I studied the aggregative responses of Common Murres and Atlantic Puffins to schools of capelin during three summers (1982–1984) at Witless Bay, Newfoundland, by conducting hydroacoustic surveys for capelin in synchrony with seabird censuses. Murres and puffins foraged offshore prior to the arrival inshore of spawning schools of capelin. Both species were abundant during peak periods of capelin abundance from late June to late July, but only puffins continued to forage inshore after capelin schools dispersed in August. On individual surveys, murre and puffin flocks were significantly correlated with capelin schools at fine and coarse spatial scales. Aggregation intensity and spatial correlations peaked at measurement intervals of 2–6 km. At that scale, murres and puffins exhibited sigmoidal (Type III) aggregative responses to capelin schools. Inflection points (thresholds) in sigmoidal aggregative response curves occurred at higher densities of capelin for murres than for puffins and foraging thresholds for both species varied daily with overall capelin abundance in Witless Bay. Murres probably foraged on denser schools of capelin than puffins because of their larger body size and associated higher food demands. The implications of differing foraging thresholds for population ecology of alcids are discussed.

Key Words: Aggregative response; capelin; murre; puffin; hydroacoustics; threshold; foraging; population ecology.

A predator's rate of food intake is limited at low prey densities by how frequently it encounters prey, and at high prey densities by how quickly prey can be captured, eaten, and digested. These constraints determine the form of various biological responses to food dispersion. In particular, the rates at which predators track prey (aggregative response), consume prey (functional response), and reproduce (numerical response), are all non-linear functions of prey density (Holling 1959, 1965; Readshaw 1973; Hassell and May 1974; Murdoch and Oaten 1975).

Predators range in behavior from those that search widely and aggregate at dense concentrations of prey to those that "sit and wait" to forage opportunistically on dispersed prey. Both foraging behaviors are evident in many feeding guilds (e.g., Davidson 1977b, Pianka 1986). Foraging responses are also influenced by such factors as hunger state, learning capacity, and prior experience of the predator, and presence of alternate prey, but, in general, predators exhibit either hyperbolic (Type II) or sigmoidal (Type III) responses to increasing prey density (Holling 1965, 1966; Murdoch and Oaten 1975). Linear (Type I) responses are rare (Hassell et al. 1977, Eveleigh and Chant 1981).

Coexisting predators often forage on different densities of shared prey (Holling 1959, Davidson 1977a). Current theory suggests this would promote the coexistence of competitors for a fluctuating food supply (Abrams 1983). Food is probably the most important resource regulating seabird populations (Birkhead and Furness 1985), and diet overlap between species is often high at seabird colonies (Belopol'skii 1957, Pearson 1968, Diamond 1984). How coexisting Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*) respond to variations in the density of capelin (*Mallotus villosus*), their main prey in Newfoundland, is the subject of this paper.

Studies of seabird aggregation behavior have revealed much about how marine predators exploit patchily distributed prey (Brown 1980, Obst 1985, Schneider and Piatt 1986), the oceanographic mechanisms for concentrating prey and predators (Briggs et al. 1984, Brown and Gaskin 1988), and the scales at which these processes occur (Hunt and Schneider 1987). However, we still do not know the minimum densities of prey required for successful foraging (Brown and Nettleship 1984), how and to what degree prey density influences choice of foraging habitats (Brown and Gaskin 1988), how fluctuations in prey abundance affect diet composition (Montevecchi et al. 1988), or why some seabirds exploit prey patches ignored by others (Ashmole 1963). With regard to population biology, Cairns (1987) hypothesized that adult survival, chick growth rates, and breeding success of seabirds are non-linear functions of prey density, but like foraging responses, the forms of these relationships have not been established for any seabird species.

I was able to address some of the foregoing questions by examining the aggregative responses of murres and puffins to schools of capelin. I censused foraging flocks of seabirds around a large breeding colony in Newfoundland while simultaneously conducting hydroacoustic surveys for capelin. Those data allowed me to assess temporal and spatial patterns of association between species, and to characterize the foraging behaviors of murres and puffins. I also consider factors that may influence aggregation behavior

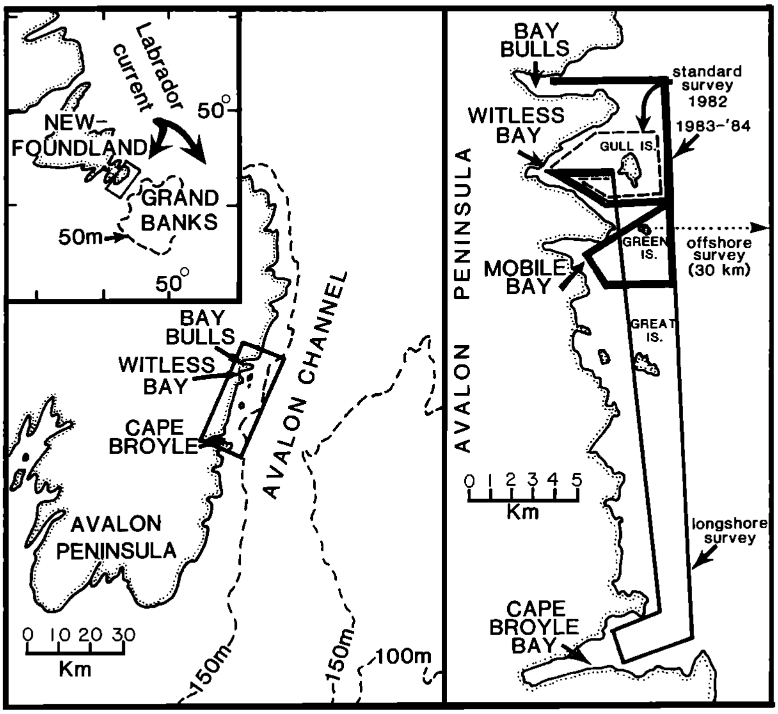


FIGURE 1. Study area in southeastern Newfoundland with survey routes in 1982–1984 indicated.

and its measurement, and discuss some implications of my results for population ecology of seabirds.

STUDY AREA AND METHODS

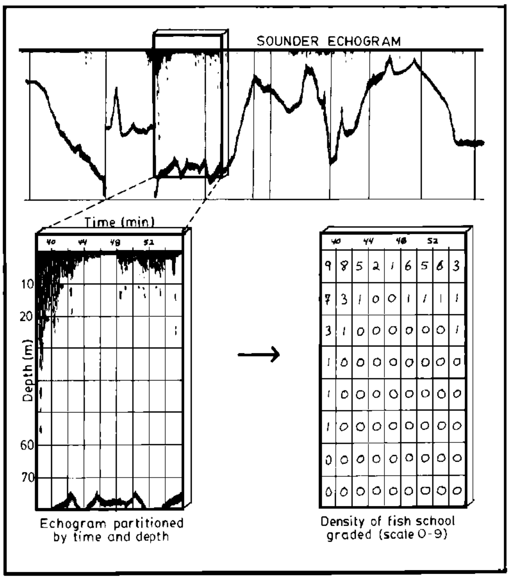
Data were collected at the Witless Bay Seabird Sanctuary (47°15′N, 52°46′W), which comprises three islands off the eastern edge of the Avalon Peninsula of Newfoundland (Fig. 1). Most seabird and capelin surveys were conducted around Gull and Green islands, which support breeding populations of about 75,000 pairs of murres (>99% Common Murres) and 74,000 pairs of Atlantic Puffins (Brown et al. 1975). Great Island is 10 km southwest of Gull Island and supports about 2800 pairs of murres and 148,000 pairs of puffins.

SEABIRD AND CAPELIN SURVEYS

Surveys were conducted at Witless Bay from May to August in 1982–1984 to record the abundance and local distribution of schooling fish (almost exclusively capelin, Piatt 1987, Methven and Piatt 1989), murres, and puffins. In 1982, surveys were conducted in a 9 m open boat with a side-mounted 38 kHz Skipper 609 echosounder. In 1983–1984, surveys were conducted in a 12 m longliner equipped with a Kelvin-Hughes echosounder (Mark 2, Model 5, 42 kHz), autopilot, and radar. Before starting each survey, the date, time, sea state, cloud cover, visibility, and approximate wind speed and direction, were recorded. Two or more observers were present on most surveys and exchanged duties at 30 min intervals. Surveys were begun by marking the sounder echogram and starting a stopwatch to synchronize (hr : min : sec) bird and capelin observations. Upon changing course, the echogram was marked and the time recorded to allow synchronization of each survey segment. Time of encounter, number of individuals, and behavior (swimming or flying) were noted on a tape recorder for all seabirds observed within a 50 m radius in front and on either side of the boat. Only birds swimming on the water were used for analyses of bird-capelin associations.

Using these general methods, four different types of surveys were conducted (Fig. 1). Standard surveys (N = 61) followed a fixed route around Gull and Green islands. This route was chosen to survey a variety of habitats: offshore (70–120 m), bays (30–70 m), inshore (5–30 m), submarine ledges, around headlands, and near islands. In 1982, the standard survey consisted of a 12 km circuit of Witless Bay and Gull Island, and in 1983–1984, surveys were extended (ca. 30 km) to include Bay Bulls, Green Island, and Mobile Bay. Standard survey data were used for analyses of seasonal variations in bird and capelin abundance at Witless Bay, and for analyses of aggregative responses.

Other sampling schemes were used to examine diurnal patterns of abundance, and the longshore and offshore distribution of birds and capelin (Fig. 1, Piatt 1987). These data are used here only for examining aggregative responses. On two occasions, standard surveys were conducted repeatedly (N = 4) over a 24-hr



9	8	5	2	1	6	5	6	3
7	3	1	0	0	1	1	1	1
3	1	0	0	0	0	0	0	1
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

FIGURE 2. Illustration of how acoustic echograms were graded to estimate capelin density (drawn from actual survey echogram).

period to detect diel variations in the abundance of birds and capelin. Offshore surveys ($N = 4$) originated on the east side of Green Island and ran east-southeast to a point 30 km offshore. Three coastal (longshore) surveys were conducted in 1984 from Witless Bay to Cape Broyle, about 25 km south.

Estimating Relative Abundance and Density of Capelin Schools

The method used to quantify capelin schools on survey echograms is illustrated in Figure 2. Each echogram was partitioned by time (1 min intervals in 1982–1984, and 2 min intervals in 1983) and depth (10 m intervals). The density of capelin registrations appearing in each block was then graded visually on a scale of 0–9 (e.g., Safina and Burger 1985).

Fish abundance is proportional to the square of echo-signal intensity (Forbes and Nakken 1972), and total capelin abundance per survey was therefore calculated as the sum of squared grades on the echogram. Mean abundance of capelin per survey or per minute was estimated by dividing the sum of abundance grades by the number of graded blocks (including zeros) in the survey or minute, respectively. Mean density of capelin schools per survey or per minute was calculated by dividing the sum of abundance grades by the number of non-zero blocks per survey or minute.

Abundance of deep capelin schools may have been underestimated because echo-signal strength attenuates with depth. Time-varied-gain (TVG) adjustments were made to compensate for that effect in 1982 (Forbes and Nakken 1972). Most capelin schools were located within 30 m of the surface, however, so signal attenuation was probably not a large source of error. The spread of acoustic signals with depth tends to overestimate deep school dimensions,but this was adjusted for in calculating capelin school volumes (Forbes and Nakken 1972).

Statistical Analyses

Aggregation intensity was quantified by computing variance-to-mean ratios (I′) for bird and capelin abundance on each survey. The dependence on measurement interval (frame size) of I′ and correlations between bird and capelin aggregations were determined by computing I′ and r^2 over increasing frame sizes for each survey (Schneider and Duffy 1985, Schneider and Piatt 1986). Measurement intervals were scaled in minutes of transect (ca. 250 m traveled per min of transect, or 4 min/km).

Plots of bird versus capelin density at varying frame sizes indicated that the aggregative response of birds to capelin schools was sigmoidal. A simple box model was used to transform sigmoidal curves, locate inflection points (thresholds), and measure the strength of bird-capelin correlations. The model used was:

$$B = k_1F \text{ if } F > F_T, \qquad B = k_2F \text{ if } F < F_T$$

where B = bird density, F = relative capelin density, F_T = test threshold capelin density, and k_1 and k_2 are the mean densities of birds above and below the test threshold F_T. An iterative procedure was used to locate the inflection point. Least squares regression was used to estimate k_1 and k_2.

Using simulated data, an example of this method is shown in Figure 3. The sigmoidal curve is transformed to a linear relationship by dummy coding the independent variable (X) according to whether it is lower (0) or higher (1) than the test threshold X_T (Fig. 3C). Regression of Y on X then reveals (r^2) how well the data fit a linear model. This analysis is performed iteratively for values of X $(0, 1, 2, \ldots, X_i)$, which generates a regression coefficient for each test threshold (Fig. 3A). In the example, a test threshold of $X_T = 2$ yields an r^2 value of 0.25; at $X_T = 5$, $r^2 = 0.89$; at $X_T = 8$, $r^2 = 0.18$. Because the relationship between Y and X is sigmoidal, r^2 increases with each iteration up to the inflection point and decreases thereafter. The best fit to the model occurs when X_T equals the true threshold, and r^2 at that point provides the best measure of correlation between X and Y.

When real data were grouped into large measurement intervals to examine the effects of scale, the number of data points available for locating thresholds decreased (e.g., grouping a 128 min survey into 16 min blocks reduced the number of data points from 128 to 8). With bird and capelin density data grouped into a small number of average points, r^2 did not always reach a maximum value and then decline in the iterative threshold test because all the high density data were sometimes grouped into an isolated, terminal data point. In such cases, if a maximum r^2 value occurred just before the terminal data point, a threshold was assumed to occur before that point.

I used Monte Carlo simulations to test the reliability of the above method for measuring correlations and locating thresholds. Two surveys were chosen at random and an International Mathematics and Statistics Library subroutine (GGPER) was used to reassign each 1 min bird count randomly to a new location along the transect (Schneider and Piatt 1986). One hundred runs were conducted for each survey and bird species. After each run, the iterative threshold test was conducted for the independent variable (relative capelin density). In total, 2400 regressions of randomized data were compared with regressions of original data. Results indicated that significance levels obtained in iterative threshold tests of original data were conservatively estimated by parametric statistics.

To determine if thresholds could occur by chance in plots of original data, the proportion of randomized surveys yielding a simple threshold (maximum r^2 whether significant or not), or a threshold with a significant regression, was determined from 400 Monte Carlo simulations. Because thresholds could also occur before terminal values of capelin density in some cases (see above), and therefore not be located by the iterative threshold test, the probability of obtaining one or two consecutive significant r^2 values anywhere in a plot was also determined from Monte Carlo simulations. The results of these additional simulations are presented and discussed below.

Like spatial correlations, the temporal association between birds and capelin depended on the time scale used in analyzing the data. I used the simple procedure of grouping data over increasing time frames (1–10 d) for the analysis of temporal correlations between birds and capelin at Witless Bay.

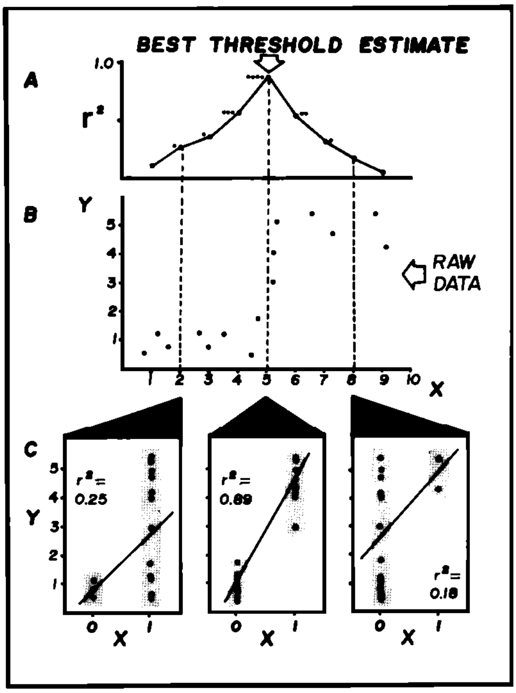


FIGURE 3. Illustration of how sigmoidal curves were transformed with a box model and how thresholds were located using an iterative procedure. Asterisks in panel A indicate significance levels of regressions: *P < 0.05, **P < 0.01, ***P < 0.001, ****P < 0.0001.

RESULTS

TEMPORAL PATTERNS IN ABUNDANCE OF BIRDS AND CAPELIN

In all years, murres and puffins were absent or occurred in low numbers on the water around their breeding colonies in May and early June (Fig. 4). Most breeders attend colonies in Witless Bay by late May (Nettleship 1972, Mahoney 1979), so birds were apparently commuting to foraging areas located farther than about 5 km from the islands. An exception occurred on 9 May 1984, when about 100,000 murres were concentrated inshore by Arctic pack ice. That unique survey was excluded from further analyses.

The abundance of murres and puffins in the survey area increased sharply in late June each year, corresponding to the arrival of spawning schools of capelin inshore (Fig. 4). Thereafter, murre and puffin abundance fluctuated with capelin abundance, although each bird species exhibited different patterns of association. Murres were better correlated with capelin over all time frames examined (1–10 d). Maximal correlations of murres and puffins with capelin were observed when data were grouped over 5-day intervals. At that scale, murre abundance was strongly correlated with capelin abundance in all years (1982: Pearson $r^2 = 0.84$, $P < 0.05$; 1983: $r^2 = 0.83$, $P < 0.0001$; 1984: $r^2 = 0.65$, $P < 0.01$). Murres, like capelin, exhibited one peak of abundance in 1982 and 1984, two peaks in 1983, and were scarce in August each year (Fig. 4). Although puffins were also abundant in late June and July, their numbers were poorly correlated with overall capelin abundance in Witless Bay (1982: $r^2 = 0.51$, $P > 0.05$; 1983: $r^2 = 0.11$, $P > 0.05$; 1984: $r^2 = 0.46$, $P > 0.05$) and puffins were often as common in August as they were in July. However, separate analyses revealed that puffins foraged mostly inshore (Piatt 1987), and using only data from inshore habitats, puffin abundance was correlated strongly with capelin abundance in all years (1982: $r^2 = 0.73$, $P > 0.05$, 1983: $r^2 = 0.75$, $P < 0.0001$; 1984: $r^2 = 0.54$, $P < 0.05$).

There was an order of magnitude decline in capelin abundance from 1982 to 1984 (Fig. 4). The mean abundance index for capelin declined from 2.3 (±0.1 SE) in 1982, to 0.83 (±0.05) in 1983, and to 0.11 (±0.02) in 1984. That trend was mirrored by a decline in overall bird abundance in Witless Bay over the same years, although puffins were less affected than murres (Fig. 4).

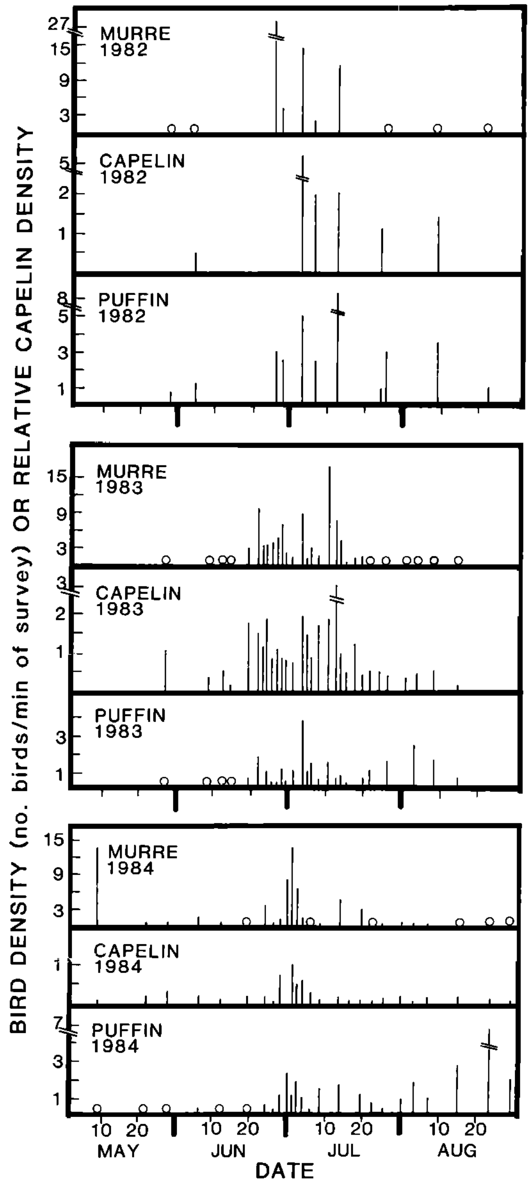


FIGURE 4. Seasonal abundance of Common Murres, Atlantic Puffins, and capelin around the Witless Bay islands, 1982–1984. Data from standard surveys only. Open circles indicate that a survey was conducted, but no birds were observed on the water.

Fine-scale Spatial Association between Birds and Capelin

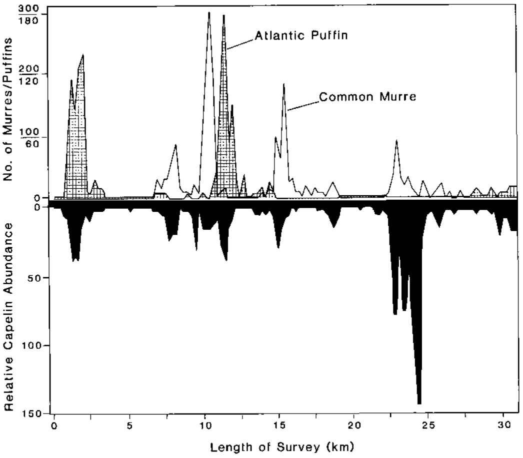


FIGURE 5. Standard survey conducted 13 July 1982, showing Common Murre, Atlantic Puffin, and capelin abundances along the survey route. Note differing scales for murre and puffin abundance.

Some hydroacoustic echograms obtained in 1982 were selected for the quality of capelin school registrations appearing on them, and schools were measured carefully to estimate volumes (Forbes and Nakken 1972, Piatt 1987). This method of measuring capelin abundance was not used for further analyses because it was too time-consuming. In conjunction with bird observations, however, these data illustrate fine-scale associations between birds and capelin (Fig. 5, Table 1).

Between minutes 3–10 (2 km) of a survey conducted on 13 July 1982 (Fig. 5), 24 capelin schools were encountered that had mean and total volumes of 399 and 9575 m^3, respectively (Table 1). The minimum and maximum depths to which capelin schools extended were 0.3 and 16.7 m. The total number of capelin present was estimated at 150,000 individuals, assuming a mean density of 15.7 fish per m^3 (Zaferman 1973). Total biomass was about 3.8 metric tons, assuming the mean weight of individual capelin in the area was 25.3 g (Piatt 1987). Only puffins fed on this shallow aggregation, and most were found over the largest schools of capelin.

Between minutes 37–49 (3.3 km) of the same survey (Fig. 5), 58 capelin schools were recorded that had mean and total volumes of 680 and 39,452 m^3, respectively. The minimum and maximum depths to which schools extended were 0.3 and 42.4 m. The total number of capelin in the aggregation was estimated at 619,000 individuals, with a total biomass of 15.7 metric tons. Both murres and puffins fed on this aggregation, but they were spatially segregated. Murres occurred over large schools concentrated between 10–30 m in the water column, whereas puffins occurred over smaller schools concentrated between 2–15 m. Similarly, most puffins were as-

TABLE 1. Fine-scale Common Murre and Atlantic Puffin Association with Selected Capelin Aggregations, 3 and 13 July, 1982

Date	Minute	No. of schools	Total[a] school volume (m^3)	Mean[b] depth (m)	No. of murres	No. of puffins
13 July	3	2	572	13.3	0	0
	4	4	599	2.5	0	30
	5	3	2213	4.7	0	100
	6	4	2229	3.7	0	75
	7	4	2055	4.2	0	110
	8	2	781	2.3	0	125
	9	4	475	4.7	0	6
	10	1	651	3.1	0	3
	37	7	350	30.1	3	0
	38	8	3698	24.7	25	0
	39	4	222	25.2	4	1
	40	12	1686	24.2	70	5
	41	5	2840	18.6	190	0
	42	4	9026	11.9	300	0
	43	5	723	19.3	201	9
	44	2	68	8.9	1	25
	45	3	7594	13.5	5	85
	46	3	12,355	11.4	15	180
	47	2	620	2.8	2	41
	48	2	254	2.6	2	78
	49	1	16	3.5	0	26
3 July	43	1	46	1.0	0	0
	44	1	743	10.4	1	3
	45	1	45	1.4	0	7
	46	2	369	0.3	0	11
	47	3	1365	4.9	0	35
	48	1	27	4.2	0	19
	49	1	8447	8.3	2	75
	50	2	144	1.4	0	32
	51	1	60	1.0	0	3
	52	1	25	10.4	0	0
	74	3	111	11.9	1	1
	75	10	3905	14.0	0	38
	76	5	3537	18.9	0	15
	77	5	16,472	27.4	50	2
	78	7	5208	22.0	5	0
	79	5	9295	32.0	21	0
	80	11	9043	32.6	6	0
	81	3	1060	12.4	1	0

[a] Total volume of all schools. School volume = $3.14\ h^2\ w/4$ (Forbes and Nakken 1972).

[b] Mean depth weighted by volume.

sociated with small, shallow (<20 m) capelin schools, whereas murres were associated with larger, deeper (20–35 m) capelin schools during a survey conducted on 3 July 1982 (Table 1).

Some important features of these and other 1982 surveys were observed also in 1983 and 1984; i.e., the combined distribution of murres and puffins matched the distribution of capelin schools, but murres and puffins were spatially segregated. They either fed in different habitats or fed on different parts of the same capelin aggregations.

Scale-dependent Aggregations and Correlations

On most surveys, murre (86%, N = 63 surveys), puffin (76%, N = 70), and capelin (88%, N = 73) aggregation intensity (I′) increased with frame size (Fig. 6), yielding significantly higher values of I′ at spatial scales of 0.5–15 km than at minimum frame sizes. In most cases, I′ increased rapidly over small frame sizes, plateaued or peaked at intermediate frame sizes (2–4 km), and decreased again at large frame sizes (8–16

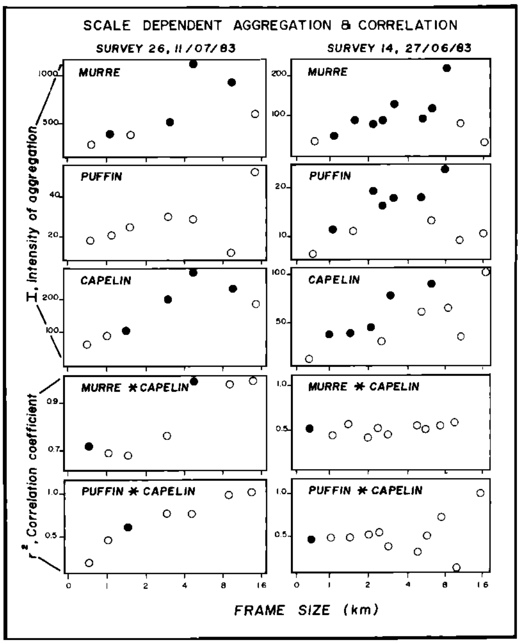


FIGURE 6. Scale dependent aggregation and correlation of Common Murres, Atlantic Puffins, and capelin. Aggregation intensity: closed circles indicate significantly higher I′ values than observed at minimum frame size (tested by Monte Carlo analysis). Correlation coefficient: closed circles at minimum frame size indicate significant correlation; at larger frame sizes closed circles indicate that the correlation was significantly higher than that calculated at the minimum frame size (tested by Monte Carlo analysis).

km). Maximal I′ values indicate the scale at which aggregations occur (Pielou 1977, Schneider and Piatt 1986) and usually peaked between 2–4 km for puffins, and between 2–6 km for murres and capelin.

Murres (68% of 63 surveys) and puffins (54% of 70 surveys) were significantly correlated with capelin at the minimum scale of measurement on most surveys. Correlations grew significantly stronger with increasing frame size on 35% and 27% of all murre and puffin surveys, respectively (e.g., survey 26, Fig. 6). Spatial correlations between birds and capelin on the remainder of surveys did not improve significantly with increasing frame size, despite significant increases in I′ (e.g., survey 14, Fig. 6).

SCALE-DEPENDENT AGGREGATIVE RESPONSE

Because fine-scale associations between birds and capelin were imperfect, plots of bird versus capelin density using fine-scale data gave the impression that large numbers of birds foraged in areas where capelin were scarce or absent (Fig. 7, 2 and 4 min frame sizes). However, when data were grouped into measurement intervals corresponding to the scale of aggregations and replotted, a more realistic picture of murre and puffin foraging behavior emerged (Fig. 7, 8 and 16 min frame sizes).

Using a 10 min frame size to examine all surveys, many plots of bird versus capelin density were sigmoidal (Figs. 7 and 8) indicating Type III aggregative responses to prey density (Holling 1959, Hassell and May 1974). An intermediate

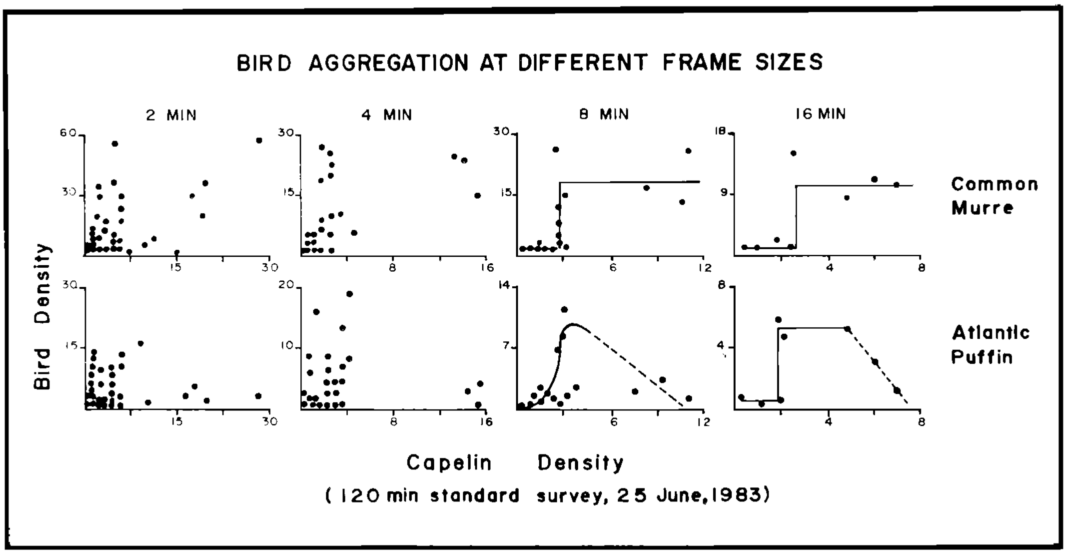


FIGURE 7. Effect of increasing frame size on the form of the aggregative response of birds to capelin.

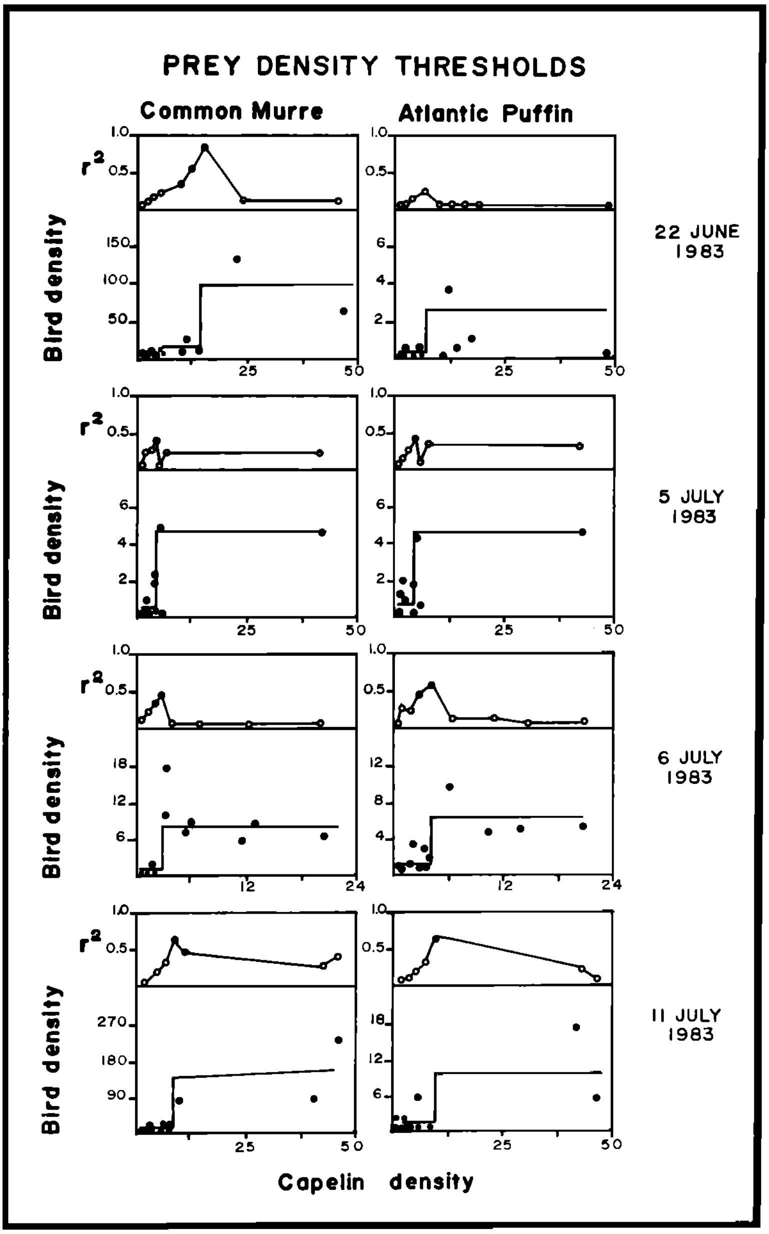


FIGURE 8. Aggregative response of Common Murres and Atlantic Puffins to capelin on four standard surveys in Witless Bay, 1983. Data grouped into 10 min frame sizes. For each date and bird species, the aggregative response is shown in the lower panel, with the estimated threshold indicated by a solid line. Corresponding upper panel shows the result of a threshold location test (closed circle indicates $P < 0.05$ for the corresponding r^2 value).

10 min (2.5 km) frame size was chosen for comparing surveys because aggregation intensity (I′) usually plateaued or peaked at frame sizes greater than about 8 min, the number of data points in an aggregative response plot decreased with increasing frame size (Fig. 7), and seabird census programs often use 10 min observation periods (e.g., Brown et al. 1975).

Estimating Thresholds to Prey Density

Using the iterative test, most plots exhibited simple thresholds, i.e., a maximum correlation

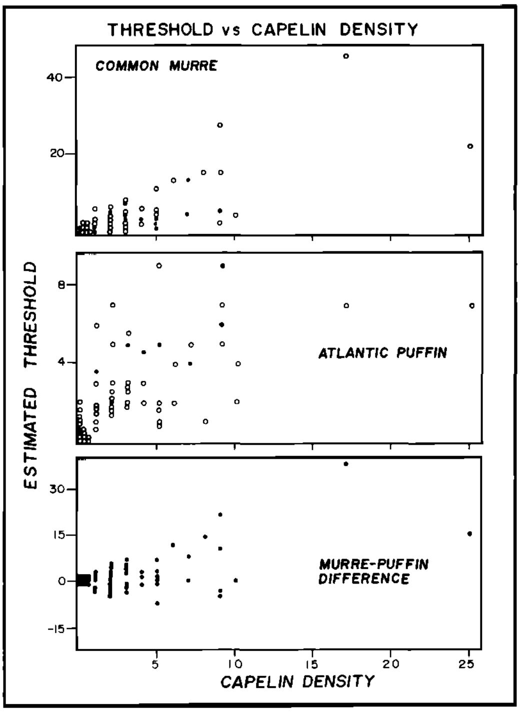


FIGURE 9. Common Murre and Atlantic Puffins prey density thresholds, and the difference between thresholds, in relation to overall capelin density in Witless Bay. Spearman rank correlations calculated using data from all surveys (open and closed circles) or using only surveys with plots exhibiting thresholds with significant regressions (closed circles). Difference plot incorporates all data. Spearman rank correlations: Common Murre—open and closed circles: $r = 0.82$, $P < 0.0001$; closed circles only: $r = 0.58$, $P < 0.05$; Atlantic Puffin—open and closed circles: $r = 0.73$, $P < 0.0001$; closed circles only: $r = 0.89$, $P < 0.001$; murre-puffin difference: $r = 0.33$, $P < 0.05$.

TABLE 3. MONTE CARLO SIMULATIONS: PROBABILITY OF FINDING THRESHOLDS AND SIGNIFICANT REGRESSIONS WHEN CONDUCTING THRESHOLD LOCATION TESTS ON RANDOMIZED SURVEY PLOTS OF BIRD VERSUS CAPELIN DENSITY

Probability[a] of obtaining:	Murre		Puffin	
	A	B	A	B
Simple threshold	0.56	0.58	0.56	0.62
Threshold with significant r^2	0.08	0.07	0.09	0.06
1 Significant r^2	0.15	0.16	0.13	0.17
2 Consecutive significant r^2's	0.02	0.03	0.07	0.05

[a] Based on 100 runs on two different surveys (A, B) for each species (conducted at 10 min frame size).

in the regression of dummy-coded bird and capelin densities occurred at some intermediate density of capelin (Table 2). However, not all regressions were statistically significant and many plots had few high density data points (or one terminal one), making it difficult or impossible to locate a threshold with the iterative test. Monte Carlo simulations revealed that:

1) There was a high probability of finding simple thresholds due to chance alone. The proportion of randomized survey plots with simple thresholds (Table 3) was similar to the proportion of original survey plots with simple thresholds (Table 2).

2) There was a low probability ($P < 0.06$–0.09) of finding a threshold with a significant regression (Table 3), and this was therefore a moderately conservative criterion for identifying true thresholds. Many more survey plots in 1983 and 1984 had thresholds with significant regressions than would be expected by chance (Table 2).

3) The probability of finding at least one significant regression anywhere in a randomized plot

TABLE 2. FREQUENCY OF THRESHOLDS AND SIGNIFICANT REGRESSIONS IN ALL BIRD-CAPELIN PLOTS, 1982–1984 (AT 10 MIN FRAME SIZE)

	1982				1983				1984			
	Murre		Puffin		Murre		Puffin		Murre		Puffin	
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
Total no. of surveys	3		5		32		35		26		25	
No. with simple threshold	2	(66)	3	(60)	17	(53)	23	(66)	7	(27)	8	(32)
No. with threshold and significant regression	0	(0)	0	(0)	10	(31)	8	(23)	5	(19)	2	(8)
No. with >2 consecutive significant regressions	1	(33)	1	(20)	19	(56)	10	(38)	8	(31)	6	(24)

TABLE 4. AVERAGE MURRE AND PUFFIN FORAGING THRESHOLDS (THR) TO CAPELIN SCHOOL DENSITY, 1982–1984 (AT 10 MIN FRAME SIZE)

		Murre			Puffin				
Case	Year	N	Thr	(SE)	N	Thr	(SE)	t[a]	P
All data	1982	3	9.7	(6.2)	5	3.6	(1.0)	1.2	NS
	1983	32	6.9	(1.6)	35	3.4	(0.3)	2.1	<0.05
	1984	26	1.1	(0.3)	25	1.0	(0.3)	0.7	NS
	Total	61	4.6	(0.9)	65	2.6	(0.3)	2.3	<0.05
If Mt and Pt significant[b]	Total	4	4.1	(3.6)	4	3.4	(2.2)	0.9	NS
If Mr and Pr significant[c]	Total	9	9.5	(2.6)	9	3.7	(0.5)	2.4	<0.05

[a] Value of t computed for paired comparisons under the hypothesis that the mean murre threshold minus the mean puffin threshold = 0.

[b] If both murre and puffin plots on the same survey had thresholds with significant regressions.

[c] If both murre and puffin plots on the same survey had ≥ 2 consecutive significant regressions.

was relatively high (Table 3). However, the probability that two or more significant regressions would occur consecutively in a plot of randomized data was low ($P < 0.02$–0.07). Consecutive regression coefficients should be high and significant around a true threshold in a sigmoidal curve (Fig. 3) and they could also indicate whether a threshold occurred before an isolated terminal data point. Thus, the existence of consecutive significant regressions was a conservative criterion for identifying true thresholds. A much higher proportion of original survey plots exhibited two or more consecutive significant regressions than would be expected by chance (Table 2).

COMPARISON OF MURRE AND PUFFIN THRESHOLDS TO PREY DENSITY

Murre foraging thresholds were usually higher than puffin thresholds on individual surveys and average murre thresholds were higher than average puffin thresholds in all years (Table 4). Considering only surveys in which murre and puffin plots both exhibited thresholds with significant regressions, the average murre threshold was higher than the average puffin threshold. Finally, considering only surveys in which murre and puffin plots both exhibited two or more consecutive significant regressions (the most conservative analysis), average murre thresholds were significantly higher than average puffin thresholds (Table 4).

The apparent difference between murres and puffins with respect to their prey density thresholds was examined for possible scale-dependency by estimating thresholds at different spatial scales. Grouping the data into larger frames lowered average bird and capelin density values, but at every frame size the average threshold for murres was greater than the average threshold for puffins (Table 5).

THRESHOLD VARIABILITY IN RELATION TO OVERALL CAPELIN DENSITY

Murre and puffin thresholds decreased progressively from 1982 to 1984 corresponding to a decline in capelin abundance (Fig. 4). Murre and puffin thresholds were strongly correlated with overall capelin density at Witless Bay in each year and over all years combined, regardless of the data set used for the analysis (Table 6, Fig. 9). The difference between murre and puffin thresholds was also correlated with overall capelin density. As overall capelin density increased, murre thresholds increased more rapidly than puffin thresholds, and the difference between thresholds widened. Conversely, as overall capelin density declined, murre and puffin thresholds converged.

DISCUSSION

SCALE-DEPENDENT AGGREGATIONS AND CORRELATIONS

In marine systems, biological and physical processes combine to impart spatial structure to plankton and fish communities, and seabird ag-

TABLE 5. EFFECT OF VARYING FRAME SIZE ON AVERAGE FORAGING THRESHOLDS (THR) USING ALL DATA IN 1983 FOR MURRES (N = 32 SURVEYS) AND PUFFINS (N = 35 SURVEYS)

	Murre		Puffin			
Frame size	Thr	SE	Thr	SE	t[a]	P
2	7.4	(1.6)	3.2	(0.4)	2.5	0.02
4	7.6	(1.5)	3.1	(0.3)	2.7	0.02
8	7.9	(1.7)	2.6	(0.4)	3.4	0.002
10	6.9	(1.6)	3.4	(0.3)	2.1	0.05
12	6.5	(1.4)	3.6	(0.4)	2.0	NS (0.06)
16	4.9	(0.9)	3.0	(0.4)	2.0	NS (0.05)

[a] Value of t computed for paired comparisons under the hypothesis that the mean murre threshold minus the mean puffin threshold = 0.

TABLE 6. Spearman Rank Correlations between Murre (M) and Puffin (P) Thresholds (Thr), the Difference between Thresholds (Diff) and Overall Capelin Density (CD), 1982–1984 (at 10 min Frame Size)

		MThr × CD			PThr × CD			Diff × CD		
Case	Year	N	r	P	N	r	P	N	r	P
All data	1982	3	0.99	0.0001	5	0.76	NS	3	0.50	NS
	1983	32	0.66	0.0001	35	0.51	0.01	32	0.38	0.05
	1984	26	0.67	0.001	25	0.76	0.0001	20	−0.09	NS
	Total	61	0.82	0.0001	65	0.73	0.0001	55	0.33	0.05
If Mt and Pt significant[a]		4	0.99	0.01	4	0.80	NS	4	0.80	NS
If Mt or Pt significant[b]		15	0.58	0.05	10	0.89	0.001	—	—	—
If Mr and Pr significant[c]		9	0.75	0.01	9	0.69	0.05	9	0.59	0.05

[a] If both murre and puffin plots had thresholds with significant regressions.

[b] Calculated using all plots in which murre or puffin plots exhibited thresholds with significant regressions. Difference (Diff) cannot be calculated because data for each species taken from different surveys.

[c] If both murre and puffin plots had ≥2 consecutive significant regressions.

gregations reflect the scale at which these processes occur (Schneider 1982). At Witless Bay, the aggregation intensity of birds and capelin varied with measurement interval and peaked at scales of 0.25 to 15 km. Most patches ranged between 2–6 km in horizontal extent. These were small compared to patches reported from other areas (i.e., 5–50 km; Zaferman 1973, Schneider 1982, Briggs et al. 1984, Woodby 1984), but they contained regionally significant concentrations of predators and prey. Thousands of tons of capelin are consumed in summer at Witless Bay by hundreds of thousands of seabirds, cod (*Gadus morhua*), and baleen whales (Brown and Nettleship 1984, Cairns et al. 1987, Methven and Piatt 1989, Piatt et al. 1989).

The present analysis of more than 70 surveys corroborates an earlier finding by Schneider and Piatt (1986) that spatial correlations between birds and capelin in Witless Bay are scale-dependent. Murres and puffins were significantly correlated with capelin on more than half of all surveys before effects of scale were examined, and spatial correlations improved with increasing frame size on about half of those surveys. At measurement intervals of 2.5 km, capelin density frequently explained over 75% of the spatial variation in bird density; it explained over 95% of the variation on nine surveys.

Elsewhere, it has proven difficult to demonstrate significant spatial correlations between seabirds and their prey (e.g., Woodby 1984, Obst 1985, Safina and Burger 1985). Scale-analysis might have been useful in these studies (Schneider and Piatt 1986), although other factors probably contributed more to the difficulty in measuring predator-prey associations. In some situations, seabirds would not be expected to track all prey aggregations, especially at great distances from their colonies or where prey schools greatly outnumber predators (Woodby 1984). Obst (1985) found that aggregations of penguins were reliable predictors of krill (*Euphausia supurba*) schools, but not vice versa. Seabirds may forage selectively in specific habitats or on specific parts of the prey aggregations they encounter (Brown and Gaskin 1988), and interference competition may exclude some species from feeding sites (Piatt 1987). Seabird and prey aggregations may be dispersed by other predators (Safina and Burger 1985) or by the activities of the research vessel or other vessels. Errors also arise from rough sea conditions, poor visibility, weak or spurious signals from the echosounder, and the time lag between bird observations and detection of prey with the echosounder. Finally, seabirds and their prey are patchily distributed and surveys may simply miss significant aggregations.

Despite these potential sources of error, I found strong spatial correlations between birds and capelin in Witless Bay. Presumably, the abundance of breeding birds, close proximity of the survey route to colonies, and the use of Witless Bay for spawning by large numbers of capelin increased the likelihood that capelin schools would be exploited by foraging murres and puffins.

The Aggregative Response

The are many examples of functional, aggregative, and numerical responses in the literature, but most are well-defined curves generated from laboratory experiments (Readshaw 1973, Hassell and May 1974, Hassell et al. 1977). Field data are more difficult to gather and interpret (Goss-Custard 1970). Response curves must contain an adequate number of high density data points to resolve their shape (Hassell and May 1974), but this requirement was generally not met outside periods of high capelin density in Witless Bay. The same biological and physical sources of error that reduced spatial correlations also affected my ability to resolve aggregative response curves. In addition, the density of puffins was occasionally suppressed at high capelin densities, possibly owing to interference competition from murres (Piatt 1987), and this made it more difficult to characterize puffin response curves.

Despite these limitations, murres and puffins exhibited sigmoidal (Type III) aggregative responses to capelin density on about one-third of the surveys I conducted. Type III responses are typical of higher vertebrates feeding on aggregated prey (Holling 1965, 1966; Goss-Custard 1970, 1977; Hassell and May 1974; Murdoch and Oaten 1975). Aggregative responses were scale-dependent and best resolved at measurement intervals corresponding to the scale of aggregations (ca. 2–4 km). Murres foraged on larger, denser concentrations of capelin than puffins and also formed larger, denser flocks while foraging (Piatt 1987).

BODY SIZE AND FEEDING THRESHOLDS

Both Common Murres (ca. 975 g) and Atlantic Puffins (ca. 475 g) search widely for aggregated prey and dive to pursue their prey underwater. Foraging ranges, diving depths, and dive times are all positively correlated with body size in piscivorous alcids (Piatt and Nettleship 1985, Piatt 1987, Wanless et al. 1988). At Witless Bay, I observed murres and puffins simultaneously as they foraged on the same species of schooling prey. Thus, the difference between species in foraging thresholds must be attributed to biological differences between them (as opposed to differences between their prey or feeding environments), and body size is one obvious difference to consider. The relationship between predator body size and prey density thresholds is predictable from well-known models of foraging behavior.

The principal feature of Holling's (1965) "disc" equation, and many subsequent models of foraging behavior (e.g., Royama 1970, Murdoch and Oaten 1975, Hassell et al. 1977, Werner and Mittelbach 1981) is that:

$$N/T \propto D/(1 + D)$$

i.e., a predator's potential rate of food intake (N/T, where N = the number of prey captured and T = time spent foraging) is a non-linear function of prey density (D). The major distinction between coexisting predators with similar foraging styles and shared prey is N_{tot}, the amount of food required for daily existence. N_{tot} is the sum of food required for maintenance and foraging, and both are functions of body size (Peters 1983, Werner and Mittelbach 1981).

Optimal foraging theory assumes that predators try to maximize their rate of food intake to allow as much time as possible for other activities (Krebs 1978, Pyke et al. 1977, Pyke 1984). Food intake rates may be maximized by foraging on the biggest or best quality food available (energy maximizer), by minimizing the time spent foraging (time minimizer), or both. To maximize N_{tot}/T, murres and puffins feeding on capelin can only adjust D, T, or the size of capelin consumed, because N_{tot} is a fixed function of body size and time spent foraging (T). Murres require about twice as much food as puffins (Brown and Nettleship 1984) and could therefore obtain their daily ration in the same time (T) as puffins if they foraged on capelin aggregations about $2[D/(1 + D)]$ times as dense as those fed on by puffins. Alternatively, murres could obtain their daily ration by foraging about twice as long on the same prey concentrations used by puffins. However, this would not be optimal behavior for murres, and in any case, evidence suggests that murres spend slightly less time foraging on prey shared with puffins (Pearson 1968). Finally, murres could obtain their daily rations in the same time as puffins if they fed on similar concentrations of much larger capelin. Although murres did take some larger size-classes of capelin than puffins at Witless Bay, the difference was not great enough to compensate for the difference in food demands. Morisita's index of overlap in weights of capelin consumed ranged from 0.82–0.96 in 1982–1984 (Piatt 1987).

Therefore, I postulate that the differing thresholds to capelin density exhibited by murres and puffins result from species-specific behavioral responses to food dispersion that have evolved in concert with metabolic constraints imposed by body size. In other words, puffins choose to exploit lower density prey aggregations than murres—a behavior that: i) is permitted because of lower metabolic demands; ii) is selected for when prey are scarce; and iii) promotes coexistence with murres (see below). An alternative explanation is that puffins were excluded by murres from high density prey patches. There is evidence that asymmetric interference competition for feeding sites occurred at Witless Bay (Piatt 1987). However, this would not explain why the gap between murre and puffin thresholds widened as overall capelin density increased. If puffins were simply tracking murre thresholds, then the difference between thresholds should have remained constant. Nor would it explain why puffins continued to forage on low density capelin aggregations after murres departed the study area, or why murres formed larger, denser feeding flocks than puffins (Piatt 1987).

VARIABLE THRESHOLDS AND FORAGING EXPECTATIONS

Most foraging models assume that predators change behavior at threshold levels of foraging success (Krebs 1978, Lima 1983), but few predict how thresholds should vary with fluctuations in overall prey density. Such behavior is well simulated in "Foraging by Expectation" models, which assume that a predator will switch patches when its current success rate drops below what it has come to expect from recent experience. As prey density fluctuates, predators should change their expectations and foraging thresholds accordingly (Green 1980, Iwasa et al. 1981, Lima 1983).

Consistent with the above predictions, foraging thresholds of murres and puffins changed from survey to survey and between years in relation to overall capelin density in Witless Bay. Brown and Gaskin (1988) noted similar behavior in phalaropes (*Phalaropus* spp.) foraging on zooplankton in the Bay of Fundy and suggested that phalaropes exploit the densest concentrations of prey available to them at any given time or place.

THRESHOLDS, BODY SIZE AND POPULATION ECOLOGY

Murres and puffins at Witless Bay colonies normally hatch chicks in late June (Nettleship 1972, Mahoney 1979) as capelin arrive inshore for spawning (Templeman 1948, this study). Murre chicks go to sea about 19–25 days after hatching, and because breeding is well synchronized, most adult murres leave the colony within 4–5 weeks after the peak of hatching (Mahoney 1979, Piatt and McLagan 1987). In contrast, puffins take about a month longer to fledge chicks and fledging is less synchronized (45–60 days, Nettleship 1972). Thus, the period of peak food demand by murres in Witless Bay corresponds well with the period of peak capelin density around the colonies (ca. 4 weeks), whereas puffin food demands extend well beyond this period. What accounts for the difference in duration of chick-rearing?

The conventional explanation for timing of reproduction in the Alcidae is that breeding coincides with peak food availability for provisioning chicks (Birkhead and Harris 1985). For murres and puffins, however, which overlap extensively in their choice of prey (Pearson 1968, Piatt 1987), this hypothesis offers little explanation for the marked interspecific difference in duration of chick-rearing. The emphasis on chicks may be misleading because only about 5% of the total food biomass taken by murres and puffins during breeding is fed to chicks (Brown and Nettleship 1984). The bulk of food required for reproduction is used to fuel adult maintenance and foraging activity (Gaston 1985). Therefore, the breeding seasons of murres and puffins may be limited to that portion of the year when local prey densities are sufficient to support adults while they are constrained to forage near their breeding colonies; this period is shorter for murres than for puffins.

Many long-term studies have been conducted on components of Common Murre and Atlantic Puffin population biology (Nettleship and Birkhead 1985) and the results are unequivocal. Where they coexist in the North Atlantic, Common Murres exhibit, on average, higher rates of breeding success (Harris and Birkhead 1985), higher recruitment rates (Hudson 1985), higher rates of adult mortality (Hudson 1985, Evans and Nettleship 1985), and more extreme population fluctuations (Hudson 1985) than Atlantic Puffins. I propose that these differences in population dynamics are related to food thresholds and body size.

At least four factors contribute to this relationship. First, because high density prey offer the greatest rate of energy extraction from the environment, any predator feeding on high density prey should be able to harness more energy for reproduction than any coexisting predator feeding on low density prey (MacArthur 1958). Field measurements of foraging energetics support this hypothesis (Nagy et al. 1984). Second, large animals have lower specific metabolic rates than small animals and can therefore channel a higher proportion of energy into reproduction than small animals feeding on the same food (Peters 1983). Third, predators feeding in dense aggregations face a higher risk of starvation and mortality from competition or stochastic events than dispersed predators feeding in the same environment. Finally, higher reproduction and mortality rates result in larger and more rapid population fluctuations (Utida 1957).

The hypothesis that prey density thresholds are linked to population dynamics in murres and puffins is corroborated by observations on other kinds of animals. Population growth rates are non-linear functions of prey density for most animals that have been studied (Holling 1959, 1965; Readshaw 1973; Murdoch and Oaten 1975), and a few studies have examined how naturally coexisting predators respond numerically to variations in density of shared prey (Utida 1957, MacArthur 1958, Holling 1959, Taylor 1978, Stemberger and Gilbert 1985). All these studies revealed that predators that could be characterized as low- or high-density foragers also exhibited a suite of population characteristics typical of the prey density to which they were adapted. Specifically, "high-density" predators were found to have higher maximal reproduction rates, higher adult mortality rates, and faster and larger population fluctuations, than coexisting "low-density" predators.

THRESHOLDS, BODY SIZE, AND COEXISTENCE

If food is the most important resource regulating seabird populations (Birkhead and Furness 1985), my hypothesis that murres and puffins specialize on different densities of shared prey offers a plausible mechanism to explain their coexistence. If species have different, non-linear responses to resource density, then coexistence of two or more competitors limited by one resource is possible regardless of the degree of overlap in use of that resource (Abrams 1983). Applying the concept of limiting similarity, it has been proposed that there is a limit to how similar resource density thresholds may be before competitive exclusion occurs (Abrams 1983). In this view, the competitive advantage shifts between high- and low-density adapted predators as resource densities fluctuate, and neither species can exclude the other. For murres and puffins, differing thresholds to prey density may be attributable to differing body sizes. Differential thresholds to food density may also be maintained by marked differences in foraging style, but it appears that animals with the same foraging style and body size do not coexist (Brown 1973; Diamond 1975; Davidson 1977a, b).

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HOT SPOTS IN COLD WATER: FEEDING HABITAT SELECTION BY THICK-BILLED MURRES

DAVID K. CAIRNS AND DAVID C. SCHNEIDER

Abstract. We used repeated transects to examine the relationship between habitat variability and the feeding distribution of Thick-billed Murres (*Uria lomvia*) near the Nuvuk Islands, northeastern Hudson Bay. Murres preferred waters between 40 and 120 m in depth, and were rarely sighted in shallow water. Abundance was correlated with degree of bottom relief, and the strength of correlation increased with the frame size at which abundance was measured. Murre abundance varied with phase in the tidal cycle, but did not consistently reach expected peaks at the midpoints of ebb and flood tides. Murre distributions were highly aggregated in space and time, and were positively correlated with densities of shoaling prey. Our data suggest that Thick-billed Murre feeding distributions are influenced by coarse-scale (1–100 km) flow gradients, and that birds track preferred feeding conditions at the scale of several kilometers.

Key Words: Thick-billed Murres; habitat selection; scale of aggregation.

Habitat selection has been investigated in a wide variety of avian species (Cody 1985), yet little is known about the spatial scale of habitat selection in birds (Wiens 1985, 1986). In marine birds, selection of feeding habitat is thought to be influenced by oceanographic processes which act at several spatial scales (Hunt and Schneider 1987). During the breeding season habitat selection is additionally constrained by the maximum foraging radius. Aggregation of feeding seabirds has been demonstrated at scales smaller than the foraging range (Schneider and Duffy 1985), and has been related to coarse-scale (1–100 km) variation in prey abundance (Schneider and Piatt 1986) or variation in physical processes that can alter prey abundance around colonies (Kinder et al. 1983). The spatial predictability of physical processes in coastal waters (Csanady 1982) suggests that seabirds may select feeding habitat relative to coarse-scale physical features that concentrate prey at food-rich "hot spots." The consistency over time of coarse scale habitat selection during the breeding season has not been investigated.

We examined habitat selection by Thick-billed Murres (*Uria lomvia*) within the foraging range of a major colony at the boundary of Hudson Bay and Hudson Strait. Adult murre diet in this area includes both crustaceans and small fish (Gaston and Noble 1985). Because of strong currents in the area, distribution of crustacean prey is likely to be influenced by drift as well as by active swimming. Fish taken by murres may feed on the same crustaceans consumed by murres (e.g., Arctic cod *Boreogadus saida*, Bradstreet and Cross 1982), so fish prey is likely to concentrate in areas of high crustacean density. Based on these considerations and on knowledge of the physical environment (Beals 1968; Griffiths et al. 1981; Prinsenberg 1986a, b), we constructed a set of hypotheses about habitat selection in Thick-billed Murres in relation to physical processes likely to concentrate prey organisms.

Our hypotheses were:

1. Abundance of murres on the water should be consistently higher in relatively shallow areas that have bottom relief, because flow gradients generated by tidal oscillations of water over uneven topography can enhance prey supply to foraging birds (Brown 1980).
2. Murre abundances in the central part of the study area will be greater during ebb tide than flood tide, because the prevailing counter-clockwise circulation in Hudson Bay (Barber 1968) will result in greater advection of nekton from the south during ebb tides than from the north during flood tides.
3. Murre abundance will be greatest during mid-tide, when effects of tide velocities on prey abundance and availability are maximal. Potentially important mechanisms include (i) production of fronts by friction against the sea floor, and (ii) generation of convergent and divergent flow above and in the wake of obstacles to tidal flow. Little relation between murre abundance and tidal stage was expected in the eastern part of the study area, because the deep water there reduces the importance of both mechanisms as concentrators of nekton.
4. The mobility of nektonic prey will produce fine-scale (< 1 km) decoupling of the distribution of murres and their prey.

Since present understanding does not permit clear predictions as to the scales at which physical processes influencing prey supplies might operate, we examined murre distributions on a range of scales from 50 m to about 5 km.

STUDY AREA AND METHODS

OCEANOGRAPHY

This study was conducted in waters near the Nuvuk Islands, N.W.T. (Fig. 1). Bathymetry of the northern

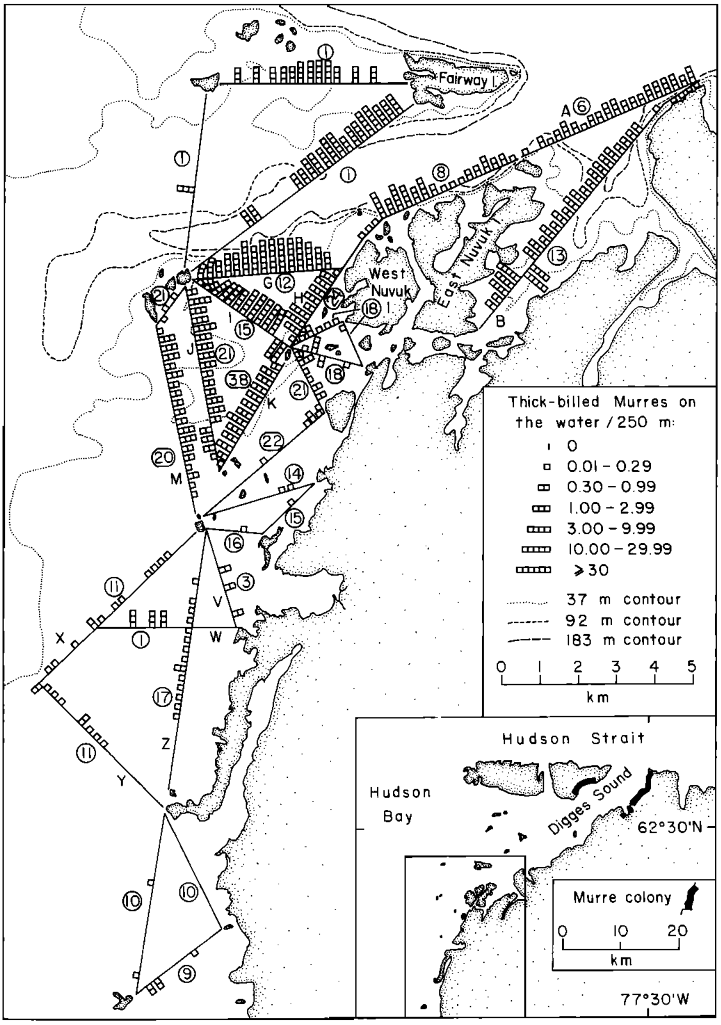

FIGURE 1. Study area, with inset-map showing its position relative to the Thick-billed Murre colonies at Digges Sound. Straight lines are transect routes. Histograms indicate mean sighting frequency per 250 m on a logarithmic scale. Circled numbers indicate how many times each transect was run.

part of the study area is dominated by a deep trench that extends west from Digges Sound and terminates off West Nuvuk Island. This trench, which attains maximum depths of 400 m, has several south-branching arms with depths greater than 50 m. In contrast, the southern part of the study area is a shallow platform with little relief and is generally less than 30 m deep.

Circulation in Hudson Bay-Hudson Strait is generally counter-clockwise (Canadian Hydrographic Service 1983). A west-trending current on the north side of Hudson Strait brings water into Hudson Bay, where it moves counter-clockwise around the bay before exiting via the south side of Hudson Strait. Overall water movement in the study area is northeastward, but flow is strongly influenced by the tidal cycle. The m_2 (principal lunar) tidal current varies from northeast at 60 $cm \cdot sec^{-1}$ to southwest at 60 $cm \cdot sec^{-1}$ (Prinsenberg 1986b:232).

The biota of the study area was described by Gaston et al. (1985) and Morrison and Gaston (1986). The large Thick-billed Murre colonies at Digges Sound, containing some 300,000 pairs, dominate the region's avifauna (Gaston et al. 1985). These birds forage over a large area in western Hudson Strait and northeastern Hudson Bay, apparently feeding up to 160 km from their colonies (Gaston and Smith 1984). Several hundred pairs of Black Guillemots (*Cepphus grylle*) and gulls (*Larus* spp.) also breed in the area.

SURVEY METHODS

The distribution of Thick-billed Murres on the water was recorded from an inflatable boat, which was run

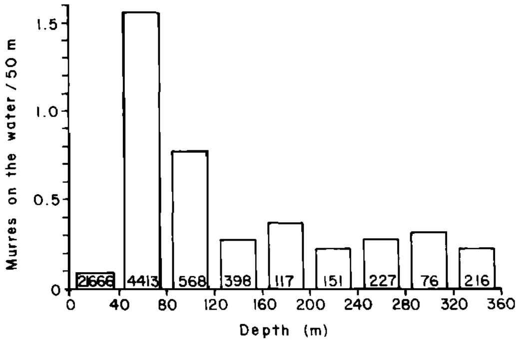

FIGURE 2. Number of murres on the water per 50-m transect segment in relation to water depth. Number of transect segments run in each depth category is given at the base of each column.

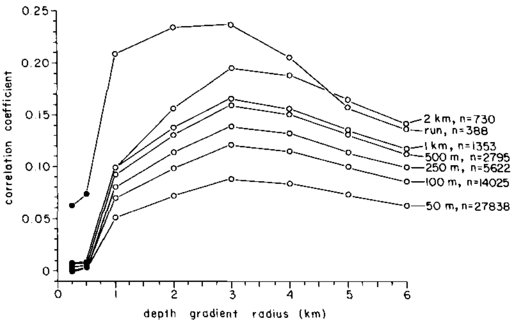

FIGURE 3. Pearson correlation coefficients between murres sighted per segment and depth gradient of that segment. Solid circles are non-significant ($P > 0.05$); open circles are significant ($P < 0.05$). Frame sizes and number of segments run are given at the right of the figure.

at constant throttle along fixed routes (Fig. 1). Murres seen within 125 m on both sides of the boat were noted on a tape recorder, together with the exact sighting time. Surveys were conducted from 22 June to 6 August 1982 and from 21 June to 27 August 1983. Distance of transect routes from the Digges Sound murre colonies ranged from 16 to 48 km. Details of survey operations are given by Cairns (1987). To obtain detailed depth profiles and information on the distribution of potential seabird prey, all routes were surveyed at least once with a continuous-trace echosounder. Density of potential prey recorded on the sounder trace was evaluated on a four-point scale, with 0 indicating no trace and 3 a high-density trace.

Times of bird sightings were converted into distance along the transect by assuming constant boat speed between the known start and end points of the transect. The basic units of analysis were 50 m segments of the transect, for which number of murres on the water and water depth were recorded. We also integrated sighting data into larger "frames" of 100, 250, 500, 1000, and 2000 m by summing sightings within adjacent 50 m segments. Depth for larger frames was the mean of the depths of the 50 m segments that composed them. The largest frame was the "run," which was the full length of each transect. We truncated data at the end of transects for frames between 250 and 2000 m if the last segment was less than one half the frame size; otherwise sightings in the last segment were multiplied by frame length and divided by segment length to correct for their shorter length.

We used depth gradients as an index of bottom relief. These were calculated for each transect segment by subtracting minimum from maximum water depths within circles of 250, 500, 1000, 2000, 3000, 4000, 5000, and 6000 m radius, centered on the midpoint of the segment.

STATISTICAL ANALYSIS

Statistical relations between murre abundance and physical parameters were calculated with the SAS package of programs. The criterion for statistical significance was 5% for all tests. Frequency of Type I error for parametric significance tests was checked by Monte Carlo randomization trials, in which murre counts were assigned to random locations along a transect (see Schneider and Piatt 1986). Twenty-nine of 800 (3.6%) correlations in our Monte Carlo runs showed significance levels greater than 5% according to standard tables, indicating an acceptable estimate of Type I error by parametric methods. Similarly, we tested ANOVA significance levels by randomly reassigning murre sighting frequencies. Six of 100 runs were significant at 5%. This indicates that parametric ANOVA procedures gave acceptable estimates of Type I error.

RESULTS

MURRE DISTRIBUTION IN RELATION TO DEPTH AND DEPTH GRADIENT

We recorded 9680 murres on the water in 1391.9 km of transect, for an overall sighting frequency of 1.74 birds per 250 m. Murre distribution was distinctly heterogeneous, and sighting frequencies differed among areas by several orders of magnitude (Fig. 1). The most favored area was west of West Nuvuk Island, where mean sighting frequencies were generally higher than 10 murres per 250 m. Murres occurred in moderate abundance north and east of the Nuvuk Islands, but were rare in the southern part of the study area.

Murre distribution was closely related to depth (Fig. 2). Water less than 40 m deep was infrequently visited by murres, which accounts for the scarcity of murres in the shallow waters of the southern part of the study area and the near-shore shallows southwest of West Nuvuk Island. Waters between 40 and 120 m deep were most frequently visited. This depth range is typical of the heavily used area west of West Nuvuk Island. Abundance was moderate in waters deeper than 120 m to the north and to the east of the Nuvuk Islands. Sighting frequencies varied little with depth in waters deeper than 120 m.

To examine the relation between murre density and bottom relief, we calculated correlation coefficients between sighting frequencies for each transect segment and the depth gradient for that segment. Correlations were low and non-significant for gradient radii of 250 and 500 m, but rose sharply with larger gradient radii, and peaked at gradients with radii of 3 km (Fig. 3). Correlations diminished with gradient radii larger than 4 km. Correlations increased with increasing size of measurement frame, and were highest when frame size was the run.

Since depth gradients were generally greater in deep water (Fig. 1), we used ANOVAs to test whether murre abundance was related to depth gradient regardless of depth. At small and medium frame sizes (≤ 500 m) depth gradient produced significant improvement in the ANOVA model over that given by depth alone (Table 1). At large frame sizes (particularly 2000 m) depth gradient gave little or no model improvement over depth alone. This suggests that depth gradient, acting independently of depth, may be an important determinant of murre sighting frequencies at small and medium scales.

MURRE DISTRIBUTION IN RELATION TO TIDE

We plotted frequencies of murre sightings on the water against stage of the tidal cycle for the areas west and east of the Nuvuk Islands. Distributions were similar for all frame sizes; Figure 4 plots data for frame size of 250 m. Birds were more abundant west of the Nuvuk Islands during ebb tide than during flood tide. Tidal response was tested with one-way ANOVAs, which compared mean number of birds sighted on the water per 250 m among tide periods grouped as two-hour blocks. Sighting frequencies differed among tidal stages west of the Nuvuk Islands (F = 14.8; df = 6,2049; P = 0.0001), although tidal stage explained only a very small part of the sighting variability ($R^2 = 0.042$). Sighting frequencies did not differ significantly with tidal stage east of the Nuvuk Islands (F = 1.28; df = 6,606; P = 0.26; $R^2 = 0.013$).

MURRE DISTRIBUTION IN RELATION TO PREY SHOALS

Correlations between murre sighting frequencies and density indices of prey shoals were calculated for 65.15 km of transect. Correlations were positive and generally highly significant (Table 2). Prey density was negatively correlated with depth gradient at small depth gradient radii and small frame sizes, and positively correlated at larger gradient radii and small frame sizes (Table 2).

TABLE 1. F-VALUES OF TYPE I ANOVAS RELATING FREQUENCY OF MURRES SIGHTED ON THE WATER (DEPENDENT VARIABLE) TO DEPTH AND DEPTH GRADIENT (SOURCE VARIABLES). THIS PROCEDURE FIRST DETERMINES VARIANCE DUE TO DEPTH AND THEN CALCULATES THE INCREMENTAL IMPROVEMENT IN VARIANCE DUE TO INCLUSION OF GRADIENT. DEPTH IS IN 20 M CATEGORIES

Depth gradient radius (m)	Frame size (m)											
	50		100		250		500		1000		2000	
	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient
250	34.2***	21.8***	37.8***	20.8***	18.1***	12.3**	15.0***	9.2**	7.4***	0.5	6.9***	1.7
500	34.2***	25.2***	37.8***	24.4***	18.1***	13.8**	15.1***	11.1**	7.4***	1.2	6.9***	2.5
1000	34.2***	1.8	37.7***	1.0	18.1***	1.0	15.0***	0.0	7.4***	4.2*	6.9***	0.2
2000	34.2***	19.3***	37.8***	15.1***	18.1***	9.4**	15.0***	3.8*	7.4***	6.9*	6.9***	2.0
3000	34.3***	39.0***	37.8***	34.2***	18.2***	21.4***	15.1***	14.4**	7.5***	10.7**	7.0***	5.6*
4000	34.2***	20.5***	37.8***	17.9***	18.1***	11.1**	15.0***	6.9*	7.4***	4.3*	6.9***	2.1
5000	34.2***	9.1**	37.8***	8.4**	18.1***	5.6*	15.0***	3.7	7.4***	2.3	6.9***	0.8
6000	34.2***	3.4	37.7***	3.4	18.1***	2.6	15.0***	1.6	7.4***	0.9	6.9***	0.3

* $P \leq 0.05$; ** $P \leq 0.005$; *** $P \leq 0.0001$.

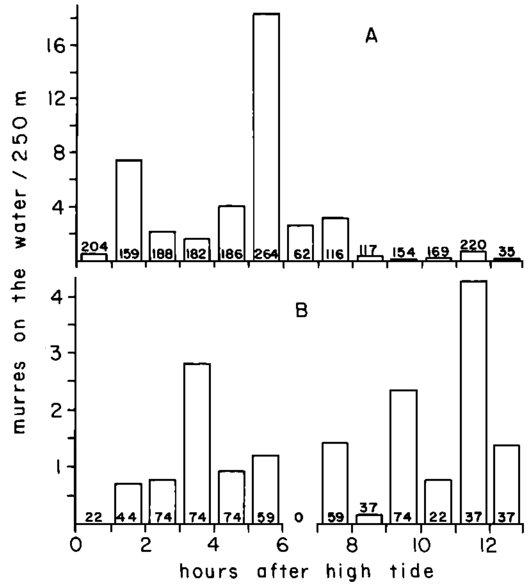

FIGURE 4. Number of murres on the water per 250 m segment in relation to time since high tide. Number of transect segments run in each tide category is given at the base of the columns. (A) shows results for an area of high murre density west of West Nuvuk Island (Routes G, H, I, J, K, and M), and (B) shows data for a medium density area to the east of East Nuvuk Island (Routes A and B). Note differing ordinal scales.

PATTERNS OF AGGREGATION

Murre distributions on the water were aggregated in space and time. For example, mean sighting frequencies along routes G, H, and I were up to two orders of magnitude higher than along routes V through Z (Fig. 1). We used a two-way ANOVA to test whether usage was significantly higher on some routes than on others and whether variation in abundance among routes could be explained by date. Counts from routes G, H, and I, which had the largest sample sizes, were used. Frame size was 500 m and only segments within the preferred depths of 40–120 m were included. Variation among routes was significant (F = 3.39, P = 0.006), but was exceeded in strength by variation among dates (F = 9.95, P = 0.0001). Variation among routes was independent of date (F = 1.21; df = 11,115; P = 0.30).

Variance/mean ratios, which increase with degree of clumping, are used to indicate aggregation intensity of murre sightings in two areas (Fig. 5). The pooled data in this figure reflect the combined effects of temporal and spatial variation, since variance/mean ratios were calculated from different segments and different days. The variance/mean ratio measured over two years in the high density area of Routes G, H, and I increased with frame size, and reached 751 when frame size equaled the run. Aggregation was much weaker in the low density area of Routes V–Z.

In the high density area of Routes G, H, and I, variance/mean ratios were much lower when measured within individual days than over seasons. Figure 5 gives typical examples of variance/mean ratios for two individual days in this area. Maximum ratios were 4.3 and 43.7. Variance/mean ratios on Routes V–Z were lower than those on Routes G, H, and I, probably because of the low numbers of birds sighted. Temporal variation, as expressed by variance/mean ratios of summed daily counts in the G–H–I and V–Z areas, were 7.9 and 0.94 for the two areas, respectively.

TABLE 2. PEARSON CORRELATIONS OF PREY DENSITY, AS INDICATED BY ECHO STRENGTH, WITH FREQUENCY OF MURRES ON THE WATER AND WITH DEPTH GRADIENT

	Frame size (m)					
	50	100	250	500	1000	2000
Frequency of murres on the water	0.35***	0.47***	0.48***	0.49***	0.21	0.54***
Depth gradient						
Depth gradient radius (m)						
250	−0.14***	−0.15**	−0.16*	−0.14	−0.16	−0.15
500	−0.11***	−0.11**	−0.13*	−0.12	−0.15	−0.14
1000	0.04	0.04	0.00	0.02	−0.13	−0.12
2000	0.12***	0.12**	0.09	0.10	−0.09	−0.07
3000	0.12***	0.12**	0.08	0.08	−0.11	−0.11
4000	0.15***	0.15***	0.12*	0.11	−0.03	−0.12
5000	0.07*	0.06	0.04	0.03	−0.08	−0.16
6000	0.07*	0.06	0.04	0.03	−0.03	−0.11

* $P \leq 0.05$; ** $P \leq 0.005$; *** $P \leq 0.0001$.

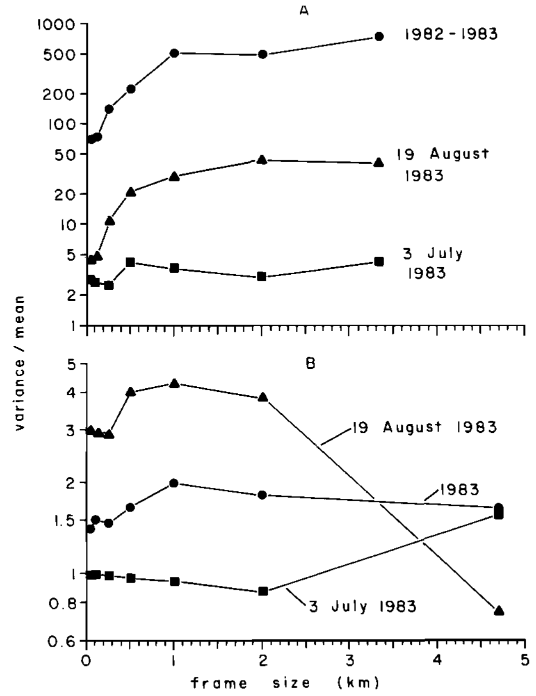

FIGURE 5. Aggregation of murres on the water, as indicated by the variance/mean ratio of birds per segment. Results are given for the pooled data set and for two individual days for an area of high murre density (Routes G, H, and I; panel A) and a low density area (Routes V, W, X, Y, and Z; panel B). The largest frame size in each panel is the run. The ordinal scale is logarithmic.

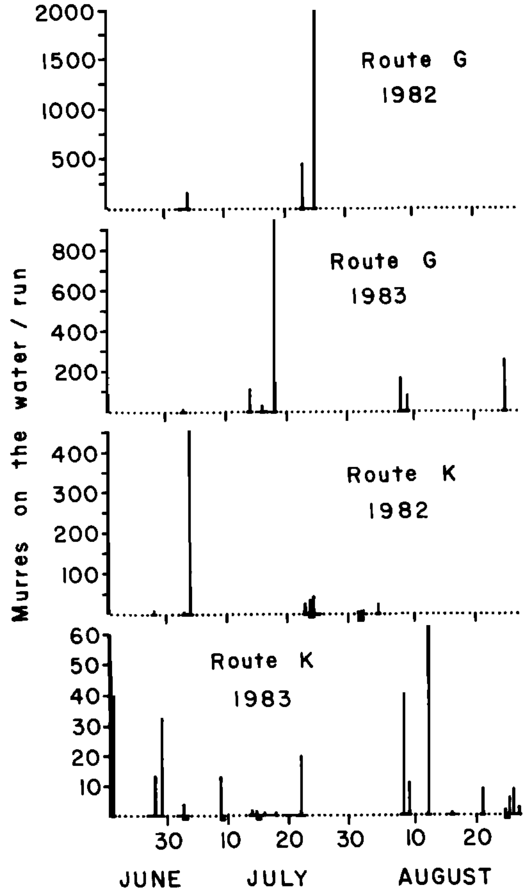

FIGURE 6. Temporal variation in number of murres sighted per run for Routes G and K. Horizontal bars on the abscissa indicate days on which transects were run. Double and triple bars indicate two and three runs on that day, respectively. Note differing ordinal scales.

Figure 6 shows temporal variation in bird numbers in the absence of spatial effects. Sighting frequencies often changed dramatically between survey dates, and variation sometimes exceeded two orders of magnitude. For example, on Route G, nine murres were counted on 17 July 1983, but on the following day 982 murres were recorded.

DISCUSSION

Qualitative predictions of the habitat requirements of marine birds can be derived from considerations of locomotory efficiency, body size, and fasting endurance. Non-diving species require vertically predictable concentrations of prey at the scale of a meter or less near the sea surface. Pursuit-diving species require vertically predictable prey within their diving range, which depends on body size (Piatt and Nettleship 1985). Diving ranges are typically 10 to 100 m. Species with flapping flight move in air at high energetic cost (Flint and Nagy 1984, Birt-Friesen et al. 1989), and hence may depend on small-scale, lateral-prey predictability to avoid extensive searching flight. Constraints on these species are modified by body size, which allows large divers to swim or fly for longer periods without food than small ones (Goudie and Ankney 1986).

Based on this qualitative model, murres require vertically predictable prey concentrations at the scale of tens of meters, and laterally predictable prey at a scale determined by fasting endurance and by the speed and cost of flight. During the breeding season the lateral range is on the order of 100–200 km (Gaston and Nettleship 1981). Lateral predictability in the ocean at this scale is typically low except in shallow (<200 m) water, where bottom topography produces spatially predictable habitat variation at the sea floor, as well as generating spatially predictable flow gradients near the sea surface (Csanady 1982). Within the constraints of locomotory efficiency and starvation resistance determined by body size, murre-sized pursuit-divers must forage either at the sea floor or in relatively shallow water columns in order to find laterally predictable prey concentrations at spatial scales on the order of hundreds of kilometers or less.

Our prediction that murres would aggregate in relatively shallow water with high topographic relief, which generates laterally predictable flow gradients that can increase the concentration or supply of nektonic prey, was confirmed: density was significantly greater in areas of strong topographic gradient than in areas of weak topographic gradient.

Previous characterizations of seabird habitat have emphasized depth (Wynne-Edwards 1935, Ashmole 1971) rather than depth gradient (but see Porter and Sealy 1981). Near the Nuvuk Islands, murre densities were strongly associated with depth, with maximum densities occurring in waters of 40 to 80 m. Within depth categories, murre abundance depended on depth gradient at small and medium scales. Preferential foraging in areas of high bottom relief has been previously found in Barrow Strait, where, in the absence of ice, murres tend to forage along the coastline instead of in the strait itself (Gaston and Nettleship 1981).

Murre abundance varied significantly with tidal stage, and murres were observed more often during ebb than flood tides west of the Nuvuk Islands, as expected. However, the predicted maxima in murre abundance at mid-tide (3 and 9 hours after high tide) was not observed. Instead, maximum counts occurred there just after high water and just before low water. Our prediction that murre abundance would peak at mid-tide was based on the assumption that maximum tidal velocity occurs at this time. Tidal phenomena in northern Hudson Bay are strong and complex (Canadian Hydrographic Service 1983, Prinsenberg 1986a), and present data are inadequate to confirm this assumption or to specify other explanations for the observed relation between bird abundance and tide cycle.

Murre distribution was correlated with acoustic estimates of the relative abundance of nekton. Correlation did not increase with increasing frame size, in contrast with the findings of Schneider and Piatt (1986) for Common Murres (*U. aalge*) and Atlantic Puffins (*Fratercula arctica*). Murre sighting frequencies were more strongly correlated with echo strength of prey schools than they were with depth gradient (Table 2, Fig. 3). Prey densities as shown by echo strength were inconsistently related to depth gradient, indicating that areas of strong bathymetric relief do not always harbor prey. The wide fluctuation of murre abundance, even in areas with high mean density (Fig. 6), may reflect strong temporal variation of prey concentration in these areas.

Spatial variation in the abundance of Thick-billed Murres was scale-dependent. Variability increased from fine (<1 km) to coarse (>1 km) measurement intervals, as has been reported in other seabird species (Schneider and Duffy 1985) including alcids (Briggs 1986, Schneider and Piatt 1986). We attribute this to coarse scale flow gradients, which appear to be a major source of coarse scale patchiness in the abundance of nekton (Olson and Backus 1985, Simard et al. 1986). Griffiths et al. (1981) predicted that local intensification of tides results in tidal fronts in the general vicinity of the Nuvuk Islands, but the scale of their analysis does not permit prediction of suitable habitat at the scale of murre censusing.

Previous transect studies around colonies have demonstrated coarse scale variability within the foraging range, but transects have not been traversed frequently enough to determine the consistency of aggregation. Repeated transects around the Nuvuk Islands showed that the abundance of murres on the water was localized, and that spatial variability was independent of temporal variability.

Coarse-scale habitat selection has important implications for the analysis and interpretation of interactions between seabirds and their prey. If spatial variation in consumption exceeds spatial variation in prey supply within the foraging range of a seabird colony, then the impact of seabird predators on local prey will be greater than that predicted from larger-scale calculations, which are typically based on a maximum or average foraging radius (Furness 1978, 1982). Calculations of prey removal at the scale of the average or maximum foraging radius may underestimate local impact on prey, even though such calculations may overestimate impact on fish stocks at a larger scale (Bourne 1983).

Models of local impact of seabirds on prey stocks around colonies must also consider the effects of larger scale lateral advection, which can act to renew local prey supplies. Assuming a foraging range of 160 km, typical advection rates can offset prey mortality estimated from respiratory requirements (Appendix 1). The importance of advective import is likely greatest in colonies that depend heavily on planktonic crustaceans for food, as fish are typically able to control their position in the water. In the Nuvuk area, Thick-billed Murres prey on both fish and crustaceans (Gaston and Noble 1985). The simple advective model shown in Appendix 1 also assumes that advectively-delivered food supplies are not previously depleted by predation from other seabird colonies. This assumption is valid for murres breeding at Digges Sound, because coastlines along eastern Hudson Bay (the advective source) lack suitable breeding habitat for murres. In some seabird communities advection may prove to be more important than production in determining impact of birds on food supplies at the scale of habitat selection, which our study suggests is on the order of 1–10 km.

Our results support earlier conclusions that breeding Thick-billed Murres favor specific "hot spots" (Bradstreet 1979). However, the strong short-term variability in bird abundance (Fig. 6) suggests that murres do not forage solely by prior knowledge of favored sites. Information exchange among foragers (Ward and Zahavi 1973, Gaston and Nettleship 1981) may also aid murres in choosing sites that are rich in food at a particular time.

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APPENDIX I.

Impact of Central Place Foragers on Passively Transported Prey

Consider a seabird colony located on a straight coastline. Birds forage in a semi-circle of radius r (km) around the colony. Advective (current-induced) import (i) is defined as the mass of prey (m) arriving per day within foraging radius r (km) of a colony $\left(\frac{\Delta m}{\Delta t} = g\cdot day^{-1}\right)$ divided by the mass (M = g) within the foraging radius.

$$i = \frac{1}{M}\cdot\frac{\Delta m}{\Delta t}, \tag{1}$$

$$\frac{\Delta m}{\Delta t} = Bvr, \tag{2}$$

where B = prey density ($g\cdot km^{-2}$), v = net advection ($km\cdot day^{-1}$), M = BA, where A is area within the foraging radius (km^2).

Then:

$$i = \frac{Bvr}{BA} \tag{3}$$

and hence

$$i = \frac{2v}{\pi r}. \tag{4}$$

Avian consumption, in dimensionally equivalent units, is:

$$a = \frac{F}{T_b} \tag{5}$$

where F = proportion of prey lost $\left(\frac{\Delta m}{M}\right)$ during the breeding season. T_b is length of the breeding season (days).

Advective import equals consumption when:

$$a = i, \tag{6a}$$

$$\frac{F}{T_b} = \frac{2v}{\pi r} \tag{6b}$$

$$v = \frac{\pi r F}{2T_b} \tag{6c}$$

If T_b = 55 days and r = 160 km, and using Furness' (1982) value of F = 30%, then v = 1.37 $km\cdot day^{-1}$ = 0.016 $m\cdot s^{-1}$. The reported advective rate in the vicinity of the Nuvuk Islands is 0.07 $m\cdot s^{-1}$ (Prinsenberg 1986b), which suggests that advective import could supply food needs even if F is much lower than 30%.

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SEABIRD DIET AT A FRONT NEAR THE PRIBILOF ISLANDS, ALASKA

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Abstract. Large concentrations of murres (*Uria aalge* and *U. lomvia*) have been reported on the water at sites where bathymetry generates flow gradients near breeding colonies in North America. One such site was located in August 1982, by following streams of murres flying away from the colony on St. George Island, Alaska. We found a well-defined tidal front where murres were diving and feeding on euphausiids on the mixed (landward) side of the front, an area of subsurface convergence. Surface-foraging birds (Black-legged Kittiwakes *Rissa tridactyla* and Red Phalaropes *Phalaropus fulicaria*) were feeding on euphausiids at the surface convergence seaward of the murre aggregation. The feeding success of surface foragers was attributed to surface convergence acting on weakly swimming (injured) euphausiids; that of murres to subsurface convergence acting on negatively phototactic euphausiids. Successful foraging at spatially predictable locations around colonies has important implications for population monitoring, impact assessment, and theoretical treatments of the foraging distribution of colonial seabirds.

Key Words: Bering Sea; marine birds; diet; fronts.

The hypothesis that bathymetrically-induced flow gradients increase the availability of prey to marine birds in shelf ecosystems was proposed to explain the patchiness of diving birds along transects away from colonies in the southeastern Bering Sea (Schneider et al. 1986). Several lines of evidence (summarized by Schneider et al. 1990) suggest that this hypothesis can be extended to colonially nesting alcids foraging around their colonies. There have been no detailed studies of the diets or feeding success of alcids in areas of flow gradient generated by bathymetry. Here we report the prey number, prey condition, and stomach volume of Common and Thick-billed murres (*Uria aalge* and *U. lomvia*) at such a site east of St. George Island, in the southeastern Bering Sea. We also report the prey of surface-foraging birds feeding at the same site.

LOCATION AND METHODS

The number of seabirds on St. George Island (Fig. 1) has been estimated at 2.6×10^6 birds, including 1.5×10^6 Thick-billed Murres (Hickey and Craighead 1977). The number of seabirds on St. Paul Island, 63 km to the northeast, has been estimated at 2.5×10^5 birds, including 1.1×10^5 Thick-billed Murres and 3.9×10^4 Common Murres (Hickey and Craighead 1977). The site that we investigated was located at 56°38.22′N, 169°22.32′W, which is 6 km east of Tolstoi Point, St. George Island. Surveys in 1977 and 1978 (Kinder et al. 1983) showed that during the summer a front associated with the 70 km isobath separates vertically homogeneous water near the island from stratified water away from the island. We attempted to relocate the front described by Kinder et al. (1983) by steaming outward from St. George on 5 August 1982 until we encountered water depths of 70 m. A series of conductivity, temperature, and depth (CTD) casts showed that the water was vertically homogeneous. During the casts we noticed streams of murres flying by the ship, so rather than searching for a front along our radial transect from the island, we simply followed the murres. Over the next hour we steamed northward through a heavy fog (visibility less than 0.5 km), while murres continued to overtake the ship from the stern and then disappear into the fog ahead. Eventually we came to a location where murres were abundant on the water as well as in the air, so we stopped and carried out a series of CTD casts normal to the prevailing bathymetry at this location. The casts showed a well-defined front, with murres confined almost entirely to the island (mixed) side. Murre abundance on the water was on the order of 10–50 birds within a 10 m radius of the bow, as we slowed to a stop over a distance of approximately 1 km.

We then carried out a more detailed CTD profile across the front. Depth casts were made at 0.5 km intervals. Surface measurements of chlorophyll and phaeopigments (a measure of phytodetritus) were obtained at each CTD station. As the fog lifted we visited the front in a skiff to collect birds. No birds were present on the stratified side of the front, but they were abundant on the mixed side of the front, where six Thick-billed Murres were collected in less than an hour.

We then returned to the ship and used the ship's depth-sounder to obtain a profile of zooplankton and nekton abundance across the front. The depth-sounder showed a dark trace at and below the depth of the thermocline identified from CTD casts. The trace was 15–20 m below the surface on the stratified side of the front, rising toward the surface on the unstratified side of the front. We made several tows with a bongo net to identify the source of the dark trace, but only a few euphausiids (primarily *Thysanoessa raschii*) were captured. The mesh size was less than 1 mm, so the poor catch may have been due to net avoidance by euphausiids (Nemoto 1983).

While making bongo tows we noticed that surface-feeding birds (Black-legged Kittiwakes *Rissa tridactyla* and Red Phalaropes *Phalaropus fulicaria*) were increasing at the slick marking the front. We revisited the front in the skiff to collect kittiwakes and phala-

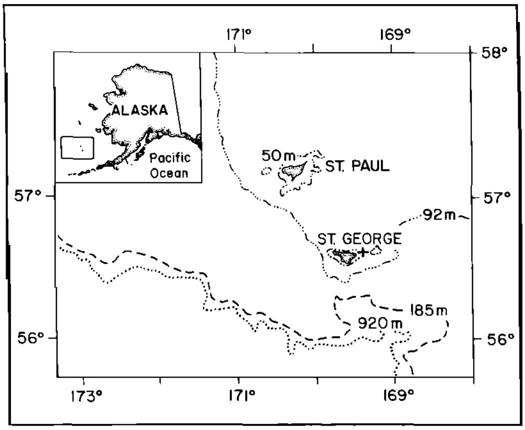

FIGURE 1. Location of bathymetrically fixed front (shown as +) east of St. George Island, southeastern Bering Sea.

ropes feeding along the surface slick. This collection was 4.2 km SSE of the earlier collection. Drift over the 6-hr period since the previous collection was 0.2 m/s. During this second trip we collected three more murres landward of the front. As before, we could not find murres at the front or seaward, for comparison with murres collected on the landward side of the front.

All birds were tagged in the skiff with a unique number. Approximately 20 ml of 95% ethanol was injected down the throat of each bird. The digestive tract of each bird was removed in the ship's laboratory within 1 hr of collection. Each tract was gently slit to allow entry of preservative, and placed in 95% alcohol. The sex, reproductive condition, and approximate mass of each bird were noted and recorded. Masses were approximate because birds had been injected with ethanol, and gravimetric measurements are unreliable on a rolling ship. Carcasses were frozen, and eventually deposited at the Los Angeles County Museum.

Crop, stomach, and gizzard contents were later identified using standard keys and a set of reference specimens. The volume of material in the stomach was measured by water displacement. The length of intact prey was measured to the nearest mm. Seabirds digest the soft parts of prey rapidly, so stomach volume and prey condition (intact or not) were used as indices of recent foraging success.

RESULTS

The front located east of Tolstoi Point in 1982 was structurally similar to the fronts described by Kinder et al. (1983). Upward deflection of the thermocline was associated with a slight change in bottom contour at the 75 m isobath (Fig. 2). Notable physical features included a surface slick at the front (Station 65, Fig. 2), thickening of the surface layer at the slick (Station 65), and upward deflection of the thermocline landward of the slick (Station 66). Gelatinous zooplankton, seaweed, and floating debris were observed at this slick. Highest chlorophyll concentrations occurred slightly seaward of the slick (Fig. 2). Chlorophyll concentrations were lower on the stratified than on the mixed side, as reported in transects across similar fronts in Europe (Le Fevre 1986). The structure of the front was consistent with Simpson's (1981) conceptual model of circulation, which is that of convergent flow marked by a surface slick running parallel to divergent flow on the landward side of the surface slick (Fig. 3). We observed considerable meandering of the front, which is also characteristic of the tidally-generated convergent fronts described by Simpson (1981).

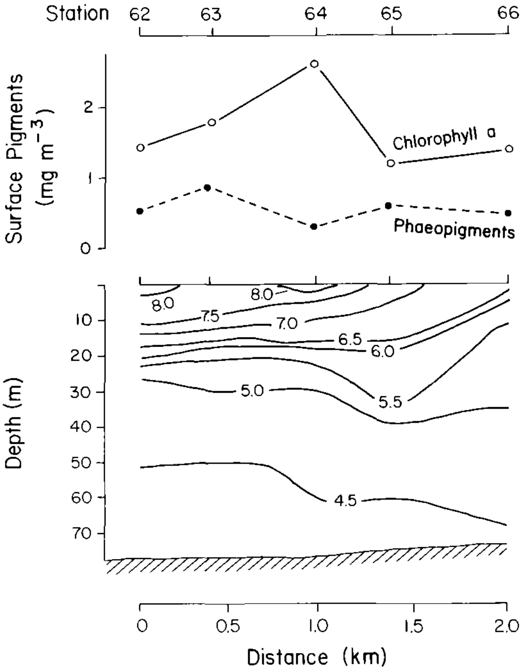

FIGURE 2. Surface chlorophyll distribution in relation to the temperature depth profile across the Tolstoi Point front.

A secondary slick occurred at Station 63, seaward of the main slick (Fig. 2). Very little debris was observed at this slick, and no birds were observed feeding there. Detailed temperature profiles (Fig. 4) showed multiple thermoclines at this minor slick (Station 63), at the major slick (Station 65), but not between the slicks (Station 64). Comparison of the horizontal profile (Fig. 2) with the detailed vertical profiles (Fig. 4) suggests that an eddy may have been present on the seaward side of the front. Other explanations for lateral variation in the depth of the thermocline (e.g., passage of internal waves) cannot be ruled

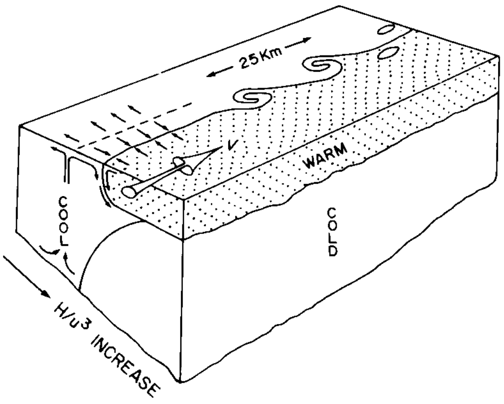

FIGURE 3. Summary of frontal structure and circulation due to bathymetrically induced gradient in rate of tidal stirring. Redrawn from Simpson (1981). Dotted lines show subsurface convergence required to maintain upwelling. The ratio of water depth to the cube of tidal stream velocity (H/u^3) measures the relative importance of buoyant and mixing energy.

out. A fully upwelled thermocline was observed landward of the front (Station 66).

Thick-billed Murres collected landward of the front had been eating euphausiids, primarily *T. raschii* (Table 1). Nearly all birds had foraged successfully, as indicated by number of intact prey and number of birds with full stomachs. Intact euphausiids ranged from 19 to 24 mm, rostrum to tail. The volume of material in the stomachs of nine murres averaged 8.5 ml, ranging from 0.3 to 21.5 ml.

Kittiwakes and phalaropes collected at the front had also been feeding actively on euphausiids. The sizes taken by Black-legged Kittiwakes and by murres were similar (Table 1). Many of the euphausiids found in the proventriculus of these birds were missing their tails, so total length could not be measured. In the field, euphausiids missing either heads or tails floated or swam weakly in the slick at the surface. This, and the fact that euphausiids are generally unavailable to surface-foraging birds during the day, suggests that euphausiids were injured by murres beneath the surface, then carried toward the slick and concentrated by the frontal circulation (Fig. 3), where they were fed on by kittiwakes and phalaropes.

DISCUSSION

Our results show that both diving and surface-foraging birds fed on the same prey at a front located east of the Pribilof Islands. However, surface-foraging birds fed along the surface convergence, while subsurface-foraging murres were observed on the landward side of the front. These observations were interpreted in light of Simpson's (1981) model of circulation at tidal fronts (Fig. 3). The feeding success of kittiwakes and phalaropes at the surface slick was attributed to convergent flow acting on dead or weakly swimming euphausiids at the sea surface. The mechanism responsible for the feeding success of murres on the landward (mixed) side of the front is less clear. We speculate that euphausiids, which are normally negatively phototactic during the day, were being concentrated by subsurface convergence beneath a surface divergence (upwelling) in a manner similar to that proposed by Simard et al. (1986) at a coastal upwelling in the Gulf of St. Lawrence.

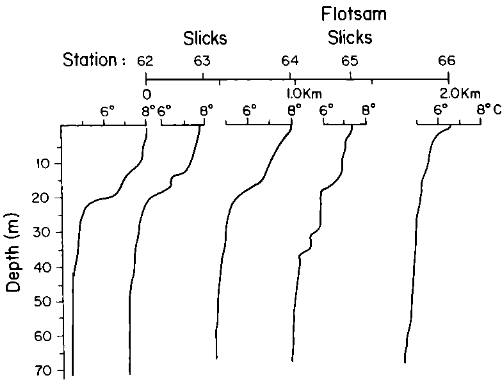

FIGURE 4. Temperature-depth profiles along transect across the Tolstoi Point front. Stations are the same as in Figure 2.

If our interpretation is correct, then the success of surface-foraging kittiwakes and phalaropes was due to a complex interaction of physical processes (surface convergence immediately adjacent to subsurface convergence) and biological processes (negative phototaxis of euphausiids unless injured). Similarly, at St. Matthew Island, injury of euphausiids by murres foraging beneath the surface increased the foraging success of surface feeding kittiwakes (Hunt et al. 1988). At St. Matthew, surface-foraging by kittiwakes occurred immediately above subsurface-foraging murres, whereas at St. George, surface-foragers were displaced laterally relative to subsurface-foragers.

During the field work and up until the work by Simard et al. (1986) on euphausiids we considered a series of alternative interpretations. These deserve brief comment.

1. Euphausiids avoid warm water, remaining just below the thermocline, and hence were closer to the surface on the landward side than the seaward side of the front. However, lack of diving birds immediately adjacent to the surface

TABLE 1. STOMACH CONTENTS OF BIRDS COLLECTED IN THE FRONTAL ZONE OFF TOLSTOI POINT AT 11:00 HR (20:00 HR GMT) AND 17:00 HR ON 5 AUGUST 1982. F = FEMALE, M = MALE. N = NUMBER. V = VOLUME (ML). B = BEAK, O = OTOLITH, T = TRACE. BS = *BOREOGADUS SAIDA*. MYCT = MYCTOPHID

	11:00															
	Thysanoessa raschii													Unidentified euphausiid		
	Length (mm)															
Predator	27	26	25	24	23	22	21	20	19	18	17	N	V	N	V	Other
Uria lomvia																
M	1	1	2	2	3	4	4	1			1	257	11.0	134	10.5	BS (O) SQUID (B)
M				1		2	1	1				28	0.9	8+	3.5	BS (O)
M					1			1				51	1.8	9	4.9	BS (O) SQUID (B)
M		1						1				30	0.8	27	6.0	BS (O)
F												4	0.1	4	1.8	BS (O) SQUID (O) MEDUSAE (T)
F		1				1	1	2				78	2.9	65	7.8	BS (O)

	17:00																	
	T. raschii													Unidentified euphausiid		*Euphausia pacifica*		
	Length (mm)																	
	27	26	25	24	23	22	21	20	19	18	17	N	V	N	V	N	V	Other
Rissa tridactyla																		
M				1	1	2	1	1	2			16	0.8	10	0.9	4	0.4	BS (O)
M										1		3	0.1	3	0.4	1	T	MYCT (O)
F					1		1	1	1			41	2.2	112	8.3	3	T	
Uria lomvia																		
M	1		1				1	1	1			113	5.7	417	14.7	3	0.3	
Phalaropus fulicaria																		
M												<1	0.2					
M												5	3.0					
M									1			8	2.4					
F												?	0.2	?	0.2			
Uria aalge																		
M												32	1.0	72	5.0			
F													0.3					

convergence suggests that proximity of prey to the surface was not responsible for the foraging success of birds at this site.

2. Water clarity was reduced on the seaward side of the front, increasing the availability of euphausiids to murres foraging visually beneath the sea surface. Water clarity at the sea surface appeared to be greater on either side of the front than at the front. If water clarity were important, then murres should have been less abundant at the front. Instead, they attained a local maximum on the landward side. Looking landward from the front, murre density first increased with distance from the front, then decreased.

3. Euphausiids aggregate in response to increased primary production. This explanation may be correct at the scale of several kilometers, as euphausiids and newly produced chlorophyll were abundant in the same area (frontal zone of Federov 1986). At a smaller scale, however, chlorophyll occurred in highest concentration on the stratified side of the front (as expected), whereas foraging murres and targets recorded on the depth sounder occurred in mixed water landward of the front.

4. Spawning behavior of euphausiids increased their availability at the sea surface. We did not observe swarms of euphausiids at the surface during the two collecting trips in the skiff.

5. Pursuit divers concentrate euphausiids near the surface, or delay the ascent of euphausiids from the surface, as has been hypothesized for fish (Hoffman et al. 1981, Grover and Olla 1983). It is possible that behavioral responses of euphausiids to murres did contribute to successful feeding by surface-foragers. This mechanism does not account for the continued association of a laterally structured foraging aggregation with a front over more than 6 hr.

The number of intact prey found in Black-legged Kittwake and murre stomachs at this site was, in our experience, high for birds collected at sea. We attempted to determine whether quantity of prey was lower away from the front, but were unable to find birds on the water there. We tabulated the number of Black-legged Kittiwakes and murres with intact prey during the same cruise. Birds were collected on 26–29 July, 30–31 July, and 2–3 August in Bristol Bay, at latitudes ranging from 54°50.3′ to 57°47.3′N, between 163°10.1′ and 167°55.3′W. Of 14 kittiwakes and one murre, only one kittiwake had intact prey in the digestive tract. Comparison with Table 1 indicates the recent foraging success of birds collected near the Pribilof front.

These data, plus our experience in observing and collecting marine birds at sea, indicate that energy gain occurs at a limited number of sites around colonies, some of which are the result of physical structuring of the fluid environment of prey by topography. This concept is based on physical theory combined with observations of prey and seabird aggregations around alcid colonies in the Bering Sea (Kinder et al. 1983, Hunt and Harrison 1990) and in the southern Labrador Current (Schneider and Piatt 1986, Schneider et al. 1990). In shelf ecosystems, flow gradients depend on topography, because upward and downward mixing act through significant fractions of the water column (Csanady 1982). These flow gradients can increase prey aggregation through a variety of mechanisms (e.g., Simard et al. 1986). Empirical support for this concept comes from the observation that feeding aggregations are observed in areas of strong flow gradient (e.g., Brown 1980), that seabird patchiness depends on the strength of salinity gradients generated by flow gradients at topographic features (Schneider et al. 1987), and that bathymetric charts have been used to locate an active feeding site (Schneider et al. 1990).

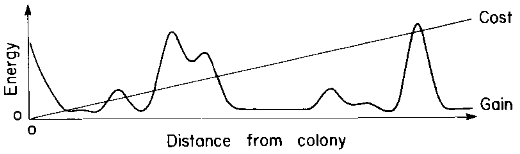

FIGURE 5. Conceptual model of foraging costs and bathymetrically fixed food concentrations along a radius running outward from a breeding colony.

Spatially predictable variation in prey supply has a number of implications. One is that the difference between energy gain and foraging costs depends on location (Fig. 5), rather than simply on distance from a colony. The recognition of spatially predictable sites of prey concentration due to bathymetric influence shows that models of foraging behavior need to include oceanographic heterogeneity in order to be realistic. Furthermore, learning where to forage may occur as birds mature and increase their foraging efficiency (Orians 1969, Porter and Sealy 1982). Another implication of spatially predictable feeding sites is that the probability of contact with a point source contaminant (e.g., oil spills) will be reduced unless contamination occurs at feeding sites. Knowledge of regularly used feeding sites near a colony will allow more effective monitoring in the event of a release of contaminants (Ford et al. 1982).

Our observations around the Pribilof Islands indicate that physical processes may contribute to the structure and function of mixed-species feeding flocks. Other investigators (Sealy 1973, Hoffman et al. 1981, Porter and Sealy 1982, Grover and Olla 1983, Chilton and Sealy 1987) have described ways that the foraging behavior of individual species can affect the formation and structure of feeding aggregations. Further study of predator behavior in relation to prey behavior and physical processes can increase our understanding of the formation, composition, and evolution of mixed species feeding flocks.

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WINTER OBSERVATIONS OF BLACK GUILLEMOTS IN HUDSON BAY AND DAVIS STRAIT

ANTHONY J. GASTON AND PETER L. MCLAREN

Abstract. Previous accounts of the habitat of Black Guillemots (*Cepphus grylle*) demonstrated that species is common in coastal waters and at land-fast ice edges throughout the year. On aerial surveys over Hudson Bay in February 1981 and Davis Strait in March 1981 we found them common in winter among offshore pack ice, where there was some open water. We suggest that offshore pack ice is an important habitat for Black Guillemots wintering in the arctic.

Key Words: Black Guillemot; *Cepphus grylle*; Arctic; ice.

The Black Guillemot (*Cepphus grylle*) breeds on rocky coasts throughout eastern Canada, from Ellesmere Island to Nova Scotia, and over most of the Canadian arctic archipelago, Hudson Bay, Foxe Basin and Hudson Strait (Brown et al. 1975, Nettleship and Evans 1985). It is considered to be characteristic of shallow, inshore waters, where it feeds mainly on benthic fishes (Bradstreet and Brown 1985, Brown 1985, Cramp 1985, Nol and Gaskin 1987). Cairns (1987) showed that, during the breeding season, bottom-feeding Black Guillemots in north-east Hudson Bay fed almost exclusively in water less than 50 m deep. They are also known to feed along the margins of land-fast ice in arctic waters in spring and summer, including those formed over water more than 50 m deep (Bradstreet 1979).

During winter, Black Guillemots retreat from those parts of their breeding range where the sea freezes over completely, but if open water is present, some may remain as far north as 79°N (Renaud and Bradstreet 1980). In Hudson Bay and Foxe Basin the species is seen regularly along land-fast ice-edges throughout the winter (Sutton 1932, Ellis and Evans 1960, AJG pers. obs.). Aerial surveys carried out in May in the High Arctic demonstrated that Black Guillemots occurred in large numbers among broken pack ice far offshore (McLaren 1982). Similarly, Black Guillemots were seen frequently among mobile pack ice in the Chukchi Sea in September and October (Watson and Divoky 1972, Divoky 1987). However, it was not clear in either case whether these birds were merely passing through en route to their breeding areas, or whether pack ice constituted the preferred habitat at that season for a segment of the population.

To address this question we present data from an aerial survey carried out over Hudson Bay on 9 February 1981 and on a series of surveys over Davis Strait during 15–31 March 1981. On both surveys Black Guillemots were widespread in offshore waters, where the pack ice was mobile. Our observations, coupled with those of previous surveys over arctic waters in late winter (Renaud and Bradstreet 1980), provide evidence that Black Guillemots occupy a wider range of habitats in winter than was previously thought.

METHODS

HUDSON BAY

This survey was made by AJG from a Canadian Ice Survey Lockheed Electra. The survey route is shown in Figure 1. Counts of birds were made from 10:30 to 17:00 hr EST. The average flight speed was 300 km/h. Altitude was about 1500 m for most of the flight, descending periodically to about 300 m. A bubble window on the side of the aircraft allowed the observer to look vertically downwards. At altitudes above 500 m the sea was scanned through 8 × binoculars; using these, Black Guillemots, in their white winter plumage, were easy to pick out on the water. Observations were recorded on cassette. Scanning with binoculars was done for 1–2 min at a time, alternating with a minute of rest, to avoid fatigue. All open water areas within a strip estimated at 0.5 km wide were scanned. Ice conditions were recorded continuously by the ice recording team, using visual estimates and radar.

DAVIS STRAIT

Aerial surveys for marine mammals were performed by LGL Ltd. between 15 and 31 March 1981 and covered the whole of Davis Strait north of 65°N (Fig. 2). A de Havilland Twin-Otter aircraft was used, with two observers counting continuously, one on each side. Procedures were as described by McLaren (1982), except that the average ground speed was 222 km/h, the altitude was 150 m and observers scanned 800 m on each side of the flight path. Numbers of guillemots were recorded by two minute periods, corresponding to an area of about 12 km^2 scanned. For both surveys water depths at locations where Black Guillemots were recorded were determined by comparison with the appropriate hydrographic charts.

RESULTS

HUDSON BAY

Weather conditions were perfect throughout the survey, with clear skies, and little or no wind at sea level, judged from a lack of ripples on the water. Thin fog over some open water areas reduced visibility periodically, but never for more

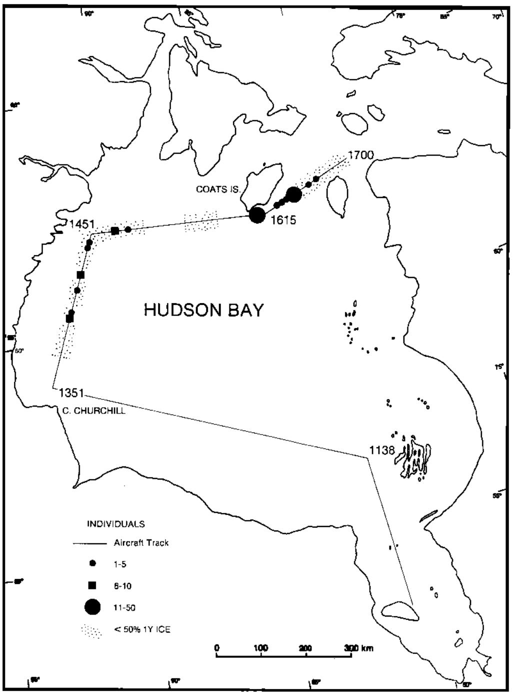

FIGURE 1. Map of survey route on 9 February 1981, showing the position of Black Guillemot sightings and the type of ice encountered.

than a minute. After 16:00 hr light conditions were poor, the sun being very low, and the detectability of the birds was probably much reduced.

Ice cover was almost 100%, except for occasional leads up to about 200 m in width. The proportion of young ice (mainly less than 30 cm thick), ranged from 30% to 100%. The rest was thicker, first-year ice. During the period up to 13:50 hr, cover was entirely first-year ice, but after 13:50 it was much more variable. No solid, land fast ice was encountered after 13:50, and none of the birds seen was associated with landfast ice edges.

Black Guillemots were seen from 14:10 hr onwards and a total of 61 was counted, including one group of 21 on a large expanse of open water about 200 × 800 m, south of Coats Island. Most other sightings were of one or two birds, often on leads estimated to be less than 5 m in width. Most birds were seen either in the western part of Hudson Bay, in an area of young ice with numerous areas of open water, or south and east of Coats Island (Fig. 1). Water depths in areas where Black Guillemots were seen were never less than 80 m.

Allowing for breaks, watching lasted for about 2 h between 13:50 and 17:00 hr, and hence a maximum area roughly 300 km^2 was scanned. The total area of Hudson Bay north of Cape Churchill (approximately the area crossed after 13:50 hr) normally covered by mobile pack ice during the winter is about 250,000 km^2 (Markham 1986). Hence, even in the unlikely event that all the Black Guillemots passing through the field of the glasses were detected, there must have been at least some thousands wintering in the mobile pack ice of Hudson Bay.

TABLE 1. DENSITIES OF BLACK GUILLEMOTS RECORDED DURING AERIAL SURVEYS OF NORTHERN DAVIS STRAIT IN RELATION TO ICE COVER

Ice cover (%)	No. of transect segments	Proportion with guillemots (%)	Density birds km^{-2}
0–25	139	5	0.103
26–50	51	6	0.029
51–75	87	10	0.044
76–90	317	15	0.038
91–100	896	21	0.076

DAVIS STRAIT

Black Guillemots were widespread throughout northern Davis Strait during 15–31 March, with 1101 being seen on transect and a further 210 off-transect during 48 h of flying, giving a mean density estimate of 0.068 birds/km^2. Densities were higher on the west side of the strait than on the east side (Fig. 2), and were probably related to ice conditions. Maximum bird densities, away from open water, were recorded where ice cover exceeded 90% (Table 1). There was a significant positive correlation between ice cover and the proportion of two-minute periods during which guillemots were recorded (Spearman rank correlation, $r_s = 1.0$, $P = 0.01$).

All Black Guillemots seen in areas of 0–25% ice cover were recorded on seven transect segments flown within 50 km of the Greenland coast south of 68°N. No ice was present in that area. Most of the water covered during these transects was reddish in color, perhaps indicating the presence of pigmented plankton. This was the only area where guillemots were seen in open water. As in Hudson Bay, virtually all observations of guillemots were made in water more than 80 m deep.

Similar surveys were flown over the western portion of Davis Strait south of 65°N between 25 March and 5 April 1981, and over the Labrador Sea up to 170 km offshore between 1 and 9 April. In southern Davis Strait densities of Black Guillemots were lower than in the northern sector, averaging 0.016 birds/km^2 (128 birds seen). Only 17 birds were seen in the Labrador Sea, all in areas with more than 50% ice cover.

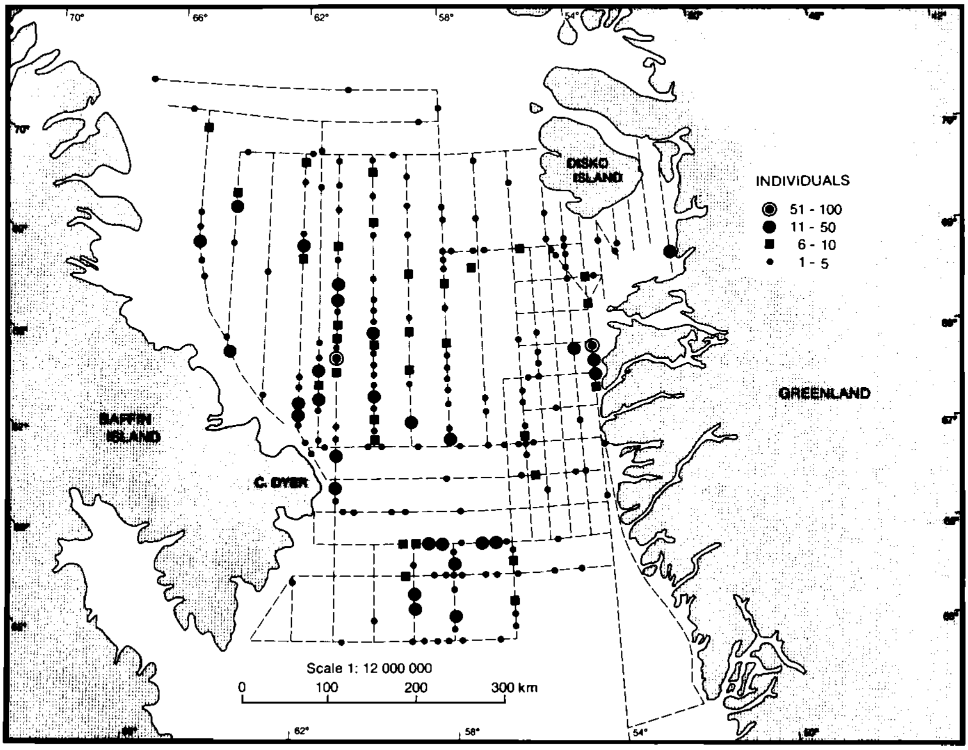

FIGURE 2. Map of surveys during 15–31 March 1981, showing the position of 2-min periods when Black Guillemots were recorded.

In both areas comparison of sightings with bathymetric charts showed that the majority of birds seen were in water more than 100 m deep.

The total area of Davis Strait between 65° and 70°N is about 230,000/km^2, yielding an estimate of 16,000 guillemots in that area during the surveys. As in the case of the Hudson Bay estimate, this is a minimum figure, because not all birds present are seen (McLaren 1982, Gaston and Smith 1984). We think that the true figure was probably in the low tens of thousands.

DISCUSSION

The total population of Black Guillemots in Hudson Bay is unknown, although Hudson Bay, Hudson Strait and Foxe Basin have been estimated to hold 13,000–26,000 breeding birds (Nettleship and Evans 1985). However, population densities are higher in Hudson Strait than in Hudson Bay (Gaston 1982, Morrison and Gaston 1986). If we assume that no Black Guillemots move into Hudson Bay during the winter, it follows that in February 1981 a considerable proportion of the local population was wintering offshore amid mobile pack ice.

Black Guillemots wintering in Baffin Bay and Davis Strait, on the other hand, may include many from the large high arctic colonies in Barrow Strait and Jones Sound (Renaud and Bradstreet 1980). Nettleship and Evans (1985) estimated the population of that area at 55,000 breeding pairs. Even if we assume that most of the Black Guillemots breeding in the eastern High Arctic and the northern part of West Greenland winter in Baffin Bay and Davis Strait, the several tens of thousands of guillemots estimated to be present offshore in late March represents a significant fraction of the entire wintering population.

On the basis of aerial surveys of the North Water polynya of Baffin Bay in March and April, Renaud and Bradstreet (1980) estimated 3900 Black Guillemots in mobile pack ice away from fast ice edges and in water more than 100 m deep. Similar numbers were estimated to be present at land-fast ice edges in the same area. A survey of western Hudson Strait in April 1982 also revealed some Black Guillemots in deep water, more than 10 km from shore, amid mobile pack (0.08/km^2, AJG pers. obs.). Because winter ice conditions throughout the eastern arctic persist until at least early May (Smith and Rigby 1981), we think that distributions observed in February to April are representative of those existing throughout the winter.

In summary, observations from aerial surveys suggest that many Black Guillemots that winter in arctic waters probably do so among mobile pack ice, in water sufficiently deep to prevent them from foraging on the bottom. As shallow coastal waters in the arctic are mainly covered in solid, land-fast ice in winter, this switch must result in changes in foraging behavior and diet. It also enables them to remain in the area, and thus provides them with an alternative to migration, the strategy preferred by most birds that breed in the arctic.

On both our surveys we found only small numbers of Black Guillemots away from pack ice, and in Davis Strait the frequency of sightings was positively correlated with pack ice cover. Although the cause of this association is unknown (e.g., the distribution of prey organisms, the influence of ice on sea conditions), we consider Black Guillemots to be 'pagophilic' rather than truly pelagic in winter.

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Allocation of Time and Energy

FLEXIBLE TIME BUDGETS IN BREEDING COMMON MURRES: BUFFERS AGAINST VARIABLE PREY ABUNDANCE

ALAN E. BURGER AND JOHN F. PIATT

Abstract. We report on a 4-year study of the relationships between parental behavior of Common Murres (*Uria aalge*) and the relative abundance of their principal prey, capelin (*Mallotus villosus*), at Witless Bay, Newfoundland. Capelin comprised 89% of the prey fed to murre chicks. Capelin abundance and the density of their schools, measured with hydroacoustic surveys, varied significantly within and between each of the murre's breeding seasons, by up to 10-fold. Despite this, the feeding rates of chicks (average 0.28 fish chick^{-1} h^{-1}) did not vary significantly between years, and were not depressed by intraseasonal capelin variations. Adult murres compensated for periods of low capelin abundance by taking more of other fish, particularly sandlance (*Ammodytes* sp.), and by spending more time at sea. Chick survival (average 93%) did not vary significantly between years. Chick feeding rates and parental resting time at the colony were not strongly affected by weather, sea conditions or chick age. We suggest that with moderate prey abundance, variable time budgets of adult murres would buffer the effects of temporal and spatial prey variability so that chick feeding rates would remain relatively constant. Under such conditions chick growth and survival might not reflect food availability.

Key Words: Seabird; fish abundance; time budgets; energetics; murre; capelin.

Herbers (1981) and Southern and Moss (1985) suggested that inactive periods in mobile animals might represent time buffers to compensate for variable food levels. The effects of periodic, unpredictable food shortages can be ameliorated if the animals have a reserve of time, available for foraging when necessary, in lieu of activities like resting or preening. Flexible time budgets might be particularly useful to seabirds feeding on pelagic prey, where the environment and prey availability are often highly variable in time and space. This would be most evident during the breeding season, when foraging ranges are restricted and time and power demands on adults are greatest (Ricklefs 1984, Gaston 1985a).

Several characteristics of breeding seabirds have been shown to vary with food availability, e.g., clutch size (Springer et al. 1986), chick growth (Gaston 1985b, Gaston et al. 1983) and brood size (Braun and Hunt 1983, Shaw 1985). Many seabirds, including murres (*Uria*), lay a clutch of one and thus cannot adjust clutch or brood size. Variations in egg size (e.g., Birkhead and Nettleship 1982) are unlikely to compensate for large variations in food availability. There are comparatively few data on the effects of food availability on parental time budgets in seabirds (Cairns 1988). At one extreme, parents may work at maximum capacity so that chick growth and breeding success are thought to reflect levels of food availability (Ashmole 1963, Diamond 1978, Gaston 1985a). In other cases, successful breeding seabirds appear to have time to spare (Pearson 1968, Furness and Barrett 1985, Cairns et al. 1987).

Following Cairns (1988), we propose that under conditions of moderate to high prey availability, parental time budgets and attendance at the colony should vary, resulting in relatively constant provisioning of chicks, despite fluctuations in prey availability. The chicks might therefore be buffered from the effects of variable food availability. An alternative possibility is that parents always maximize their foraging time and effort, perhaps constrained only by physiological limitations (Drent and Daan 1980) or digestive bottlenecks (Diamond et al. 1986).

We studied the activity-time budgets of Common Murres (*Uria aalge*) rearing chicks at a colony on Gull Island (47°16′N, 52°46′W) in Witless Bay, Newfoundland, over four consecutive breeding seasons. The abundance and distribution of the murre's principal prey, capelin (*Mallotus villosus*), were estimated from hydroacoustic surveys made in and near Witless Bay in each season (Piatt and Methven 1986, Piatt 1987). These data allowed us to assess inter- and intraseasonal variations in chick diets, chick feeding rates, and parental activities at the colony, relative to independent assessments of prey abundance on the birds' foraging grounds. To our knowledge, this has never been done with pelagic seabirds.

METHODS

DETERMINATION OF CAPELIN ABUNDANCE

Relative capelin abundance was determined from hydroacoustic surveys made as part of a study of seabird-capelin interactions (Piatt and Methven 1986, Schneider and Piatt 1986, Piatt 1987). The vessel's survey routes were 16–28 km long, required 2–2.5 h travelling and encircled Gull Island. Survey routes varied slightly between some years (Piatt 1987), but were always within 10 km of the study colony, within the average foraging range of the murres from Gull Island (Cairns et al. 1987, Piatt 1987).

Hydroacoustic echograms were divided into blocks representing 1 min of travel (approx. 250 m) and 10 m of water depth, and the intensity of the traces of fish within each block were visually graded (scale 0–9). Because fish abundance is proportional to the square of the intensity of the echo signal (Forbes and Nakken 1972), all grades were squared before averaging to obtain a relative abundance index (mean intensity grade per min of transect, see Piatt and Methven 1986, Piatt 1987 for details). The frequencies of capelin schools per min of transect were also calculated from the hydroacoustic traces, and these were the only estimates of capelin abundance available from 1985. In 1982 through 1984 the frequencies of schools were highly correlated with the relative abundance index (Piatt 1987). In 1982, hydroacoustic surveys were sparse and only three surveys coincided with observations at the murre colony. Consequently, data from 1982 were omitted from intraseasonal analyses.

Observations at the Colony

Observations were made from a blind positioned 8–17 m above a cliffside colony of Common Murres on Gull Island (sites 4 and 5 used by Mahoney, 1979). In each season, 20–25 pairs of murres were marked with picric acid dye squirted from the clifftop. Observations of the marked birds provided data on the following: the parental resting time (PRT), defined as the % time that the off-duty (non-brooding) bird was present at the colony, i.e., the pair was together at the colony; the chick feeding rate (CFR), defined as the rate at which fish were delivered by both parents (fish chick^{-1} hour^{-1}); the type and size of prey delivered to the chick; and the duration of the adults' foraging trips at sea.

Observation shifts ranged from four to 17.5 hours, the latter covering the entire day from first light (ca. 04:00, Newfoundland Daylight Saving Time) to dark (21:00–21:30). Observations commenced 30 min after the observer entered the blind. Arrivals and departures of adults were recorded to the nearest minute. The presence of each marked adult was recorded at 5 min intervals to ensure that marked birds that wandered away from their breeding site were not overlooked. Daily means of parental activities and chick feeding rates were compared with estimates of capelin abundance made on the same day, or where that was not possible, with three-day averages covering the day of observation. Growth rates of chicks were not measured.

The birds were close enough for the observer, using binoculars, to identify 88% of the 1150 fish delivered to chicks over four years. Mature capelin were sexed on the basis of the shape of the anal fin, which has an enlarged base in males, or the presence of eggs exuding from the cloacas of females. Fish lengths were estimated relative to the gape lengths of adult murres (mean gape length = 70.3 ± 3.6 mm, N = 21). In 1982, 1983 and 1984, fish were collected by fitting chicks at nearby sub-colonies on Gull Island with collars to prevent them from swallowing for 3-h periods. Comparisons within each year showed no significant differences between visual identifications and samples of fish from collared chicks, in the proportions of prey species, mature and immature capelin or in the sex ratios of mature capelin (A. E. Burger, unpubl. data). Visual observations are thus presented here as valid estimates of prey composition.

Shaded air temperatures, visibility (ability to see landmarks of known distance), sea conditions (calm, moderate or rough seas), windspeed (Beaufort scale later converted to km h^{-1}), wind direction and the occurrence of clouds, fog and rain, were recorded hourly at the colony. Data from 4-hr observations (12:00–16:00) were used to test the effects of weather and sea conditions, because these factors can change dramatically during longer watches.

The non-parametric Kruskal-Wallis analysis of variance and Mann-Whitney tests were used to analyze behavioral and dietary data, using QSTAT programs (Biderman 1985). Throughout, means are given ± one SD.

RESULTS

Factors Affecting Parental Activities of Murres

Before examining the effects of capelin abundance on the parental activities of murres, it is necessary to determine which periods of observation may be used for valid comparisons, and to examine possible confounding influences, such as chick age, weather and sea conditions.

Selecting an appropriate observation period

All observations were made during daylight, and there was no evidence that the murres fed their chicks at night (see also Verspoor et al. 1987). A 4-h subsample was selected from each day of observation, to allow comparisons between days of unequal observation time. Careful selection of the time of this period was needed, because the frequency of many activities, including chick feeding (Fig. 1), varied through the day. Using data from dawn-to-dark watches, we found that feeding rates (CFR) and resting times (PRT) measured in most 4-h subsamples were significantly correlated with the dawn-to-dark values, but only in the period 12:00–16:00 were the magnitudes of both CFR and PRT sufficiently similar to the dawn-to-dark values (Table 1). Consequently, data from this period were selected, and identified as CFR-P3 and PRT-P3 to distinguish them from dawn-to-dark values, designated CFR-DD and PRT-DD.

Effects of environmental conditions

No clear trends or significant correlations were found between either feeding rates (CFR-P3) or resting times (PRT-P3) and visibility, windspeed, wind direction, temperature and sea state in 1983 (N = 8 observation days), 1984 (N =

10) or 1985 (N = 10), possibly due to small sample sizes in each season.

With data from all years pooled, CFR-P3 was not markedly affected by prevailing weather conditions affecting visibility (Table 2). CFR-P3 was not correlated with air temperature at the colony ($r = 0.123$, $df = 27$, $P > 0.05$), or sea condition ($r = -0.162$, $df = 24$, $P > 0.05$), but was negatively correlated with windspeed ($r = -0.376$, $df = 27$, $P < 0.05$), due largely to reduced feeding rates during two days of moderately strong offshore winds. Overall, CFR-P3 was similar on days with onshore (mean 0.25 ± 0.07 fish chick^{-1} h^{-1}, N = 6), longshore (0.30 ± 0.07, N = 5) or offshore (0.26 ± 0.08, N = 17) winds (Kruskal-Wallis test, $H = 1.91$, $df = 2$, $P > 0.05$).

Parental resting time (PRT-P3) appeared unaffected by weather and visibility (Table 2). PRT-P3 was not correlated with windspeed ($r = -0.132$), or sea condition ($r = 0.071$, $df = 27$, $P > 0.05$ in both tests), but was negatively correlated with air temperature ($r = -0.390$, $df = 27$, $P < 0.05$). This reflected occasional periods of intense insolation when heat-stressed off-duty adults left the colony. PRT-P3 was not significantly different on days with onshore (mean 38.9 ± 16.4%, N = 6), offshore (24.9% ± 11.1, N = 17) or longshore winds (21.9% ± 14.1, N = 5; Kruskal-Wallis test, $H = 3.989$, $df = 2$, $P > 0.05$).

Effects of chick age

Within each year there were no consistent correlations between chick age and daily measures of feeding rate, parental resting time, duration of foraging trips or proportion of adult capelin in the diet (Table 3). Fish size was positively correlated with chick age in each year (significant in two years, Table 3), because chicks 1–2 d old are fed a higher proportion of small, immature capelin than older chicks (A. E. Burger, unpubl. data).

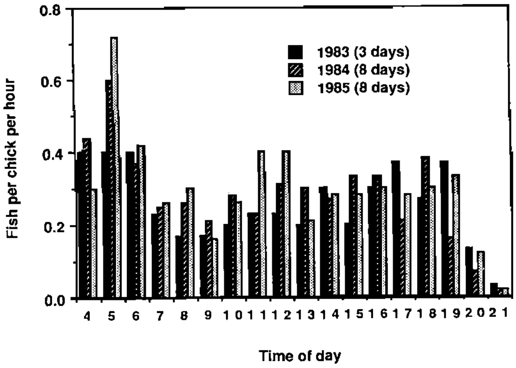

FIGURE 1. Mean hourly chick feeding rates of Common Murres at Gull Island in 1983, 1984 and 1985. The time intervals are labelled with the starting time of each interval (i.e., 4 = 04:00–05:00). Data from complete dawn-to-dusk days only.

The correlation between chick age and proportions of adult capelin in their diets in 1984 probably reflected the scarcity of capelin in the early part of that season (see below), when many chicks were newly hatched.

VARIATIONS AMONG YEARS

Variations in capelin abundance

Schools of capelin first appeared in Witless Bay in late May. Their abundance usually peaked in the last ten days of June and first two weeks of July, and declined markedly by early August (Figs. 2 and 3). The annual means of relative capelin abundance varied by an order of magnitude during the study, showing a significant decline between 1982 through 1984 (Fig. 4, One-way ANOVA, $F_{2,57} = 28.2$, $P < 0.001$). Frequency of capelin schools followed a similar trend, but in-

TABLE 1. COMPARISON OF CHICK FEEDING RATES (FISH CHICK^{-1} H^{-1}) AND PARENTAL RESTING TIMES (% DAYLIGHT TIME WITH OFF-DUTY ADULT AT THE COLONY) FOR VARIOUS PERIODS OF OBSERVATION, INCLUDING THE MIDDLE EIGHT HOURS (MD) AND THE WHOLE DAWN-TO-DARK DAY (DD). ALL DATA FROM 17 DAYS OF COMPLETE DAWN-TO-DARK OBSERVATIONS IN 1983 (3 D), 1984 (7 D) AND 1985 (7 D), WITH AN AVERAGE OF NINE PAIRS OBSERVED PER DAY

Observation period (time)	Chick feeding rate (CFR)			Parental resting time (PRT)		
		Comparison with DD rate[1]			Comparison with DD rate[1]	
	Mean ± SD	t	r	Mean ± SD	t	r
P1 (04:00–08:00)	0.41 ± 0.10	6.25***	0.519*	16.5 ± 9.3	3.52**	0.691**
P2 (08:00–12:00)	0.26 ± 0.09	1.55 NS	0.578*	15.4 ± 7.5	6.88***	0.846**
P3 (12:00–16:00)	0.26 ± 0.08	1.81 NS	0.692**	22.6 ± 10.5	0.16 NS	0.678**
P4 (16:00–dark[2])	0.23 ± 0.07	3.28**	0.425 NS	31.9 ± 10.9	5.90***	0.796**
MD (08:00–16:00)	0.26 ± 0.07	2.07 NS	0.734**	19.7 ± 8.4	2.35*	0.846**
DD (04:00–dark[2])	0.28 ± 0.05	—	—	22.3 ± 7.4	—	—

[1] Two-tailed paired t-test; Pearson correlation (r); *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, NS not significant ($P > 0.05$).

[2] Darkness occurred between 21:00 and 21:30.

TABLE 2. EFFECT OF WEATHER AND VISIBILITY ON CHICK FEEDING RATE (CFR-P3) AND PARENTAL RESTING TIME (PRT-P3) IN COMMON MURRES. MEANS ± SD FROM 4-H OBSERVATIONS (12:00–16:00), 1983–1985 POOLED

Weather	Visibility (km)	CFR-P3 (fish chick^{-1} h^{-1})	PRT-P3 (% of 4 h)	N
Clear, sunny	Excellent (>10)	0.28 ± 0.09	32 ± 13	8
Overcast but bright	Good (5–10)	0.24 ± 0.08	22 ± 9	8
Heavy overcast, rain	Moderate (1–5)	0.27 ± 0.08	23 ± 20	3
Moderate fog	Moderate-poor (0.3–1)	0.31 ± 0.07	26 ± 14	6
Thick fog	Poor (<0.30)	0.22 ± 0.02	38 ± 20	3
Kruskal-Wallis H-value		3.82 ($P > 0.05$)	3.65 ($P > 0.05$)	

creased slightly in 1985 (Fig. 4, ANOVA, $F_{3,86} = 36.3$, $P < 0.001$).

Diets of the chicks

The diets of Common Murre chicks at Gull Island in 1982–1985 comprised 72% mature capelin (91% females), 11% immature capelin, 6% unclassified capelin, 9% sandlance *Ammodytes* sp. and 2% other fish (N = 1017 fish in visual observations). Diets differed significantly between years, with fewer capelin, particularly mature females, delivered in 1984 (Fig. 5; $\chi^2 = 85.33$, df = 12, $P < 0.001$).

The size/frequency distributions of fish delivered to chicks, estimated visually, differed significantly between years (Fig. 6; χ^2 test with Yate's correction, $\chi^2 = 50.23$, df = 12, $P < 0.01$). This was due to increased numbers of large sandlance and fewer small female capelin in 1984, and more small fish in 1982. Mature female capelin obtained intact from collared chicks were, on average, heavier in 1984 (17.1 ± 3.4 g, N = 13) than in 1982 (13.7 ± 2.4 g, N = 17) and 1983 (13.8 ± 4.1, N = 25; Mann-Whitney tests, $P < 0.05$ in each case). Mature capelin caught in traps were generally also larger in 1984 than 1982 or 1983 (Piatt 1987). Samples of other fish from collared chicks were too small for inter-year comparisons. The mean masses of immature capelin and sandlance were 6.7 ± 3.2 g (N = 5) and 14.5 ± 6.6 g (N = 10), respectively.

Feeding rates and parental activities

For 17 dawn-to-dark watches in 1983, 1984 and 1985 the mean chick feeding rate (CFR-DD) was 0.28 ± 0.05 fish chick^{-1} h^{-1} (4.8 ± 0.9 fish chick^{-1} per 17-h day), and the mean resting time (PRT-DD) was 22 ± 7% (3.7 h d^{-1}). Each off-duty adult thus averaged 1.9 h per day at the colony. Feeding rates (CFR-P3) and resting times (PRT-P3) from the partial day 4-h watches included more days, from all four years, and averaged 0.25 ± 0.07 fish chick^{-1} h^{-1} and 30 ± 14%, respectively (N = 41 days, average 9 chicks per day). Mahoney (1979) reported a feeding rate of 0.23 fish chick^{-1} h^{-1} for the same sites in 1977, but did not sample the most active period between 04:00 and 06:00.

The mean chick feeding rates (CFR-DD and CFR-P3) did not vary significantly among years (Table 4), despite the significant changes in capelin abundance. Feeding rates were higher in 1984, when capelin were least abundant. Parental resting time measured in dawn-to-dark watches did not differ among years, but the sample sizes were small (Table 4). The larger samples from 4-h watches (PRT-P3) did differ significantly, showing that murres spent less time resting at the colony in seasons when fewer capelin were detected on hydroacoustic surveys (Table 4).

The durations of foraging trips preceding fish deliveries were compared using dawn-to-dark

TABLE 3. CORRELATION COEFFICIENTS OF CHICK AGE COMPARED TO PARENTAL BEHAVIOR AND CHICK DIET IN COMMON MURRES AT GULL ISLAND. DATA FROM VISUAL DAWN-TO-DARK OBSERVATIONS ONLY

Parameter	Year		
	1983	1984	1985
Chick feeding rate (CFR-DD)	−0.408*	−0.168	0.009
Parental resting time (PRT-DD)	0.165	0.136	−0.157
Duration of foraging trips	0.045	0.114	0.243
Percentage of adult capelin fed to chicks	−0.085	0.425**	−0.216
Size of fish fed to chicks	0.479*	0.210	0.401*
No. bird-days	26	68	39

** $P < 0.01$, * $P < 0.05$, all other correlations not significant ($P > 0.05$).

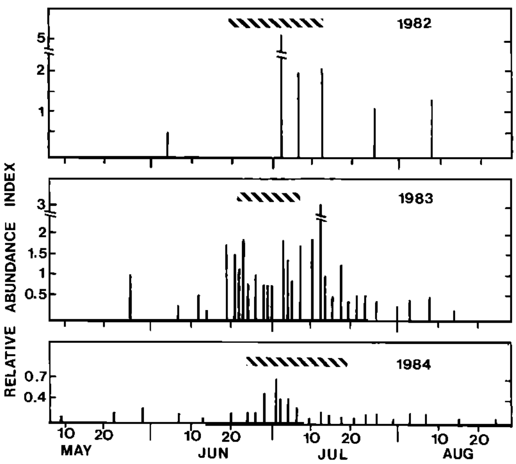

FIGURE 2. Relative abundance indices of capelin in Witless Bay, estimated from hydroacoustic surveys (from Piatt 1987). Horizontal hatched bars indicate the periods of observations of Common Murres at Gull Island. Capelin were recorded on all days surveyed.

data and showed no significant differences between years (Fig. 7, Kolmogorov-Smirnov Test, $P > 0.05$).

By combining estimates of feeding rates, proportions of prey in the diet and mean mass and energy content of prey, we calculated the average mass and caloric intake of murre chicks in each year (Table 5). Differences among the years did not correspond to differences in estimated capelin abundance, and the highest intake was in 1984, the year of lowest capelin abundance.

Survival of eggs and chicks

Survival of eggs, excluding those which had not hatched at the end of the field season, was 76% ($N = 29$), 73% ($N = 33$), 80% ($N = 35$) and 67% ($N = 15$) in 1982 through 1985, respectively. These were maximum survival rates since observations commenced 2–3 weeks after the peak of laying. No mortality occurred among chicks > 13 d old, and only two chicks died when > 3 d old. Chicks that were > 15 d old at the end of each year's field season were therefore assumed to have a high probability of fledging. Survival of chicks to fledging, or to > 15 d old at the end of each year's field season, was 82% ($N = 17$), 100% ($N = 21$), 92% ($N = 25$) and 100% ($N = 9$) for 1982 through 1985, similar to that in other murre colonies in the Atlantic (Harris and Birkhead 1985). There was thus no evidence that egg or chick survival was affected by changes in capelin abundance in these years.

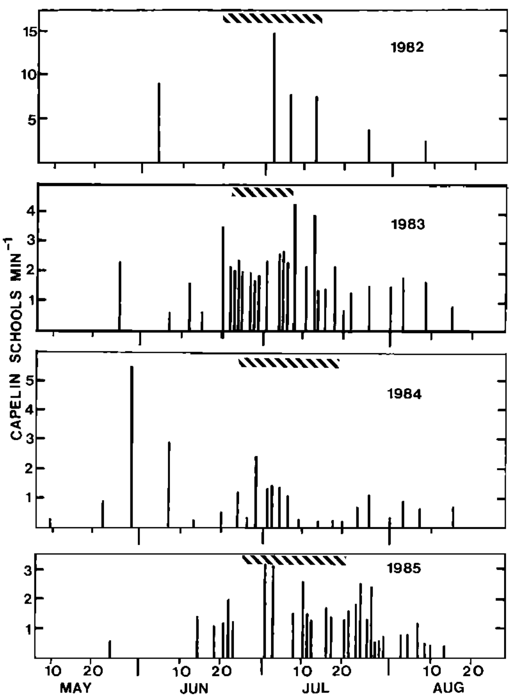

FIGURE 3. Estimates of the frequency of capelin schools in Witless Bay made from hydroacoustic surveys (J. F. Piatt and D. A. Methven, unpubl.). Horizontal hatched bars indicate periods of observations of Common Murres at Gull Island. Schools were detected on all days surveyed.

VARIATIONS WITHIN SEASONS

Daily variations in murre activities and capelin abundance

Daily variations in feeding rates (CFR-P3) were significantly correlated with resting times (PRT-P3) in 1984 ($r = 0.671$, $df = 10$, $P < 0.05$), but not in 1982 ($r = 0.135$, $df = 10$, $P > 0.05$), 1983 ($r = 0.097$, $df = 8$, $P > 0.05$), 1985 ($r = -0.571$, $df = 9$, $P > 0.05$), or in the pooled data from all years ($r = -0.276$, $df = 40$, $P > 0.05$). We calculated correlation coefficients to test whether daily averages of relative capelin abundance (1983 and 1984) and the frequency of capelin schools (1983 through 1985) might be related to changes in daily values of feeding rate (CFR-P3), resting time (PRT-P3), mean fish size and % adult capelin in the chicks' diets. Out of 20 pairs of comparisons, only one (CFR-P3 and frequency of schools) showed a statistically significant relationship. Since this result might be obtained by chance alone, we concluded that there was too much variation or "noise" in the daily estimates of both murre behavior and capelin abundance to detect short-term trends with small samples.

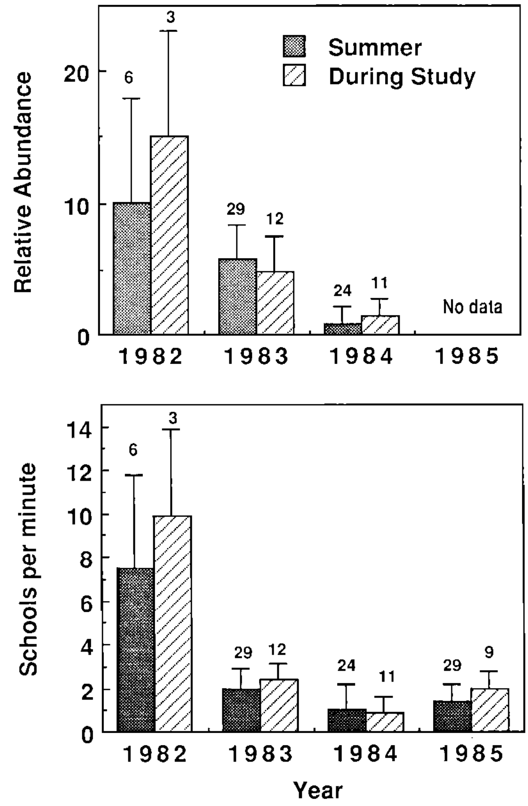

FIGURE 4. Mean ± SD (error bars) measures of the relative abundance index, and the frequency of schools of capelin in Witless Bay during the entire summer (shaded bars) and during the study of murres at Gull Island (hatched bars, see Fig. 2 for duration of study in each year). The number of surveys in each sample is shown. Data from J. F. Piatt and D. A. Methven (unpubl.).

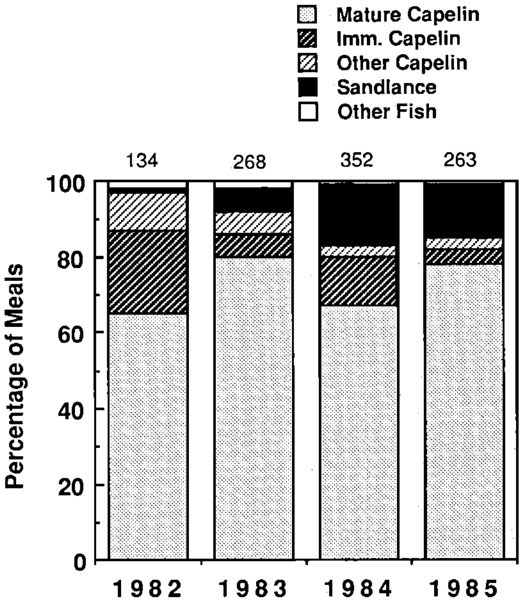

FIGURE 5. Proportions of fish types in the diets of Common Murre chicks at Gull Island, based on visual observations. Fish were classified as mature capelin, immature (imm.) capelin, other (unclassified) capelin, sandlance and other species. The number of meals sampled is shown.

Relationships were therefore examined by grouping data into periods of several days with notably different estimates of capelin abundance. There were three of these periods in 1984 (Figs. 1 and 8) and two in 1985 (Figs. 2 and 9) but none during observations in 1982 or 1983. In 1984 the relative abundance of capelin was initially very low (Fig. 8, 20–26 June), increased seven fold (28 June–6 July), and then decreased

TABLE 4. ANNUAL MEANS (±SD) OF CHICK FEEDING RATES (FISH CHICK^{-1} H^{-1}) AND PARENTAL RESTING TIMES (% DAYLIGHT TIME WITH OFF-DUTY ADULT AT THE COLONY), CALCULATED FROM THE MEAN OF EACH DAY OF OBSERVATION FOR DAWN-TO-DARK AND 4-H (12:00–16:00) PERIODS OF OBSERVATIONS

Measure	Year				Kruskal-Wallis test
	1982	1983	1984	1985	
Chick feeding rates CFR-DD (dawn–dark)	—	0.26 ± 0.04	0.28 ± 0.03	0.29 ± 0.06	H = 0.333 (P > 0.05)
CFR-P3 (12:00–16:00)	0.22 ± 0.05	0.24 ± 0.06	0.29 ± 0.06	0.26 ± 0.10	H = 6.012 (P > 0.05)
Parental resting time PRT-DD (dawn–dark)	—	21.5 ± 4.2	18.8 ± 6.0	26.1 ± 8.6	H = 2.879 (P > 0.05)
PRT-P3 (12:00–16:00)	41.2 ± 10.8	33.5 ± 15.6	19.4 ± 9.7	28.4 ± 13.0	H = 14.557 (P < 0.01)
Sample sizes (days)					
Dawn-to-dark watches	0	3	7	7	
Four hour watches	11	9	11	10	

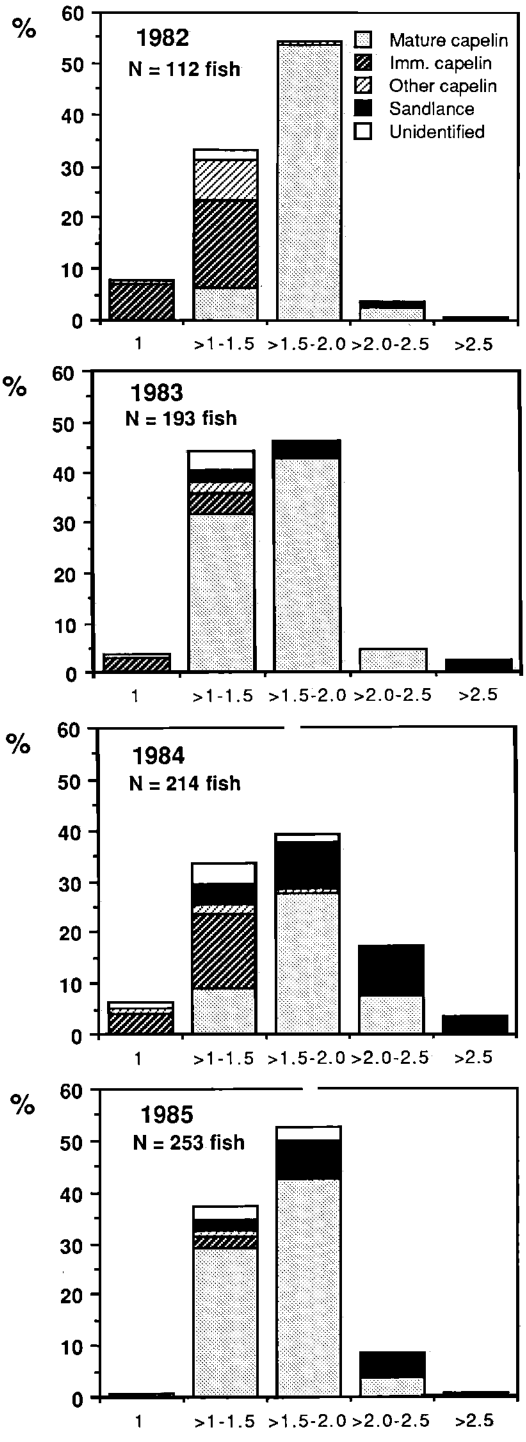

FIGURE 6. Size-frequency distributions of fish delivered to Common Murre chicks at Gull Island. Fish sizes were estimated visually and are presented in units of gape length in adult murres.

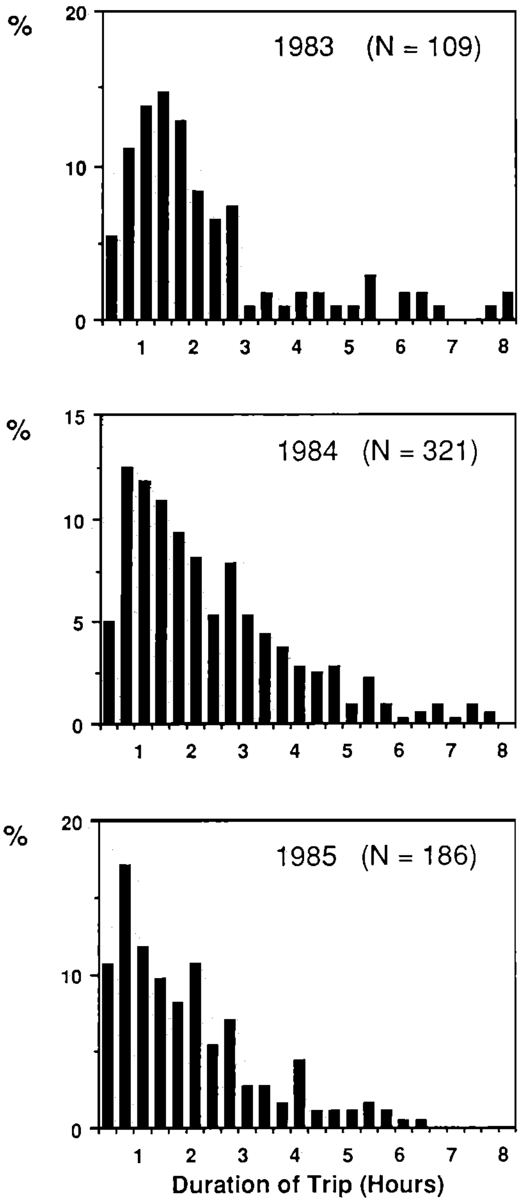

FIGURE 7. Variations between seasons in the durations of foraging trips preceding deliveries of fish to chicks, by Common Murres at Gull Island. Data from dawn-dark observation periods only.

again (9–20 July). Chick feeding rates (CFR-DD) were not significantly affected by these large changes (Fig. 8; Kruskal-Wallis test, $H = 3.07$, $df = 2$, $P > 0.05$), but there were significant differences in the parental resting times (Fig. 8, $H = 11.31$, $df = 2$, $P < 0.05$) and proportions of prey in chicks' diets (Fig. 8, Chi-squared test,

TABLE 5. ESTIMATES OF THE DAILY FEEDING RATE, MEAL SIZE, FOOD AND ENERGY INTAKE PER CHICK OF COMMON MURRES AT GULL ISLAND

Measure	1982	1983	1984	1985	Mean
Chick feeding rate (meals d^{-1})[1]	3.74	4.08	4.93	4.42	4.29
Mean meal size (g)[2]	12.1	13.7	13.4	14.1	13.3
Total food intake (g)	45.3	55.9	66.1	62.3	57.4
Energy intake (kJ)[3]	339	417	485	460	425

[1] From CFR-P3 (Table 4) assuming 17 h daylight.

[2] Calculated using proportions (Fig. 5) and mean weights (A. E. Burger unpubl. data) of fish types delivered to Gull Island chicks.

[3] Calculated using the method and caloric values of fish given in Birkhead and Nettleship (1987), and food intake data from Gull Island.

$P < 0.05$). The most likely explanation for these results is that capelin were generally scarce during the first period, forcing murres to take more sandlance, which demanded increased foraging time. During the third period, capelin were scarce within the surveyed areas, but appeared to have been available elsewhere, since mature capelin made up the bulk of the chick meals and the adults spent only slightly less time at the colony.

In 1985 (Fig. 9), during the late-season period of low capelin abundance, the feeding rate was significantly higher (Mann-Whitney test, $U_{14,26} = 315$, $P < 0.01$), and the resting time significantly lower ($U_{14,26} = 255$, $P < 0.05$), but the chicks' diets did not change (χ^2 test, $P > 0.05$). Again, the parents appeared to work harder when capelin were less abundant locally, but in this year the feeding rates were also affected. The duration of foraging trips preceding fish deliveries was not affected by changes in relative abundance of capelin in 1984 or 1985 (Kolmogorov-Smirnov tests, $P > 0.05$ in each year).

DISCUSSION

EFFECTS OF OBSERVATION PERIODS, WEATHER, AND CHICK AGE

Hourly variations in chick feeding rates and parental activities occur in many seabird populations (e.g., Gaston and Nettleship 1981; Harris and Wanless 1985; Birkhead and Nettleship 1987, this study). Despite this, it is standard practice to determine breeding activities from observation subsamples of 2–8 h per day (e.g., Birkhead 1976; Birkhead and Nettleship 1981, 1987; Gaston and Nettleship 1981; Wehle 1983). We have shown that rates determined in 4-h subsamples were generally strongly correlated with complete dawn-to-dark rates, which would justify some intrastudy comparisons, but rates from subsamples and complete days did not always have the same magnitude. Careful selection of representative sampling periods, as we have done, would facilitate comparisons between studies where observation times differ.

Common Murres at Gull Island were relatively unaffected by most weather and sea conditions at the time of breeding. Chick feeding rates were maintained even in thick fog and fairly strong winds. These findings are consistent with other studies of murres (Birkhead 1976, 1978; Slater 1980; Gaston and Nettleship 1981; Piatt and McLagan 1987). High seas were found to reduce the chick feeding rates of Common Murres in one study (Birkhead 1976) but not in another (Harris and Wanless 1985). The trends in feeding rates and resting times in our data could not therefore be attributed to short-term influences of the weather.

Parental activities and chick feeding rates were relatively unaffected by chick age, except that a greater proportion of small, immature capelin was fed to chicks of 1–2 d old. Gaston and Nettleship (1981) found a similar trend among Thick-billed Murres (*Uria lomvia*). The energy intake of murre chicks studied over two seasons in Labrador increased with chick age in both seasons among Thick-billed Murres, but in only one season among Common Murres (Birkhead and Nettleship 1987). Other studies of Common Murres showed no significant changes in provisioning rates with increasing chick age (Birkhead 1977, Hedgren and Linnman 1979, Harris and Wanless 1985). The lack of consistent evidence for increased parental effort as the chick grows is surprising, because the maintenance requirements of Common Murre chicks are thought to increase about six fold while they are at the colony (Coulson and Pearson 1985). Since murres at Gull Island maintained high feeding rates but usually had time to spare at sea (Cairns et al. 1987) or at the colony (this paper), these results do not support the hypothesis that murre chicks fledge at <30% of adult mass due to the inabilities of parents to provision them adequately at the colony (Tuck 1961, Sealy 1973, Birkhead 1977, Gaston 1985b).

RESPONSES OF COMMON MURRES TO VARIABLE PREY ABUNDANCE

Large scale variations in capelin abundance are normal off Newfoundland (Carscadden 1984), and some of the effects of these variations on

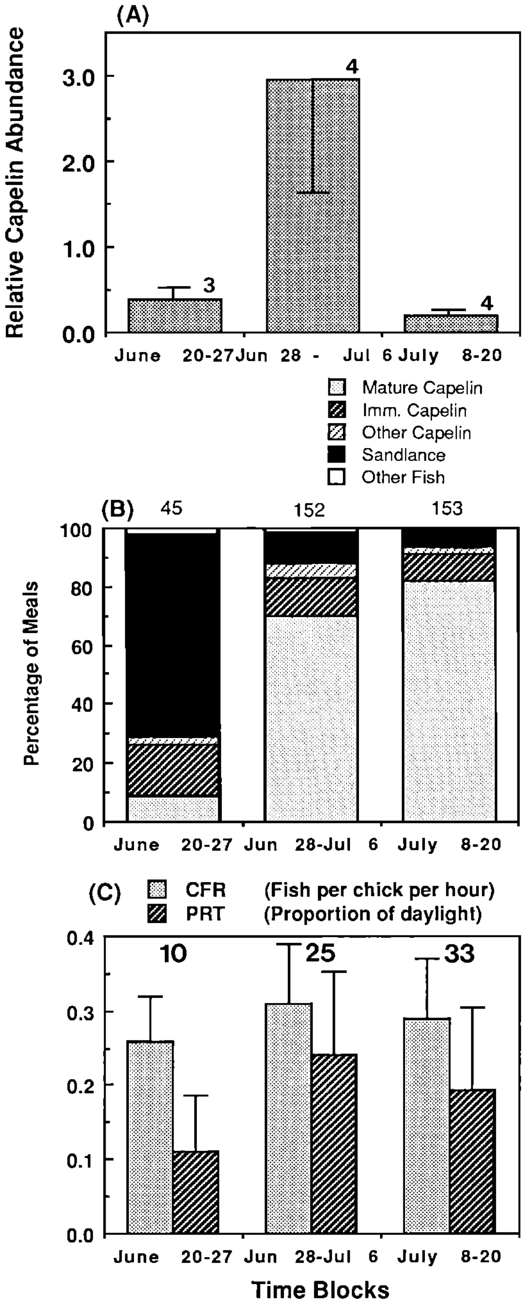

FIGURE 8. Intraseasonal changes in 1984, including: A) the relative abundance index of capelin in Witless Bay (N = number of surveys); B) the proportions of fish types in diets of Common Murre chicks (N = number of meals); and, C) chick feeding rates and parental resting times of Common Murres at Gull Island (N = pair-days). Error bars show SD.

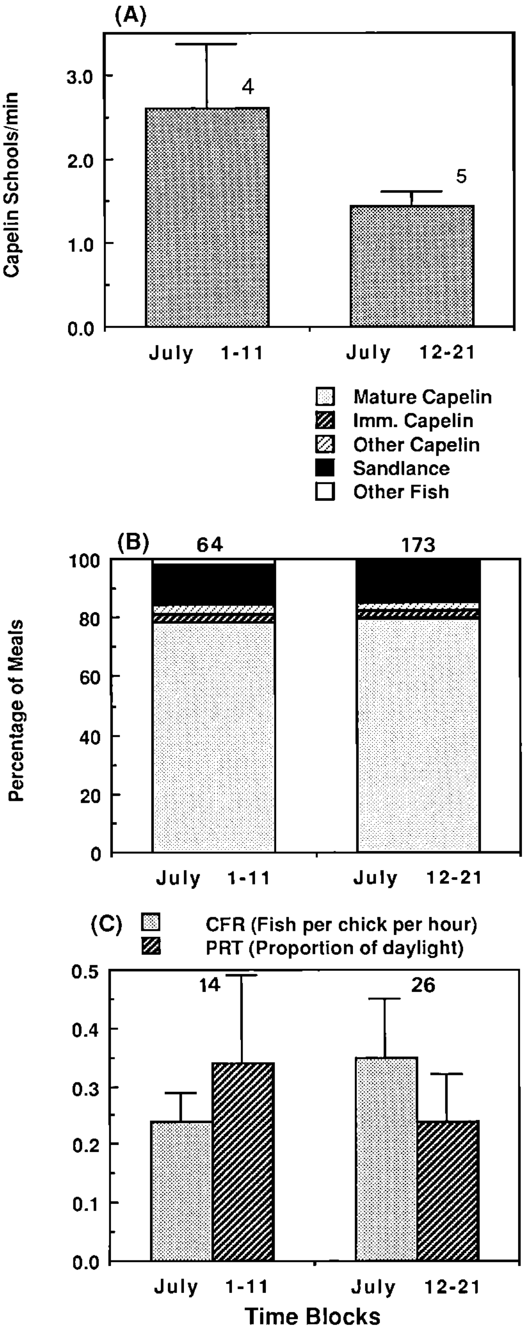

FIGURE 9. Intraseasonal changes in 1985, including: A) the frequency of capelin schools per minute of transect; B) the proportions of fish in the diets of Common Murre chicks; and C) chick feeding rates and parental resting times of murres (N = pair-days). Error bars show SD. Numbers indicate sample size, as in Figure 8.

TABLE 6. ESTIMATES OF THE TIME SPENT AT THE COLONY BY OFF-DUTY PARENTS (PRT) BY MURRES AT VARIOUS LOCATIONS

Species	Location	Day-length (h)	PRT (% day-light)	PRT (h d^{-1})	Reference
Common Murre	Witless Bay, Newfoundland	17	22	3.7	This study
Common Murre	Isle of May, Scotland	18	32[1]	5.9	Wanless et al. (1985)
Thick-billed Murre	Pr. Leopold I., High Arctic	24	4	1.0	Gaston and Nettleship (1981)
Thick-billed Murre	Hornøy/Reinøy, North Norway	24	53	12.7	Furness and Barrett (1985)

[1] Each adult was at the colony for 66% of the day, so the time when both would be ashore together should average 32%.

seabirds have been reviewed (Brown and Nettleship 1984, Piatt 1987). Capelin abundance off Newfoundland during this study (1982–1985) was intermediate (Carscadden et al. 1987, Carscadden in litt. 1987, Piatt 1987), and higher than in 1981, when the breeding success of Atlantic Puffins (*Fratercula arctica*) in Witless Bay was markedly poor (Brown and Nettleship 1984). Analysis of commercial catches of inshore spawning capelin off eastern Newfoundland (averaging 12.3, 19.5, 22.2, 17.2, and 21.0 t d^{-1}, for 1981–1985, respectively) also shows that fewer capelin were available in 1984 than in the other years of our study (Carscadden et al. 1987).

Common Murres at Gull Island varied their activities in response to variations in capelin abundance, and thereby ameliorated the effects on the chicks. Chick feeding rates were relatively invariable within and between seasons, despite variations in relative capelin abundance and frequency of schools of up to 10 fold, near the colony. The estimated food and energy intake of the chicks was not markedly affected by these changes either. The murre parents compensated for reduced capelin availability in two ways: by including a greater proportion of large mature sandlance in their catches, and by spending more time per day at sea.

Significant interactions between capelin abundance and murre activities were evident at time scales ranging from several days to complete seasons. Trends were less obvious when day-to-day variations were analyzed, but this was not unexpected, since the food demands of the chicks and adults on any day would be affected by foraging success on previous days. In addition, the "snapshot" estimates of capelin abundance, made during shipboard surveys, covered only a small portion of the space and time normally available to the murres at the colony. Murres at sea in Witless Bay have been found to respond rapidly to small scale temporal and spatial variations in capelin abundance (Schneider and Piatt 1986; Piatt 1987; Piatt, this volume).

IMPLICATIONS OF FLEXIBLE TIME BUDGETS

The time spent ashore by off-duty, breeding seabirds is very variable, ranging from 0.4% of the trip time in Grey-headed Albatrosses (*Diomedea chrysostoma*, Prince and Francis 1984) to over 90% of the day in the Shag (*Phalacrocorax aristotelis*, Pearson 1968). Among murres, where one parent almost always remains on duty at the nest site, resting at the colony by the off-duty bird (PRT) varied between 4 and 53% of the daylight time (Table 6). Pearson's (1968) estimate of only 16% of the day spent at sea by Common Murres at the Farne Islands was not well supported by data and seems too low, even though food was apparently abundant.

Seabirds spend part of their time ashore preening and interacting with chicks, mates or neighbors. The extent to which such activities are essential to survival or breeding success is not known for any seabird, and would be very difficult to assess. The murres we watched used very little time ashore in overt activity. Digestive bottlenecks affect time budgets of some birds (Diamond et al. 1986), and might affect the activities of murres feeding large fish to small chicks. Energy and physiological limitations also constrain activities (Drent and Daan 1980, Walsberg 1983). Flight and diving are energetically very demanding in murres (Gaston 1985a), and some recuperation time might be essential following long flights or bouts of diving. Cairns et al. (1987) showed that the Gull Island murres spent 4–5% of their total day in flapping flight, which is much higher than expected for a 990 g bird (Walsberg 1983).

Despite these potentially confounding factors, our data from four years, and comparisons between colonies, indicates that breeding murres do have discretionary time ashore, which varies inversely with food availability. Where colonies were large and birds fed on distant prey stocks, time at the colony was low (Gaston and Nettleship 1981, 1982; Gaston 1985a), but where food was apparently abundant near the colony, murres spent more time ashore (Furness and Barrett 1985, this study).

Thick-billed Murres at Prince Leopold Island and Digges Island, in the Canadian Arctic, foraged far from their colonies and appeared to work much harder than Common Murres at Gull Island (Gaston and Nettleship 1981, Gaston 1985a). Adults with chicks spent ca. 36% of their time away from the colony in flight, and appeared to be functioning near their maximum sustainable limit (Gaston 1985a). In contrast, murres rearing chicks at Gull Island spent 10.5% of their trip times in flight and were not considered to be stressed (Cairns et al. 1987). Because of the distant distribution of food, and possible intraspecific competition at the large colonies, the murres in the high Arctic, unlike those in Newfoundland, seemed unable to adjust their time budgets to buffer environmental effects on their reproductive performance. At Prince Leopold Island, the parental resting time averaged about 1 h d^{-1} (Table 6), and did not vary much between and within seasons, but food intake, chick growth and maximum chick mass at the colony all varied between years and within seasons (Gaston and Nettleship 1981, 1982).

Birkhead and Nettleship (1987) studied murres breeding in Labrador in two seasons. The average daily energy intake of chicks (296 and 336 kJ in 1982 and 1983, respectively) indicated less favorable conditions than at Gull Island (Table 5). In 1982, a poor year, adult Common Murres made about 20% more, but shorter, feeding trips, delivered smaller capelin and a greater proportion of poor quality alternative fish, and left their chicks unattended more frequently than in 1983. By working harder, the adults appeared to compensate for poor conditions in 1982. Mortality of chicks was similar in the two years, and fledging weights were only 6% lower in 1982 than in 1983.

The activities of murres at sea are largely unknown but are obviously critical parts of time and energy budgets. Cairns et al. (1987) used gauges to determine time on or under water, and estimated that Common Murres with chicks at Gull Island in 1985 spent 10.5% of their time away from the colony in flight and 16.8% actively foraging. Thus, 73% of the time at sea was spent swimming or resting on the sea surface. It is not known what proportion of this time was used in essential activities, but Cairns et al. (1987) hypothesized that time at sea was flexible and could be adjusted with changing fish availability.

Among other seabirds, there is both evidence for (Pugesek 1981, Shea and Ricklefs 1985) and against (Ricklefs 1987) the concept that parental effort varies with changing conditions while breeding. Attempts to increase feeding rates in seabirds by experimentally adding a second chick to the brood have been successful in a few species, but have failed in others (Ricklefs 1987). We anticipate that time budgets would be most flexible in seabirds that lay a single egg clutch, since clutch and brood size adjustments are precluded.

CONCLUSIONS

The role of flexible time budgets of seabirds as buffers against variable food resources is not clear, but needs to be considered. In our view, growth rates or survival of chicks should not be assumed to be strongly correlated with food availability (e.g., Gaston et al. 1983, Ricklefs et al. 1984) until the buffering role of variable time budgets has been considered (cf. Cairns et al. 1987, Cairns 1988). Deleterious effects of food shortage on chick growth and survival might occur only in situations where adults have inflexible time budgets, or face excessive energy demands. Furthermore, our data show that parental time budgets might provide a sensitive indicator of prey stocks under conditions of moderate prey abundance. More rigorous examinations of behavioral time buffers are required, with simultaneous measurements of prey availability, diets, provisioning rates, and reproductive performance. Such studies are essential if seabird breeding activities are to be considered as valid indicators of the local abundance and distribution of commercial fish stocks.

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ENERGY EXPENDITURES, ACTIVITY BUDGETS, AND PREY HARVEST OF BREEDING COMMON MURRES

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Abstract. We used doubly labeled water and electronic timers to measure field metabolic rates (FMRs) and activity budgets of Common Murres (*Uria aalge*) breeding in eastern Newfoundland. Mean FMR (1789 ± 265 kJ·day^{-1}) was about 50% higher than predictions for seabirds. The high FMR may be related to thermal costs in a cold ocean environment and to high locomotion costs associated with a wing structure that is a compromise between flying and diving needs. Basal metabolic rates ($\bar{X}$ = 360 ± 69 kJ·day^{-1}) were also higher than allometric predictions. While absent from the colony birds spent most (70.2–84.9%) time on the sea surface. Potential foraging range as estimated by flight time was greater during incubation than during chick rearing in two study years. Rates of prey exploitation were highest near the colony, but high exploitation rates may also have occurred about 60–70 km from the colony during incubation. Murres associated with the Witless Bay colony consumed an estimated 7579 tonnes of food, primarily capelin (*Mallotus villosus*).

Key Words: Common Murre; field metabolic rate; energy budget, activity budget; seabird prey harvest.

Seabird biology has traditionally been practiced either on land, where the activities of individual animals can be recorded in detail, or at sea, where shipboard observers tally bird distributions in relation to oceanographic features. The cross-product of these approaches is an understanding of the ecology and behavior of individual birds at sea. Until recently, technological limitations effectively precluded the study of individual birds at sea. Innovative techniques have now opened the subject to scientific scrutiny. These include the doubly-labeled water (DLW) method of measuring metabolism (Nagy 1980), activity timers (Prince and Francis 1984), maximum depth recorders (Burger and Simpson 1986, Burger and Wilson 1988), time-depth recorders (Wilson and Bain 1984a) and swimming speed meters (Wilson and Bain 1984b).

We developed a new type of activity timer that allows seabird time budgets to be measured nonintrusively during consecutive foraging trips (Cairns et al. 1987b). The present paper reports field metabolic rates (FMRs) of Common Murres (*Uria aalge*) breeding in eastern Newfoundland and extends earlier activity measurements of murres in the same area (Cairns et al. 1987c). Activity and energy data are integrated in a bioenergetics model that estimates the magnitude and location of the murres' prey harvest. Accurate characterization of food exploitation by murres in eastern Newfoundland is important because of their large population (ca. 500,000 pairs, Cairns et al. 1989) and their dependence on capelin (*Mallotus villosus*). Capelin migrate in large numbers to inshore Newfoundland waters in June and July, where they are a primary food source for many seabirds, marine mammals, and commercially harvested fish, and are themselves subject to an important commercial fishery (Carscadden 1984, Birkhead and Nettleship 1987, Piatt 1987).

METHODS

ENERGY AND ACTIVITY MEASUREMENTS

This study was conducted at Gull (47°16′N, 52°46′W) and Great (47°11′N, 52°49′W) islands, Witless Bay, Newfoundland. These islands and nearby Green Island are the site of a multi-species seabird community that includes some 77,000 pairs of Common Murres (Cairns et al. 1989). On Gull Island in 1985 murres were captured from breeding ledges by noose-pole. On Great Island in 1986 birds were captured at a cliff-top subcolony with a noose-pole or wire neck-hook. All study birds were breeders; we observed them from distances of 15–18 m on Gull Island and 1–3 m on Great Island. The close observations at Great Island were made possible by a 30-m tunnel (Cairns et al. 1987a) that allowed undetected access to blinds fitted with one-way glass (Purdy 1985).

In 1986, we injected 0.3 mL of ^{3}HH^{18}O containing 95 atom % $H_2{}^{18}O$ and 0.051 MBq·mL^{-1} ^{3}HHO into the pectoral muscles of four chick-rearing murres. Birds were weighed, banded, fitted with timers, and individually color-marked on the breast with airplane dope. They were then confined in cotton sacks for 2–3 h to allow equilibration of isotopes with body fluids. Following this, 1–2 mL of blood was sampled from the brachial vein, and the bird released. Birds were recaptured about two days later, when a second blood sample was taken. Water distilled from the blood was assayed for levels of tritium and ^{18}O on a Beckman LS7500 scintillation counter and a Micromass 903E mass spectrometer, respectively (Birt-Friesen et al. 1989).

CO_2 production rate (mL·g^{-1}·day^{-1}) was calculated for each bird, assuming that changes in body water volume were negligible (Nagy 1980). Total body water was estimated from ^{18}O dilution space (Nagy 1983). FMR (kJ·day^{-1}) was calculated assuming an energy equivalent of 0.025 kJ·mL^{-1} CO_2 for a diet of capelin

TABLE 1. INPUT PARAMETERS FOR POPULATION MODEL OF COMMON MURRE ENERGETICS AND FORAGING AT WITLESS BAY, NEWFOUNDLAND

Parameter	Value	Source
Breeding population	77,487 pairs	Cairns et al. 1986
Egg mass	108.4 g	Mahoney and Threlfall 1981
Assimilation efficiency	76%	Montevecchi et al. 1984
Pre-breeding period	40 days	personal observation
Incubation period	31 days	Mahoney 1979
Chick-rearing at colony	23 days	Mahoney 1979
Post-nesting period	7 days	personal observation
Non-breeding population as a percent of breeding population	30.5%	see text
Yolk as a percent of egg	32	Montevecchi unpubl.
Hatching success	74%	Burger and Piatt 1990
Fledging success	94%	Burger and Piatt 1990
Chick fledging mass	241 g	Mahoney and Threlfall 1981
Adult field metabolic rate	1789 $kJ \cdot day^{-1}$	present study
Chick metabolic rate	425 $kJ \cdot day^{-1}$	Burger and Piatt 1990
Adult diet by mass		Piatt 1987
Ovid female capelin	50.7%	
Spent female capelin	4.8%	
Adult male capelin	26.3%	
Immature capelin	0.9%	
Total capelin	83.0%	
Atlantic cod	7.6%	
Sand lance	9.7%	
Chick diet by mass		Piatt 1987
Ovid female capelin	56.3%	
Spent female capelin	20.8%	
Adult male capelin	9.2%	
Immature capelin	4.4%	
Total capelin	90.7%	
Atlantic cod	0.2%	
Sand lance	8.0%	
Other	1.0%	
Energy density of prey		
Ovid female capelin	4.6 $kJ \cdot g^{-1}$	Montevecchi and Piatt 1984
Spent female capelin	3.9 $kJ \cdot g^{-1}$	Montevecchi and Piatt 1984
Adult male capelin	3.8 $kJ \cdot g^{-1}$	Montevecchi and Piatt 1984
Immature capelin	3.8 $kJ \cdot g^{-1}$	Montevecchi and Piatt 1984
Atlantic cod	4.5 $kJ \cdot g^{-1}$	Birkhead and Nettleship 1987
Sand lance	7.3 $kJ \cdot g^{-1}$	Montevecchi et al. 1984
Other	4.0 $kJ \cdot g^{-1}$	mean of other fish
Flight speed	64.4 $km \cdot h^{-1}$	Pennycuick 1987a

(Montevecchi et al. 1984). Mean values are given ± SD.

Basal metabolic rates (BMRs) were measured at Great Island in 1987 by the closed-system respirometry method of Ricklefs et al. (1984). Drierite® and soda lime were placed beneath a plastic mesh floor in 11.5 and 16.3 L chambers to absorb water and CO_2, respectively. Birds were captured at dusk and held in chambers for 2–3 hours before trials. Murres digest food rapidly; Gaston and Noble (1985) suggested that stomachs empty in 1–2 hours, and an X-ray experiment indicated that all food reached the rectum within 95 min of ingestion (Partridge 1986). We therefore believe that little if any food remained in the gut during the metabolism trials. O_2 uptake was calculated from water displacement in a manometer during two 15 min tests during which the manometer showed smoothly decreasing fluid levels. Trials in which manometer levels changed irregularly or in which birds moved vigorously were discarded. Mean chamber temperature during trials, monitored by Yellow Springs Instruments telethermometers, was 18.7 ± 0.4°C. BMR was calculated using the equation of Ricklefs et al. (1984).

All captured birds were fitted with electronic activity timers (Cairns et al. 1987b) on the tail and a leg. When used in conjunction with continuous colony watches, these devices permit a bird's time budget to be partitioned into colony, flying, sea surface, and diving times. Unit mass of timers was 12.5 g in 1985 and 7.5 g in 1986. Timers represented 2.7 and 1.6% of body mass for the two years, respectively. Timers appeared to have little effect on birds' behavior and locomotion (Cairns et al. 1987c).

Potential foraging ranges were calculated from flight

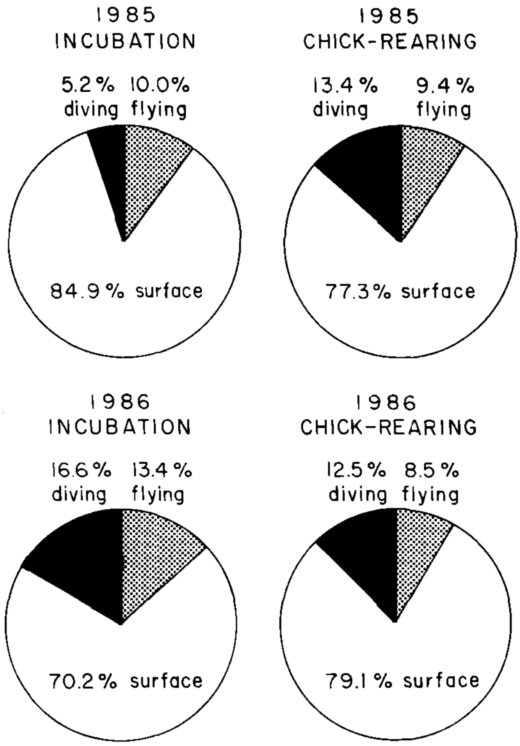

FIGURE 1. Time allocation of breeding Common Murres during absence periods from the colony at Witless Bay in 1985 and 1986. Diving, flying, and surface times were calculated from 1, 16, and 1 trips for incubation in 1985; from 38, 48, and 30 trips for colony-based chick-rearing in 1984; from 29, 23, and 18 trips for incubation in 1986; and from 8, 6 and 6 trips for colony-based chick-rearing in 1986 (all numbers given respectively).

times during individual trips, assuming that birds flew at 64 $km \cdot h^{-1}$ (Pennycuick 1987a) and flew to and returned from feeding sites along straight lines radiating from the colony.

Bioenergetics Model

We modeled prey consumption and harvest distribution of Common Murres during the breeding season at Witless Bay using measured FMRs and activity data and literature values for breeding and other parameters. The model was written on VP-Planner, a microcomputer spreadsheet package. Input parameters are listed in Table 1. Although non-breeders are exempt from the demands of incubation and chick-feeding, we assigned them energy expenditures equal to breeders because they are probably less efficient food-gatherers (Gaston 1985). Activity patterns were also assumed to be equivalent between the two groups.

To estimate numbers of non-breeders associated with the Witless Bay colonies we assumed age of first breeding and annual adult survival as five years and 0.9, respectively (Hudson 1985). Using these values, we iterated a life table with various values of pre-breeding survival until population stability was reached. Non-breeders represented 67.8% of the breeding population (individuals) at this point. Pre-breeding murres are generally absent from the colony area at age one, and gradually increase their attendance until breeding age is attained (Piatt et al. 1984, Hudson 1985). We assumed presence at the colony of 0, 40, 80, and 90% of non-breeders of ages one through four, respectively. This yielded an estimate that total non-breeder numbers at the colony were 30.5% of breeder numbers.

We assumed that murre numbers near the colony increase linearly from zero at the beginning of the pre-breeding period until the full breeding population is reached at the start of incubation, and that the reverse occurs following nest-leaving. Non-breeding immature birds tend to arrive in the colony area later than breeders (Hudson 1985), and we assumed that non-breeders are present only during incubation and chick-rearing at the colony.

Egg production cost was estimated from percentage yolk composition by Carey et al.'s (1980) formula for semi-precocial chicks. Chick energy requirements were summed over the nestling period from mean daily consumption derived from observations of food deliveries (Burger and Piatt 1990). Based on the tendency for chick mortality to occur soon after hatching (Burger and Piatt 1990), chicks that die were assumed to receive no food from the parent.

RESULTS

Energy Expenditures

We obtained simultaneous DLW and activity measurements on four murres rearing chicks at the colony. FMRs ranged from 1542 to 2054 kJ·

TABLE 2. Energy Expenditures and Activity Budgets of Four Common Murres Breeding at Great Island, Newfoundland, in 1986

Bird	Mass (g)	Days	Field metabolic rate: $ml\ CO_2 \cdot g^{-1} \cdot day^{-1}$	Field metabolic rate: $kJ \cdot day^{-1}$	FMR[a]/BMR	Percent time allocation: At colony	Flying	Surface	Diving
Orange	927	2.24	2.84	1580	4.61	25.2	5.0	57.8	12.0
Green	972	1.71	3.40	1979	5.50	43.8	4.9	51.3[b]	
Purple	898	1.85	3.82	2054	6.18	10.8	16.6	66.6	6.1
Black	963	1.87	2.67	1542	4.33	41.4	4.2	48.2	6.2
Mean	940	1.92	3.18	1789	5.16	30.3	7.7	57.5	8.1
SD	34	0.23	0.53	265	0.85	15.4	6.0	9.2	3.4

[a] Based on BMR of 0.370 $kJ \cdot g^{-1} \cdot day^{-1}$ (present study).

[b] Sum of surface and diving time.

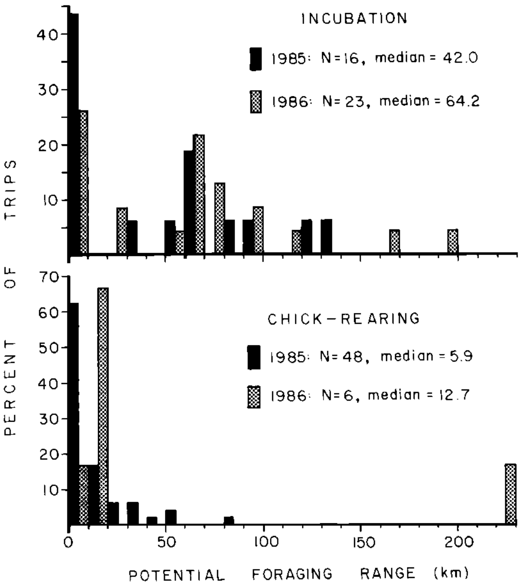

FIGURE 2. Frequency distributions of potential foraging ranges of Common Murres at Gull Island in 1985 and Great Island in 1986.

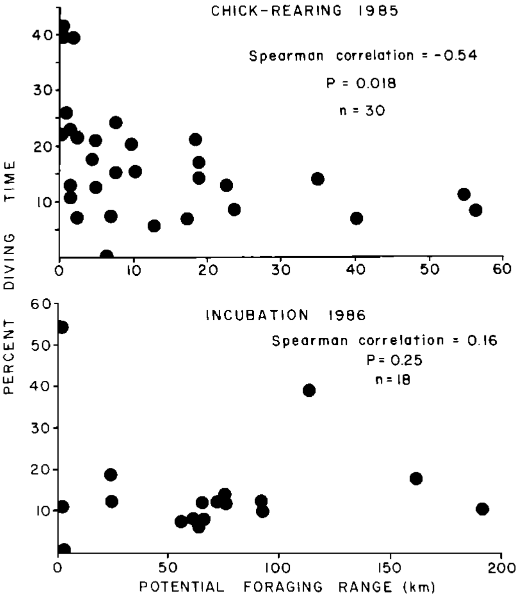

FIGURE 3. Relationship between potential foraging ranges and percent diving time during absence periods from the colony.

day^{-1} ($\bar{X}$ = 1789 ± 265) (Table 2). Mass-specific FMR was 1.90 ± 0.31 $\mathrm{kJ \cdot g^{-1} \cdot day}$. During trials birds spent a mean of 57.5 ± 9.2% of their time on the surface of the water, with the remainder of their time divided among flying, diving, and colony (Table 2).

BMRs of three murres of mean body mass 972 ± 24 g were 283, 381, and 416 $\mathrm{kJ \cdot day^{-1}}$ ($\bar{X}$ = 360 ± 69 $\mathrm{kJ \cdot day^{-1}}$). Mass-specific BMR averaged 0.370 ± 0.078 $\mathrm{kJ \cdot g^{-1} \cdot day^{-1}}$. Using this value of BMR, the ratio of FMR to BMR varied from 4.33 to 6.18 ($\bar{X}$ = 5.16 ± 0.85, Table 2).

TIME ALLOCATION

Proportions of time spent flying, on the sea surface and diving are shown in Figure 1. In all periods, most (70.2–84.9%) time away from the colony was spent on the surface. The proportion of time spent diving did not vary significantly among the four time periods (incubation and colony-based chick-rearing, 1985 and 1986; Kruskal-Wallis H = 3.7, $P < 0.3$), but the proportion of time flying varied significantly among these periods (H = 12.8, $P < 0.01$).

Modal potential foraging range was <20 km in all time periods (Fig. 2). During incubation, a secondary mode appeared at 60–70 km, but during colony-based chick-rearing few foraging trips could have exceeded 20 km in range. Potential foraging range was significantly greater during chick-rearing in 1986 than during chick-rearing in 1985 (Mann-Whitney test; z = 1.72, P = 0.043), but was not significantly different between incubation in 1985 and 1986 (z = 0.86, P = 0.2). Proportion of time diving decreased significantly with potential foraging range during chick-rearing in 1985, but not during incubation in 1986 (Fig. 3).

PREY CONSUMPTION

Common Murres associated with the Witless Bay colony were estimated to require 7579 tonnes of food per breeding season (Table 3). Based on diet composition reported by Piatt (1987), capelin comprised 83% of this requirement, and Atlantic cod (*Gadus morhua*) and sand lance (*Ammodytes* spp.) accounted for most of the remainder. About 68% of estimated food harvest was directed to maintenance and activity of breeders. Food harvest required for egg production (0.3%) and chick feeding (2.7%) was a very small portion of total consumption.

The model estimated that Common Murres at Witless Bay require 103 tonnes of food$\cdot \mathrm{day}^{-1}$ during incubation and 110 tonnes$\cdot \mathrm{day}^{-1}$ during chick-rearing at the colony. If we assume that birds take prey only at their most distant point from the colony during a foraging trip, the geographic distribution of predation intensity can be calculated from the distribution of potential foraging ranges (Fig. 2). We have done this under two foraging regimes. Noting that the Witless

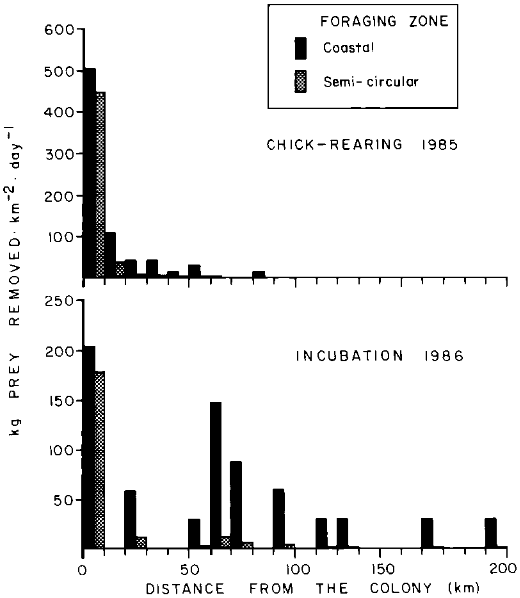

FIGURE 4. Potential prey harvest intensities in kg of prey·km^{-2}·day^{-1} by Common Murres during the breeding season in relation to distance from the colony. Harvest intensities for coastal foraging zones assume that birds feed only in an 8 km wide strip running north and south of the colony. Harvest intensities for semi-circular zones assume that birds use semi-circular foraging zones centered at the colony. See text for additional assumptions.

Bay breeding sites are located just off the straight eastern face of Newfoundland's Avalon Peninsula, we first assumed that murres foraged only in a coastal strip 8 km wide running north and south of the islands. This assumption is supported by distributions of murres recorded during boat transects, which show higher densities on long-shore than offshore transects (Piatt 1987). However, murres from Witless Bay also feed offshore (Schneider et al. 1990). We therefore postulated a second regime in which feeding occurred in a semi-circular area centered at the colony.

Figure 4 plots predation intensity in kg of prey removed·km^{-2}·day^{-1} under these regimes. When a coastal feeding zone was assumed, the pattern of prey removal·km^{-2}·day^{-1} with respect to distance from the colony closely paralleled the distribution of potential foraging ranges (Fig. 2). However, when feeding was assumed to occur in semi-circular zones, predation intensity was relatively high only near the colony, and very low beyond 10 km.

DISCUSSION

ENERGY EXPENDITURES

FMRs of Common Murres tested at Witless Bay fall well above the allometric regression line of other seabirds, which tend to have higher FMRs than birds in general (Nagy 1987, Birt-Friesen et al. 1989). Mean FMR was 1789 ± 265 kJ·day^{-1}, compared to the predicted 993 kJ·day^{-1} for seabirds in general (Nagy 1987) and 1661 kJ·day^{-1} for seabirds with flapping flight occurring in cold oceans (Birt-Friesen et al. 1989; all calculations assume a mass of 940 g).

The high value of FMR may be related to locomotory inefficiencies caused by a wing structure that allows both aerial flight and wing-propelled diving, but which is optimal for neither (Storer 1960, Pennycuick 1987b). It may also be related to the high cost of thermoregulation in cold, windswept marine environments (see Kersten and Piersma 1987, Birt-Friesen et al. 1989).

FMRs of Common Murres overlapped with those of three Thick-billed Murres (*Uria lomvia*) measured in the eastern Canadian arctic (1432–1763 kJ·day^{-1}, Gaston 1985). These findings suggest that Thick-billed Murres may not have higher FMRs than Common Murres, despite their colder environment (Birt-Friesen et al. 1989).

BMR measurements ($\bar{X}$ = 360 ± 69 kJ·day^{-1}) exceeded allometric predictions for non-passer-

TABLE 3. ESTIMATED FOOD CONSUMPTION BY COMMON MURRES AT WITLESS BAY DURING THE BREEDING SEASON

	Estimated consumption (tonnes)					
Prey	Breeders	Non-breeders	Egg formation	Chicks	Total	Percent of total
Ovid female capelin	2624	1104	10.0	116	3854	50.9
Spent female capelin	248	104	0.9	43	397	5.2
Adult male capelin	1361	572	5.2	19	1958	25.8
Immature capelin	47	20	0.2	9	75	1.0
Total capelin	4280	1800	16.0	187	6284	83
Atlantic cod	393	165	1.5	0.4	561	7.4
Sand lance	502	211	1.9	16	732	9.7
Stichaeidae	0	0	0	2	2	0.03
Total	5176	2177	19.8	206	7579	
Percent of total	68	29	0.3	2.7		

ines (313 $kJ \cdot day^{-1}$, Lasiewski and Dawson 1967) and birds in general (231 $kJ \cdot day^{-1}$, Bennett and Harvey 1987), but were similar to those for seabirds in general (374 $kJ \cdot day^{-1}$, Ellis 1984). BMRs reported here (0.370 $kJ \cdot g^{-1} \cdot day^{-1}$) were considerably lower than those reported for Common and Thick-billed Murres in the Bering Sea (0.626 $kJ \cdot g^{-1} \cdot day^{-1}$, Johnson and West 1975) and Thick-billed Murres in Svalbard (0.535 $kJ \cdot g^{-1} \cdot day^{-1}$, Gabrielsen et al. 1988).

The FMR:BMR ratio calculated from our data ($\bar{X} = 5.16$, Table 2) exceeds the proposed avian ceiling of 4.0 (Drent and Daan 1980), which has been recently supported by the empirical and theoretical arguments of Kersten and Piersma (1987). However, the ratio of 4.0 cannot be considered an absolute ceiling for seabirds, as FMR: BMR ratios of four of 18 seabird species reviewed by Birt-Friesen et al. (1989:table 1) exceed this value.

It must be noted that sample sizes in our energetic trials are small, and further FMR measurements should be made to test the generality of our results. Reported metabolic rates also depend on the reliability of measurement techniques.We have confirmed the validity of our DLW procedures through cross-comparison with isotopic assays performed by two other labs (see Birt-Friesen et al. 1989). Similar comparisons among closed-system respirometry techniques (Ricklefs et al. 1984) used in this study, open system techniques, and DLW would also be useful.

THE MAGNITUDE AND DISTRIBUTION OF PREY HARVEST

Brown and Nettleship (1984) estimated that Common Murres at Witless Bay consume 3246 tonnes of food each year between 1 July and 15 August. Chick-rearing begins approximately 1 July, and their estimate therefore applies both to the time when chicks are reared at the colony and to the time they spend on the water following nest-leaving. Our model estimates consumption at 2774 tonnes for this period. The difference between the two estimates is due chiefly to large differences in two input parameters. Brown and Nettleship (1984) assumed that murres consume 200 $g \cdot day^{-1}$ of food, which is much lower than the 511 $g \cdot day^{-1}$ we derived from DLW measurements. Their lower consumption rate was offset by their assumption that all murres remain in the colony area until 15 August. However, desertion by murres of the colony area proceeds rapidly following the third week in July (personal observations), so that most birds are present in the area during only about half the 1 July–15 August period.

Bioenergetics models that compare estimates of harvest by breeding seabirds with fishery landings and stock size (e.g., Furness 1978, Furness and Cooper 1982) require information on the area over which seabird predation occurs. The foraging areas used in models are usually based on sparse and anecdotal data (Bourne 1983). In addition, the models generally assume that predation is equally intense throughout the foraging area, although foraging effort is often spatially heterogeneous (e.g., Cairns and Schneider 1990). The use of activity timers to calculate flight times and therefore potential foraging ranges during individual trips can aid in clarifying the geographical pattern of resource exploitation around colonies.

Figure 4 shows that predation intensity by Common Murres around Witless Bay may be high at substantial distances from the colony during incubation, but that intensity decreases rapidly with distance from the colony during chick-rearing. It is important to note that predation intensities calculated from potential foraging ranges give maximum distances at which given foraging intensities may occur, and are subject to other limitations. To the extent that foraging birds deviate from straight line courses radiating from the colony, and to the extent that they feed during transit to and from the end-points of these courses, foraging intensities in distant zones will be overestimated. The assumption of straight flight paths seems generally valid; with the exception of birds within 1–2 km of the colony, murres seen in flight during the breeding season are nearly always flying directly toward or away from the colony (Schneider et al. 1990, DKC and WAM pers. obs.). It is not known how frequently murres feed en route to or from their most distant stopping points.

Seabird prey and seabird feeding effort are generally patchily distributed in space and time (e.g., Brown 1980, Schneider and Duffy 1985). Predation intensities calculated from potential foraging ranges apply to concentric rings around colonies, and these intensities indicate local conditions better than do feeding rates that apply to a colony's entire foraging range (e.g., Furness 1978). However, these calculated intensities will not reflect variation within rings. Detailed mapping of foraging intensity is possible only when modeling approaches are combined with fine-scale surveys of distributions at sea (e.g., Cairns and Schneider 1990, Schneider et al. 1990). These two approaches to the study of distribution of foraging intensity around colonies are complementary, because flight time measurements give a picture for the colony as a whole but lack geographic precision, whereas at-sea surveys may precisely locate feeding "hot spots" but are rarely extensive enough to cover more than a fraction of potential feeding area. A third method of mapping foraging intensity, that of long-range telemetry (Trivelpiece et al. 1986, Anderson and Ricklefs 1987) also has potential, although the transmitters now available usually lack sufficient power to allow tracking of offshore and pelagic seabirds to the limit of their foraging range.

Several lines of indirect evidence (Furness 1978, Gaston et al. 1983, Furness and Birkhead 1984, Cairns 1989) and recent direct measurements of prey density around colonies (Birt et al. 1987) have been invoked to suggest that seabirds may deplete prey around colonies. The simultaneous availability of foraging range and dive time data on individual foraging trips suggests a test of this hypothesis. If seabird predation reduces prey density in waters around a colony in which initial prey density is uniform, then foraging success should rise with distance from the colony as successively less-depleted waters are encountered. Central place foraging theory (Orians and Pearson 1979) also predicts that foraging success should rise with distance, because long trips are economical only if they lead to better feeding areas which allow predators to recoup additional transportation costs. In the case of breeding seabirds, prey depletion near the colony should produce an inverse correlation between foraging range and proportion of diving time during individual trips, since birds should require fewer dives to meet food requirements in distant, less-depleted waters.

Potential foraging range and percentage of time diving were inversely correlated during colony-based chick-rearing in 1985, but not during incubation in 1986 (Fig. 3). Although the negative correlation found in chick-rearing in 1985 is consistent with the prey depletion hypothesis, other explanations cannot be ruled out. Capelin, the major food for breeding murres and their chicks at Witless Bay, undergo a spawning migration to coastal beaches in June and July. Migratory or advective flow of food (Cairns and Schneider 1990) will not prevent prey depletion effects if predation is large in comparison with prey influx. However, the arrival of large schools of capelin at sites distant from the Witless Bay colonies could produce a negative correlation between foraging range and dive time in the absence of near-colony prey depletion.

The demonstration of prey depletion by seabirds will remain problematic until difficulties in the measurement of prey distribution and abundance are resolved. However, new techniques such as those used in this study will help clarify the patterns and magnitude of seabird predation and focus questions for future investigation. These are essential steps towards understanding the role of seabirds in marine food webs.

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DAILY FORAGING BEHAVIOR OF MARBLED MURRELETS

HARRY R. CARTER AND SPENCER G. SEALY

Abstract. Patterns of at-sea dispersion, flocking, distribution, flights, and fish-holding behavior of Marbled Murrelets (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia, were synthesized into a descriptive model of daily foraging behavior. Murrelets were clumped in coastal and sill areas in Trevor Channel and used the same feeding sites each day. Adults rearing nestlings flew to and aggregated at feeding sites at or before dawn, fed themselves there early in the day, flew to other areas later in the day to search for prey for nestlings, and returned to nest sites to feed chicks mainly at or after dusk. At this time, adult murrelets minimized time required to feed themselves by specializing on abundant and easily-found prey. Consequently, this maximized time to obtain prey for nestlings, which were less abundant and more difficult to locate. This system may be facilitated by solitary foraging.

Key Words: Marbled Murrelet; *Brachyramphus marmoratus*; British Columbia; foraging; habitat selection; flocking behavior.

The foraging behavior of alcids has been difficult to study because the birds typically forage long distances from nest sites over wide expanses of ocean without obvious landmarks. Thus, foraging behavior has been inferred only roughly from diet, patterns of attendance at colonies or nest sites, and general aspects of their distribution at sea (e.g., densities within specific marine habitats) (Brown 1980, Nettleship and Birkhead 1985). While inter-seasonal and inter-year differences in these aspects of alcid biology have been examined (e.g., Gaston and Nettleship 1981; Ainley and Boekelheide, 1990), the daily foraging behavior of any alcid has never been examined directly in the field. Daily foraging behavior causes variation in the numbers and distribution of birds at sea throughout the day and reflects variability of prey resources, foraging movements at sea, and movements to and from nest sites.

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small alcid that uses nearshore waters year round and often aggregates in small, well-defined feeding areas (Sealy and Carter 1984, Carter and Erickson 1988). While we know little about actual nest sites, their accessible feeding aggregations provide a focus on which to examine distribution and movements at sea. Carter (1984) determined that Marbled Murrelets are most aggregated during the nestling period, when the single chicks are left unattended at solitary nests during the day while adults forage at sea (Sealy 1974, Simons 1980). Adults must forage efficiently when feeding themselves and their chicks, and this should be reflected in their temporal and spatial distributions at sea.

We integrated patterns of dispersion, flocking, distribution, flights, and fish-holding behavior with the few known aspects of nesting biology to construct a descriptive model of daily foraging behavior of Marbled Murrelets in Barkley Sound, British Columbia. This unique approach permitted us to infer foraging behavior from direct observations of birds at sea without following focal birds or monitoring attendance patterns at nest sites. Thus, we were able to elucidate factors affecting the selection and use of feeding areas by murrelets that would not have been possible otherwise.

METHODS

CENSUSES

Marbled Murrelets were censused at sea 37 times between 16 June and 6 July 1980 in south Trevor Channel, Barkley Sound, British Columbia. A contiguous-quadrat grid covering 23.7 km^2 of water surface was used (Fig. 1) and the size of all flocks of murrelets on the water was recorded in each of 96 0.25 km^2 quadrats on each census. Flying birds were recorded but not included in quadrat totals. Censuses began at four times (PDT) of day: dawn (05:00, N = 6), morning (10:00, N = 10), afternoon (15:00, N = 9), and dusk (20:00, N = 12). Each census was conducted by HRC from a pneumatic boat powered by an outboard engine. Dawn, morning, and afternoon censuses averaged 2.1, 2.1, and 2.2 hours, respectively, whereas dusk censuses averaged 1.7 hours. One to four censuses were conducted each day and none was carried out on eight days of the 21-day period that generally coincided with the nestling period of Marbled Murrelets in this area (Carter 1984, Carter and Sealy 1984).

A sitting flock was two or more birds observed within 1 m of one another. A flying flock was two or more birds that flew in the same direction, at the same speed, within 5 m of one another, and usually less than 10–15 m above the water. Single individuals were treated as a type of flock for ease of analysis. Flocks landing or taking off were classified as sitting flocks.

Dispersion indices

We used a comprehensive method for analyzing spatial patterns in contiguous grids based on the relation of Lloyd's (1967) mean crowding index (m^*) to mean density (m) (Iwao 1968, 1972, 1977; Iwao and Kuno 1971). The m^*/m ratio is called patchiness (Lloyd 1967) and measures relative concentration. Often, m^* is linearly related to m. The intercept, α, is called the index

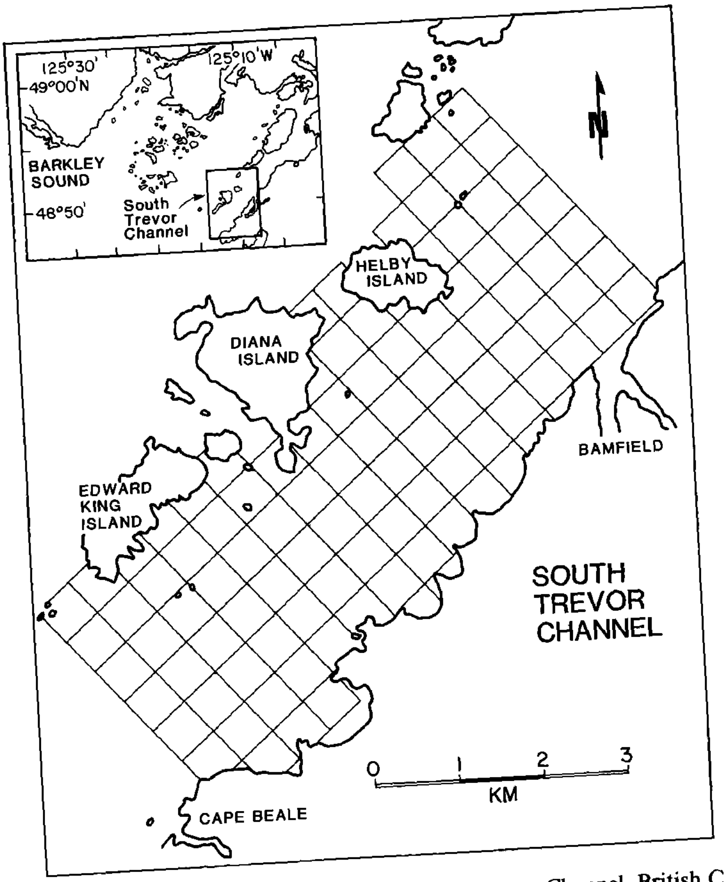

FIGURE 1. Contiguous grid of 96 quadrats in south Trevor Channel, British Columbia.

of basic contagion, and indicates whether a single individual or a group of individuals is the basic component of the distribution. The slope, β, is the density-contagiousness coefficient and indicates how the basic components distribute themselves over the habitat (Iwao 1968). The p index, obtained by successive changes in m^*/m with quadrat size, provides information about the spatial structure of the population (Iwao 1972).

We studied quadrats that differed in size by modifying Greig-Smith's (1952) method for contiguous grids. To use the entire grid, three quadrats were combined first and then quadrat size was increased by a factor of two (see Carter 1984). This method produced six quadrat sizes (q): 0.25, 0.75, 1.5, 3.0, 6.0, and 12.0 km^2.

Grid regions and areas

We divided the grid into 12 regions (see Carter 1984), using three considerations (see Cliff et al. 1975): 1) the system of regions should be simple; 2) the quadrats within a region should be similar to promote homogeneity; and 3) the regions should be compact (i.e., only contiguous quadrats should be combined and they should be closely knit rather than forming a long string). Quadrats in coastline regions were less than 500 m from shore (measured from the center of the quadrat).

Regions were grouped into areas both along and across the channel (see Carter 1984). Murrelets usually flew in straight lines in the grid, typically along or across the channel. The direction of flight was recorded when birds were first observed. Subsequent changes of direction were not examined. Because murrelets flew in small flocks below tree tops, all birds that flew over each quadrat were detected.

The number of birds observed flying depended mainly on how much time the observer spent in each quadrat, which was proportional to the size of the area. Means of 0.5, 0.4, 0.5, and 0.6 hours were spent in south, south-middle, north-middle, and north along-channel areas, respectively, and 0.6, 1.0, and 0.4 hours in west, center, and east across-channel areas, respectively. The number of birds/hr was used to examine flights over different areas of the grid.

Statistical tests

All means in this paper are expressed ± SD (standard deviation). Before analyses, densities (sitting birds/km^2) and numbers of birds flying/hr were transformed logarithmically ($\log_{10}[x + 1]$) because sample variances were greater than sample means; 1 was added to each count (some regions and areas contained no birds). This eliminated the dependence of the variance on the mean, and ensured that the components of the variance were additive. Post-hoc comparison tests (Sheffe's S test and Games-Howell procedure) were used to identify pair-wise differences between means after one-way ANOVA had indicated that differences existed.

To justify using regional changes in mean density (regardless of variation around the mean) to indicate murrelets' use of the grid, the $\log_{10}$(mean density + 1) of Marbled Murrelets was plotted against log S (or variance). The power law states that the variance of a population is proportional to a fractional power of the arithmetic mean. The linear regression $y = 0.13 + 1.89x$ indicated that the log transformation was appropriate because the slope was approximately equal to 2. Log mean density accounted for 87% of the variance of the log variances.

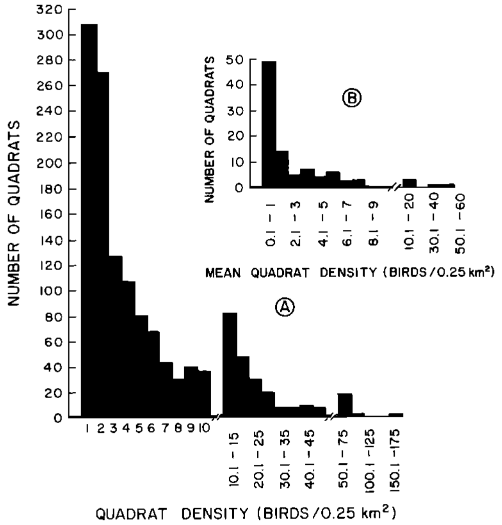

FIGURE 2. Frequency distributions of: A, the number of birds per quadrat (N = 3462 q); and B, the mean number of birds per quadrat (N = 96 q).

RESULTS

DISPERSION OF MARBLED MURRELETS AT SEA

Quadrat use

Numbers of birds/quadrat were positively skewed with a mean of 2.8 ± 7.9 and ranged from 0 to 161 (Fig. 2A). This indicated that birds were clumped within the grid (χ^2 variance-to-mean ratio test, $d = 310.6$, $P < 0.01$). Also, 61.1% of quadrats censused (N = 3462 [90 omitted due to poor observing conditions]) contained no birds. Similarly, mean numbers of birds/quadrat were positively skewed with a mean of 2.9 ± 5.8 and ranged from 0 to 43.2 ± 28.5 (Fig. 2B). This indicated that birds often were clumped in particular quadrats (χ^2 variance-to-mean ratio test, $d = 33.6$, $P < 0.01$).

Occupied quadrats (N = 1347) were arbitrarily divided into four classes of low, medium-low, medium-high, and high density containing 1–10, 11–30, 31–50, and 50+ birds, respectively. Most occupied quadrats (82.2%) were low-density; medium-low, medium-high, and high-density quadrats represented 13.4%, 2.7%, and 1.7%, respectively. Although Marbled Murrelets were clumped, 38.7% of the population occurred in low-density quadrats; medium-low, medium-high, and high-density quadrats represented 32.3%, 13.8%, and 15.3%, respectively (N = 9626 birds).

Dispersion pattern

The regression of mean crowding (m^*) on mean density (m) (Fig. 3) was linear, $m^* = 4.84 + 5.79\,m$ ($F = 21.2$, $P < 0.001$, $r = 0.38$), showing that birds were dispersed in a density independent pattern over the range of mean densities. Residual plots did not indicate any curvilinear relationship. Separate regression lines of m^* on m for each time of day did not differ significantly (ANOVA, $F = 1.8$, $P > 0.05$), although the dawn line (with highest mean densities) fell below other times of the day indicating that the distribution was less clumped. Numbers of empty quadrats also were lower at dawn (55.0%) than morning, afternoon and dusk (60.1%, 62.3%, and 64.3%, respectively). The slope was significantly greater than 1 ($t = 28.8$, $P < 0.05$), indicating that the dispersion of basic components was non-random, being clumped in some quadrats.

Different quadrat sizes

Regressions of m^* on m for each of six quadrat sizes all fitted linear models, although degree of fit increased as quadrat size increased (Carter 1984). Regression lines differed significantly (ANOVA, $F = 17.8$, $P < 0.001$), including differing slopes (ANCOVA, $F = 11.9$, $P < 0.001$) and adjusted means (ANCOVA, $F = 18.9$, $P < 0.001$). All slopes were significantly greater than 1 except at $q = 12.0$ km², indicating clumped dispersions in all but the largest quadrats. Separate regressions for each time of day within each quadrat size did not differ significantly.

In all graphs of mean p-index values by time of day (see Carter 1984) positive correlations resulted between adjacent quadrats. Largest values occurred at smaller quadrat sizes, whereas values fluctuated around 1 at larger quadrat sizes. The general shape of the p-graph indicated that basic components (>1 individual) were clumped and peaks in p-graphs revealed that clumping occurred at 3 spatial levels: ≤0.25, 1.5, and 6.0 km². At the smallest quadrat size ($q = 0.25$ km²),

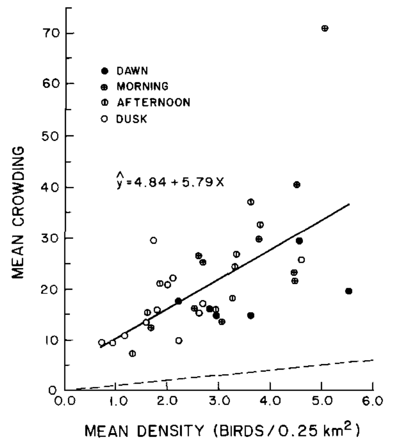

FIGURE 3. Linear regression of mean crowding on mean density. The dashed line indicates the random dispersion of basic components composed of single individuals.

the p index equalled the m^*/m ratio or Lloyd's patchiness index, which increased from dawn to dusk. This further supported the trend that birds were less clumped at dawn but became more clumped towards dusk.

Flocking Behavior

Flock sizes

Sitting flocks were positively skewed with a mean of 2.0 ± 1.9 and ranged from 1 to 55 individuals (Fig. 4). Of 4880 sitting flocks observed, most were single individuals (43.7%) or pairs (39.0%). Of 9626 sitting birds, pairs contributed most birds (40.7%) followed by single birds (22.5%). Flying flock sizes also were positively skewed with a mean of 1.4 ± 1.0 and ranged from 1 to 25 (Fig. 4). Of 885 flying flocks observed, most were of single birds (68.8%), although pairs were common (25.5%). Of 1248 flying birds observed, single birds were most prevalent (48.8%), followed by pairs (36.2%).

Sitting flock sizes were similar throughout the day but were larger as quadrat density increased ($\chi^2 = 42.6$, $P < 0.01$, Table 1). Flocks in low-density quadrats were excluded from the latter analysis because low numbers alone precluded larger flocks from forming. In fact, the preponderance of low-density quadrats partly accounted for the large proportion of small flocks (90.9% of singles and pairs). Medium-low, medium-high, and high-density quadrats also contained large proportions of singles and pairs (77.7%, 75.7%, and 67.9%, respectively). Flock sizes increased with increasing quadrat density only in morning censuses ($\chi^2 = 32.4$, $P < 0.05$). Flying flocks were largest at dawn ($\chi^2 = 18.9$, $P < 0.05$).

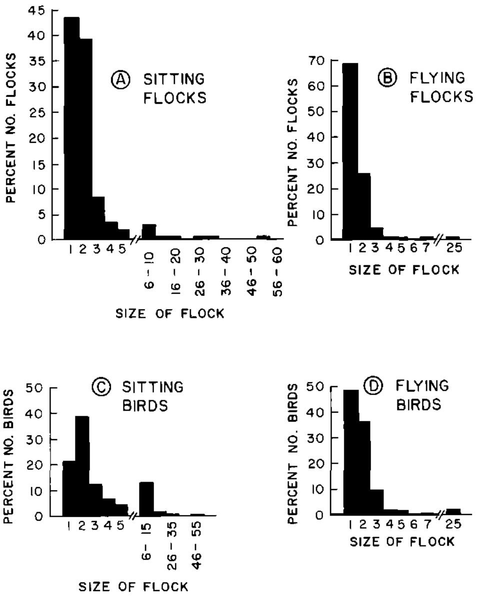

FIGURE 4. Percent frequency distributions per size of flock of: A, the number of sitting flocks (N = 4880); B, the number of flying flocks (N = 885); C, the number of sitting birds (N = 9626); D, the number of flying birds (N = 1248).

Because sitting flocks were significantly larger than flying flocks ($\chi^2 = 201.8$, $P < 0.01$), most must have formed when flocks coalesced on the water. While flying singles joined other birds in flight or landed beside birds already on the water, pairs often flew and landed alone. Larger flying flocks (maximum 25) invariably broke apart as birds landed and other flock members flew on or landed elsewhere. Large sitting flocks seemed to form only temporarily but did not take off as a unit.

Diving behavior

Only single birds and pairs were observed diving. Members of pairs were often seen swimming towards each other on the surface before diving again. Thus, pairs may have been underestimated if birds were apart or if one was under water. Three or more birds never dove together in a coordinated fashion. They often occurred in side-by-side lines which also suggested that they were not feeding (see Bédard 1969). Larger flocks sometimes included fish-holding birds that were not feeding at the time (Carter and Sealy 1987a), although most birds that held fish were alone (80.0%) or in flocks of two (9.6%).

On 8 and 10 June 1980, between 14:00 and 21:00, behaviors noted above were confirmed through observations of murrelets diving in water 10–30 m deep near Taylor Islet. Dive times of 42 single birds averaged 27.8 ± 12.8 sec (range = 2–87 sec; N = 119 dives). Dive-pause ratios, excluding fish-holding birds, averaged 3.9 ± 3.0 (range = 0.17–24.00; N = 105 dives).

DENSITIES

Numbers of sitting birds averaged 265.8 ± 118.3/census (range = 74–518) and densities averaged 11.3 ± 5.0 birds/km^2 (range = 3.1–21.9). Mean densities were significantly higher at dawn and morning (14.4 and 13.9 birds/km^2, respectively) than at dusk (7.7 birds/km^2) (Sheffe's S Test, $\alpha = 0.05$), whereas afternoon densities were intermediate (11.0 birds/km^2) and did not differ significantly from other times (Table 2). Neither tidal state nor weather affected densities (see Carter 1984). When four censuses were conducted in one day, highest numbers twice were recorded at dawn, twice in the morning, and once in the afternoon; numbers were always lowest at dusk, when only 37.1 ± 16.7% (range 17.5–51.6%) of the highest number counted that day remained in the grid. The number at dusk was higher than at other times of day only once (see Carter and Sealy 1984).

Highest mean densities occurred in regions 2 and 3 (50.0 and 24.6 birds/km^2, respectively). Mean densities were higher in west than east regions of the channel, which partly reflected more coastline habitat on the west (7.3 km^2) than east (4.6 km^2) side. Mid-channel regions generally supported lower mean densities than did coastal regions. Region 5, over the shallow sill, had the highest mid-channel mean density (6.3 birds/km^2). In general, regions near or over the sill at the mouth of south Trevor Channel had the highest mean densities.

Mean densities decreased progressively in most regions from dawn/morning to dusk (Table 2). Significant decreases were found in five regions of intermediate density located across the sill (regions 1, 5, and 9) and in regions 10 and 11 where shallow water extended inwards from the sill. Low-density regions (6, 7, 8, and 12) and high-density regions (2, 3, and 4) did not exhibit significant decreases. The densities in the five regions were similar to high-density regions at dawn and in the morning, whereas they were similar to low-density regions later in the day.

FLIGHTS

The number of flying birds averaged 33.7 ± 29.5/census (range = 7–163), which corresponded to a mean of 16.3 ± 12.7 birds flying/hr (range = 3.0–64.7) (Table 3). More birds flew/hr at dawn (37.4 birds/hr) when highest numbers were on the water; morning, afternoon, or dusk (11.1, 9.3, and 15.2 birds/hr, respectively) did not differ significantly from each other (Table 3). North and south flights accounted for 75.5% of daily flights (Table 3). Most flights occurred over west, center, and south areas of the grid, which were associated with intermediate and high densities of birds on the water.

TABLE 1. NUMBER AND SIZES OF FLOCKS IN QUADRATS OF DIFFERENT DENSITIES OF MARBLED MURRELETS BY TIME OF DAY (N = 4880 FLOCKS)

		Quadrat density[1]				
Time of day	Flock size class	Low	Medium-low	Medium-high	High	Total
Dawn	1	204	156	82	18	477
	2	187	154	54	12	436
	3	23	43	15	2	87
	4+	13	33	17	6	73
Morning	1	322	166	76	49	613
	2	266	192	68	74	600
	3	36	51	23	27	137
	4+	30	54	29	51	164
Afternoon	1	308	99	49	51	509
	2	224	99	62	63	448
	3	45	26	12	18	101
	4+	21	24	19	31	104
Dusk	1	398	91	26	19	534
	2	245	108	42	23	418
	3	27	33	13	4	83
	4+	23	42	19	7	97

[1] Density of birds in 0.25 km^2 quadrats: low (1–10 birds), medium-low (11–30 birds), medium-high (31–50 birds), and high (51–161 birds).

At dawn, more birds flew into the grid from the south and north than flew out of the grid. Many birds flew directly towards the sill and west areas (Fig. 5), where there was no difference between northward and southward flights over south-middle and north-middle areas at dawn. After dawn a few more flights occurred near the sill, when densities decreased there (Table 2). Fewer flights in morning and afternoon represented lower within-channel flights as well as few birds leaving the grid area. Although dusk flights did not differ significantly from morning and afternoon (Table 3), the lowest number of birds were in the grid at this time. Increased flights probably occurred relative to the proportion of flying birds that originated from birds sitting in the grid. Directions of flight were the reverse of those at dawn (Fig. 5).

MURRELETS HOLDING FISH

Sitting birds holding fish averaged 3.9 ± 4.9 individuals/census (range = 0–26) and densities averaged 0.2 ± 0.2 birds/km^2 (range = 0–1.0). Few flying birds that carried fish were counted (range = 0–5 birds/census), corresponding to 0 to 3.3 birds/hr. However, at least one fish-hold-

TABLE 2. Mean (±sd) densities (Birds/km^2) of Marbled Murrelets in each Region of South Trevor Channel by Time of Day (N = 37 Censuses). Mean Log Densities that Were Not Significantly Different Are Underscored by a Line (Scheffe's S Test for All Pair-Wise Comparisons (α = 0.5) or are Indicated by NS (One-Way ANOVA, α = 0.05)

Region	Total	Time of day: Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	Differences between ranked log means
1	14.2 ± 14.9	23.4 ± 12.4	26.0 ± 19.3	8.7 ± 6.1	3.9 ± 3.3	M DN A DK
2	50.0 ± 24.2	47.6 ± 26.2	61.2 ± 29.4	55.6 ± 21.1	37.5 ± 16.2	NS
3	24.6 ± 15.2	21.0 ± 7.2	29.3 ± 19.3	25.1 ± 15.5	22.2 ± 14.7	NS
4	15.7 ± 12.3	25.7 ± 17.1	16.9 ± 11.3	14.2 ± 8.2	10.9 ± 11.2	NS
5	6.3 ± 6.5	14.2 ± 10.2	7.0 ± 5.5	4.6 ± 4.5	3.1 ± 2.3	DN M A DK
6	2.6 ± 3.4	3.8 ± 2.9	2.8 ± 4.6	0.8 ± 1.0	3.1 ± 3.4	NS
7	2.2 ± 2.2	2.7 ± 2.9	2.7 ± 3.1	1.3 ± 1.2	2.3 ± 1.6	NS
8	1.1 ± 1.3	1.2 ± 1.1	0.6 ± 1.0	1.1 ± 0.9	1.6 ± 1.8	NS
9	11.0 ± 12.4	14.2 ± 8.0	18.4 ± 17.7	8.4 ± 4.9	0.8 ± 0.8	M DN A DK
10	16.1 ± 18.3	23.9 ± 20.1	20.1 ± 22.7	20.5 ± 18.8	5.5 ± 7.1	DN A M DK
11	8.5 ± 7.8	8.7 ± 7.1	10.0 ± 7.3	11.2 ± 5.0	5.1 ± 9.8	A M DN DK
12	0.9 ± 1.4	0.6 ± 1.1	0.6 ± 0.9	1.7 ± 2.3	0.9 ± 0.8	NS
Total	11.3 ± 5.0	14.4 ± 4.8	13.9 ± 4.6	11.0 ± 3.8	7.7 ± 4.1	DN M A DK
Differences between ranked log means[2]	2	2	2	2	2	
	3	4	3	3	3	
	4	3	1	10	4	
	10	1	10	4	1	
	1	10	4	11	5	
	9	9	9	9	10	
	11	5	11	1	11	
	5	11	5	5	6	
	6	6	7	12	7	
	7	7	6	7	8	
	8	8	8	8	12	
	12	12	12	6	9	

ing bird was observed on 86.5% of the 37 censuses. Fish-holding birds comprised only 1.5% of mean density and only 2.5% of mean birds flying/hr.

Highest numbers of fish-holding birds on the water or flying occurred at dusk (0.27 birds/km^2 and 1.0 birds/hr, respectively), although significant differences were found only between dawn

TABLE 3. Mean (±sd) Numbers of Marbled.Murrelets Flying/Hour by Time of Day and Direction of Flight in Trevor Channel (N = 37 Censuses). Symbols and Tests as in Table 2

Flying direction	Total	Time of day: Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	Differences between ranked log means
North (N)	6.0 ± 5.2	14.1 ± 6.6	4.3 ± 2.6	2.4 ± 2.0	6.1 ± 3.4	DN DK M A
South (S)	6.3 ± 5.9	14.6 ± 9.8	3.6 ± 2.1	3.6 ± 2.1	6.3 ± 3.7	DN DK A M
West (W)	2.7 ± 2.4	6.6 ± 3.0	2.0 ± 1.5	1.5 ± 1.0	2.4 ± 1.6	DN DK M A
East (E)	1.6 ± 2.5	2.2 ± 1.2	1.3 ± 1.5	1.9 ± 4.5	1.2 ± 1.6	NS
Differences between ranked log means	S	N	N	S	N	
	N	S	S	N	S	
	W	W	W	W	W	
	E	E	E	E	E	
Total	16.3 ± 12.7	37.4 ± 16.6	11.1 ± 5.2	9.3 ± 4.0	15.2 ± 7.5	DN DK M A
Total with fish	0.4 ± 0.8	0.1 ± 0.2	0.1 ± 0.2	0.3 ± 0.2	1.0 ± 1.2	DK A M DN

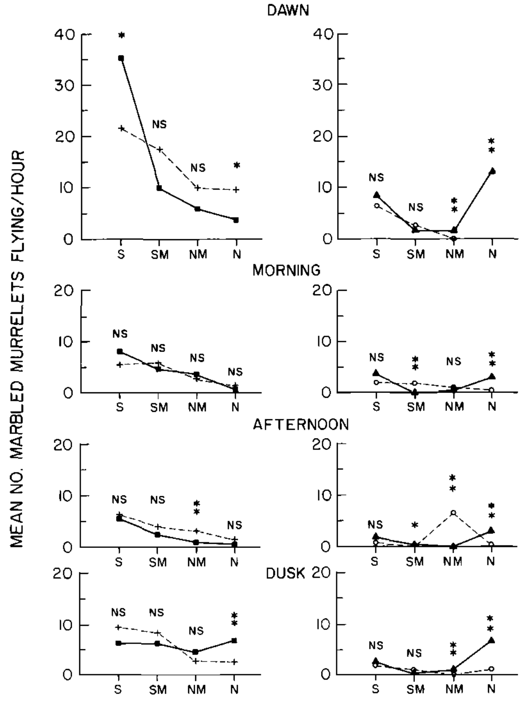

FIGURE 5. Mean numbers of Marbled Murrelets flying/hour by time of day, along-channel area and flight direction. In the left column, the numbers of birds flying north (solid line) are compared with those flying south (dashed line); in the right column, birds flying west (solid line) are compared to those flying east (dashed line). Along-channel areas are coded: S, south; SM, south-middle; NM, north-middle; N, north area. Significant differences between directions of flight in each area are indicated by * ($\alpha = .10$) and ** ($\alpha = .05$); nonsignificant differences are indicated by NS (one-tailed t-test).

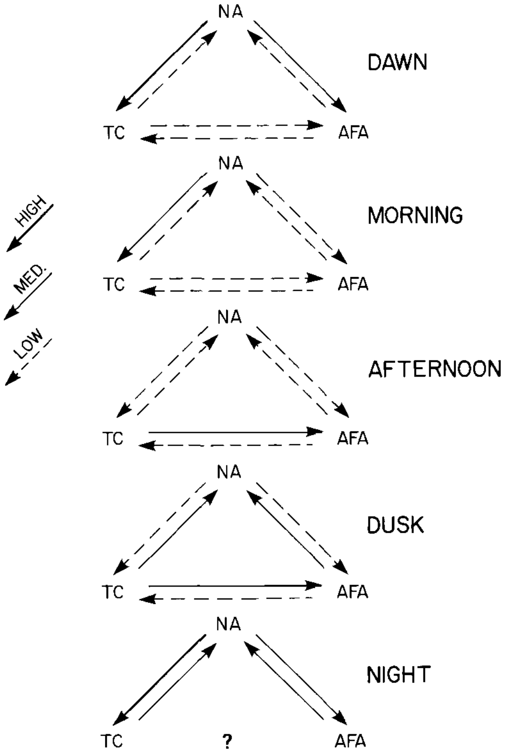

FIGURE 6. Daily movements of breeding Marbled Murrelets between nesting areas (NA), the Trevor Channel feeding area (TC), and alternative feeding areas (AFA) during the nestling period in Barkely Sound, British Columbia. Movements by chick-rearing adults occur throughout the day whereas those by off-duty incubating adults primarily occur between dusk and dawn (see text). Non-breeding birds are assumed not to move in a regular fashion at sea or to nesting areas and are not included.

and dusk (Table 3). The proportion of fish-holding birds increased from 0.2% to 3.5% of mean density and 0.3% to 6.6% of mean birds flying/hr from dawn to dusk. Numbers of sitting and flying birds did not differ significantly between regions or most areas.

DISCUSSION

DIURNAL FORAGING

Each breeding season Marbled Murrelets aggregate daily in south Trevor Channel (Carter 1984, Sealy and Carter 1984). This area evidently provided a reliable source of food because large numbers of murrelets flew there at dawn directly from nesting areas each day (Fig. 6). Adult murrelets fed primarily on juvenile Pacific herring (*Clupea harengus*) and Pacific sandlance (*Ammodytes hexapterus*) in Barkley Sound (Carter 1984). During the murrelets' nestling period these prey are concentrated each year in this traditional nursery area, which is located in sheltered water inside a small-scale oceanographic front at the south entrance of the channel (Hourston 1959; see Carter 1984). Murrelets appeared to travel substantial distances (over sea and land) from nesting areas to reach the feeding area, as indicated by high flight activity over water to the north and south of the grid. Marbled Murrelets probably nest solitarily in trees around Barkley Sound that could be up to 75 km inland (Sealy and Carter 1984, Carter and Sealy 1986). Thus, murrelets in the feeding area probably come from many different nesting areas. While other alcids are known to aggregate at larger-scale prey patches often far from shore (e.g., Schneider et al. 1990), prey availability there is most likely much less stable over time than it is in Trevor Channel for murrelets.

The clumped distribution of foraging murrelets in the grid probably reflected small patches of prey along coastlines and over the sill near the south end of the channel (Hourston 1959; see Carter 1984). The consistent use of specific quadrats and flights directly to intermediate- and high-density regions at dawn indicated that birds returned to known feeding sites or were continually attracted to these sites, perhaps by the continual presence of other birds. However, as the numbers of birds increased, some birds apparently chose not to forage where other birds were clumped, evidenced by the constant dispersion pattern over the range of densities observed, the regular spacing of birds in coastal regions, and the wide use of the feeding area on every census.

Few flights and a distribution similar to that at dawn indicated that birds moved little in the morning and afternoon (Fig. 6). After morning, more birds left than arrived in the feeding area. Flights over the sill after dawn possibly indicated birds shifting to coastal regions as also indicated by clumps of birds being more conspicuous over the sill at dawn but along coastlines later.

FORAGING BY BIRDS FEEDING NESTLINGS

Most murrelets seen holding fish were observed near dusk, just before they fly to their nests to feed nestlings (Simons 1980, Hirsch et al. 1981). A few birds, however, were observed holding fish at dawn and in the morning. Adults that hold fish intended for their nestlings are precluded from capturing more fish until after they have fed the chick. Therefore, we infer that some individuals may feed chicks during the day (Fig. 6), and mainly within a few hours of dawn. This is supported by observations of birds in flight over known nesting areas at these times (Carter and Erickson 1988).

Infrequent fish-holding behavior indicated that prey for nestlings (second-year Pacific sandlance, Pacific herring, and Northern anchovy [*Engraulis mordax*]) in Trevor Channel was less available during the day than the juvenile fish that adults consumed (Carter 1984). Indeed, fish taken for nestlings occur deeper during the day than prey consumed by adults (Hourston 1959, Macer 1965, Baxter 1967).

Increased fish-holding by birds toward dusk coincided with the decrease in overall numbers of birds in the feeding area. The proportion of birds (about 65%) that had left by dusk corresponded roughly to the expected proportion of the population that was feeding nestlings. We presumed that many birds moved to and obtained prey for nestlings later in the day at alternative feeding areas that were distributed widely in Barkley Sound but were used by only a few birds at a time (Carter 1984, Sealy and Carter 1984).

Simons (1980) suggested that murrelets fed nestlings several times on some nights. This was supported further by adults with food in their stomachs being drowned in gill nets at night in Trevor Channel, and by observations of birds apparently feeding at night at inland lakes (Carter 1984, Carter and Sealy 1984, 1986). Thus, if murrelets foraged at night to take advantage of fish (especially for nestlings) closer to the surface, this might explain why some birds were present in the feeding area at dawn.

The foraging behavior of Marbled Murrelets feeding nestlings resembled a "time minimizer" (Schoener 1971, Norberg 1977). By flying directly to Trevor Channel at dawn, birds minimized the time required to feed themselves by specializing on the abundant and easily found resources. This enabled birds to fly to alternative feeding areas some time before dusk and thereby maximized the time needed to obtain less abundant and more difficult-to-locate fish for young on a regular basis. The fast growth rate of nestling Marbled Murrelets compared with other alcids (Simons 1980, Hirsch et al. 1981) may result from regular feedings of relatively large prey loads (Carter and Sealy 1987a), in concert with multiple diurnal and nocturnal feedings, or both, by at least some individuals. This system is enhanced by rearing young when prey are most abundant (Hourston 1959, Carter 1984).

SOCIAL AND FEEDING BEHAVIOR

In Trevor Channel, murrelets occurred primarily as singles and in pairs, as has been reported elsewhere in summer and winter. Pairs probably were mated with chicks at the nest (see Sealy 1975a). Larger flocks of up to 50 individuals also have been reported previously and contain subadults and adults (Sealy 1975b).

Marbled Murrelets apparently fed solitarily because only singles and pairs were observed diving and presumably feeding. Although members of pairs may dive together, this does not imply cooperative foraging. Larger flocks were loafing groups that formed after feeding. Large loafing flocks formed from positive attractions between individual flock members, evidenced by the large sizes of certain flocks (up to 55 birds), increases in flock size with quadrat density, and cohesive formations of flocks on the water. This occurred especially in the morning when fewer murrelets were actively feeding, enabling larger flocks to form and remain together for some time. Larger flock sizes, however, occurred frequently in high-density quadrats regardless of time of day. Larger flocks may involve social interaction, although birds also interact in flight over nesting areas at dawn and dusk (Carter, unpubl. data).

We considered that murrelets were highly solitary feeders because they occurred mainly as singles and pairs in low- as well as high-density quadrats and tended to be more dispersed in the feeding area at higher densities. Thus, murrelets appeared to aggregate where food was clumped but otherwise avoided other individuals while feeding, perhaps to avoid interference or competition (see Leyhausen 1965, Goss-Custard 1970, Duffy et al. 1987).

Feeding solitarily may be necessary to maximize time required for foraging in alternative feeding areas for nestling prey, which occurred in a widely dispersed and low-density fashion in Barkley Sound. Thus, solitary foraging allowed both aggregated and dispersed prey to be exploited efficiently (see Bédard 1969, Asbirk 1979). This may partly account for the continuous occurrence of Marbled Murrelets in high and low densities along much of the coast of the North Pacific, as well as providing a basis for the development of solitary nesting (Day et al. 1983, Sealy and Carter 1984, Carter and Sealy 1987b).

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Chick Rearing at Sea

OFFSHORE DISTRIBUTIONAL PATTERNS, FEEDING HABITS, AND ADULT–CHICK INTERACTIONS OF THE COMMON MURRE IN OREGON

J. MICHAEL SCOTT

Abstract. From 1969 to 1973 I observed 1554 Common Murre (*Uria aalge*) chicks at sea during 365 nautical miles (NM) of surveys near Newport, Oregon. Chicks were most abundant within 1.75 NM of a colony but were also observed farther offshore than were unaccompanied adults. Single chicks were unaccompanied by an adult 87 times (10.7%), accompanied by one adult 704 times (86%), and accompanied by two adults 19 times (2.3%). This pattern persisted throughout each breeding season. Seventeen of 18 adults accompanying chicks at sea were males. I determined dive durations of adults (maximum 153 sec), which fed chicks 80.3% (N = 66) of the times they surfaced with prey.

Key Words: Common Murre; *Uria aalge*; Oregon; distribution; parental behavior.

The Common Murre (*Uria aalge*) is one of seven alcid species in which the young leave the nest prior to obtaining full juvenal plumage and go to sea accompanied by adults. I conducted studies to provide additional information on the at-sea behavior, feeding habits, and distribution of adult–chick groups. My objectives were to determine: 1) the type of adult–chick pairing patterns, 2) what seasonal or yearly variations in pairing patterns existed, 3) the sex of the accompanying adults, 4) offshore distributional patterns of juveniles and unaccompanying adults, and 5) feeding habits of adults and young.

MATERIALS AND METHODS

I conducted my studies off Newport, on the central Oregon coast, and at Yaquina Head during May–October, 1969–1973. Transects were run near the breeding colony at Yaquina Head; one ran parallel to shore in water less than 21 m deep and originated off Newport Jetty, 4.5 NM south of Yaquina Head; the other originated 0.25 NM off Yaquina Head in water 20 m deep and ran 10 NM offshore to water 82 m deep. I made other observations of adult–chick groups from a small boat. The transects were surveyed under standard conditions of vessel speed, location, and wind and sea conditions (Scott 1973). I ran transects weekly during the summer months May–August, 1969–1973, and monthly for the remainder of the year, weather permitting. I began the first transect during any given day 3–4 hours after sunrise.

The 11 m Research Boat, *Paiute,* was used during all transects. I observed birds from the right side of the flying bridge, 3.5 m above the water line. All birds observed in a 180° arc around the bow of the vessel were counted and their occurrence noted by 0.25 NM segments. The behavior, direction of flight, group size, and age of each murre sighted were recorded on standardized forms.

The vessel's engine was run at a constant speed of 2200 RPM allowing for a speed of 9 NM under calm sea conditions. The vessel's position was determined by using a stopwatch, allowing 100 sec for each quarter mile traversed. Compensation for currents, winds, and sea conditions was made by adding or subtracting as much as 10 sec to the elapsed time for each 0.25 NM traversed. The accuracy of these position estimates was verified using radar, reference points on land, and on the offshore transect, a depthmeter at the end of the run. These methods were accurate to within ±0.25 NM (2.5% error) in a 10 NM run. Runs that deviated more than this were not analyzed.

Weather and sea conditions (wind velocity, chop, fog, swell height) were held within a minimum range of values by the extremely limited weather conditions under which the vessel could run the transects. The effect of glare and possible effects of time of day on the behavior of the birds and my ability to see them were minimized by running the first transect of the day between 4–5 hours after sunrise and by confining surveys to conditions of at least 200 m visibility.

Information on the feeding habits of chicks and their accompanying adults was obtained by direct observations of food items handled at the surface and examination of the contents of the proventriculus of birds collected at sea. Whenever possible, I tried to collect isolated adult–chick pairs to avoid confusion as to which adult was accompanying which chick.

I obtained dive times by observing murres from distances <50 m. I first located a bird that was sufficiently isolated so that its diving behavior could be monitored without confusion. A timing sequence was always begun with a dive. When the bird initiated a dive, a stopwatch was started and run until the bird emerged. A second stop-watch was used to record the rest period. If a bird surfaced with a prey item, I calculated separate dive-rest ratios for that dive.

RESULTS

Accompanying adults

Chicks accompanied by adults normally swam within 2 m of and behind the adult, calling frequently. During a bout of dives by the adult, the chick would generally swim in the direction the

TABLE 1. Yearly Variation in the Number of Adult–Chick Common Murre (*Uria aalge*) Groups Observed on Longshore Transects off Yaquina Head, 1970–1972

	One adult–one chick		Two adults–one chick		One adult–two chicks		Unaccompanied chick	
	N	(%)	N	(%)	N	(%)	N	(%)
1969	450	(84.4)	12	(2.7)	3	(0.6)	68	(12.8)
1970	101	(95.3)	3	(2.8)	0	0	2	(1.9)
1971	103	(83.1)	4	(3.2)	0	0	17	(13.7)
Total	704	(86.6)	19	(2.3)	3	(0.4)	87	(10.7)

adult headed upon submergence and called frequently. When the adult emerged it swam toward the chick and usually the chick reciprocated. Adults seldom emerged at distances more than 75 m away. Pairs were not always reunited before the adult dove again. Adults occasionally gave loud raucous calls, to which the chicks immediately responded by calling and swimming toward the adult.

I observed murre chicks: 1) unaccompanied by an adult, 2) with a single adult, 3) accompanied by two adults, 4) with another chick, and 5) with another chick and a single adult. I occasionally observed two adults associated with a chick. However, when it was possible to observe such groups for 300 sec, one adult always left.

I observed no variation among years in the number of adults (unaccompanied chicks were not included in this test) accompanying chicks ($\chi^2 = 1.78$, $P > 0.776$, $df = 4$), and therefore, combined data from all three years (Tables 1 and 2). Most chicks were observed with a single adult (Table 1). No variation in the type of grouping was observed within a summer ($\chi^2 = 0.471$, $P > 0.925$, $df = 3$).

During July–August, 1969, many murres were found dead on Oregon beaches, including the vicinity of Yaquina Head (Scott et al. 1975). The percentage of chicks observed without an accompanying adult was significantly different among years ($\chi^2 = 83.39$, $P < 0.001$) with the number in 1969 being greater than 1970 ($\chi^2 = 8.65$, $P < 0.005$) but not significantly different from that observed in 1971 ($\chi^2 = 0.0029$, $P > 0.950$).

Sex of adult accompanying chicks

I collected 18 adult–chick groups at sea. In all but one of these groups, the accompanying adult was a male ($P < 0.005$). In one group that consisted of two adults and one chick, only one of the adults collected was a female. The weight of the chick was 653 grams or 66.8% of the accompanying female's weight (977 g). Other chicks collected that same day weighed 302, 780, and 893 grams, suggesting that the chick was not a late fledging bird (see Discussion).

Weight of accompanied chicks at sea

Common Murre chicks that I judged to be 75% or more of adult size were frequently accompanied by adults. Four of 15 juvenile birds collected while accompanied by adults weighed 800 g or more. One juvenile still accompanied by an adult had obtained a weight equal to that of the accompanying adult.

Diving behavior

I observed adult Common Murres making dives as long as 154 s and one series of dives lasted 118 min (Table 3).

TABLE 2. Composition and Occurrence of 629 Adult–Chick Common Murre (*Uria aalge*) Groups during the Four 2-Week Periods Following the Observation of the First Adult–Chick Group at Sea. Data Are Only from First Transect of the Day to Avoid Duplicate Counts. These Data Are from Transects Run 4.5 Miles Longshore or 10 Miles Offshore of Yaquina Head, Oregon (1970–1972)

	30 June to 14 July	15 July to 29 July	30 July to 12 Aug.	13 Aug. to 26 Aug.
Nautical miles surveyed	30	60	60	35
No. of adult-chick groups observed[1]	46	239	142	202
Percent of groups having one adult and one chick	97.7	96.9	99.1	95.3
Total adults observed on the water	304	616	343	284
Percent of adults associated with chick	15.1	38.8	41.4	71.1
Adults/transect/mile	10.1	10.3	5.7	8.1
Unaccompanied adults per mile	8.7	6.3	3.4	2.3

[1] Unaccompanied chicks are included in this category and assumed to be accompanied by one adult.

TABLE 3. DIVE/REST SEQUENCES OF ADULT COMMON MURRES (*Uria aalge*) ACCOMPANIED BY CHICKS IN WATER THAT WAS AT LEAST 40 METERS DEEP. ONLY DIVE/REST SEQUENCES WITH MORE THAN 3 DIVES DURING WHICH THE BIRD DID NOT HANDLE PREY ITEMS

		Duration (s)		
	N	$\bar{X}$	SD	95% C.I.
Dives after which prey handled at surface				
Dive	50	104.1	32.9	94.8–113.4
Rest	50	56.8	27.1	49.1–64.5
Dive/rest ratio	50	2.1	1.1	1.82–2.42
Dives after which prey not handled				
Dive	137	100.6	36.4	94.4–106.8
Rest	137	44.5	26.7	39.9–49.1
Dive/rest ratio	137	3.0	2.2	2.63–3.39

TABLE 4. INDICES OF RELATIVE IMPORTANCE (SANGER AND JONES 1984) (0–99 = LOW IMPORTANCE, 100–999 = MEDIUM IMPORTANCE, 1000–9999 = HIGH IMPORTANCE) OF VERTEBRATE PREY ITEMS TAKEN BY JUVENILE MURRES ACCOMPANYING ADULTS AND ADULT MURRES UNACCOMPANIED BY JUVENILES COLLECTED AT THE SAME TIME. BIRDS WERE COLLECTED DURING JULY AND AUGUST OF 1970, 1971, AND 1972

	Adult/chick groups		Unaccompanied adults
Prey item	Adults (N = 7)	Juveniles (N = 9)	(N = 11)
Fish			
Engraulidae	2269	5591	1615
Osmeridae	100	—	—
Scorpaenidae (except *Sebastes*)	1536	309	448
Sebastes	4654	2625	537
Ammodytidae	100	—	555
Anoplopomatidae	—	36	—
Unidentified fishes	227	1064	37

I observed adult–chick groups for 1023 min. During this period 242 dives were made by adult birds and six by chicks. One hundred fifty-four (82.4%) of the dives were 100 sec or longer (Table 3). Prey items were handled at the surface immediately following 66 of the 242 dives by adults (27.3%). On 53 of these occasions (80.3%) the chick was fed by the adult. I observed only one chick capture food. The longest dive by a chick was 30 s (range 18.7–30), and I observed no chick make more than 3 consecutive dives.

The average dive time for accompanied adult murres on dives in which prey was handled at the surface was 104.1 sec, while those for dives in which prey was not handled at the surface averaged 100.6 sec (Table 3).

Feeding habits

Of 60 food items observed being fed to chicks at sea, 31 were items too small to be identified. The identified items ranged from flatfish to anchovies.

Comparison of food items taken by adult murres accompanying chicks and those unaccompanied by chicks collected at the same time shows that juvenile rockfish (*Sebastes* sp.) were a more important part of the diet for unaccompanied adults than accompanied adults (Table 4). One murre chick had an empty stomach, while the accompanying adult had large numbers of euphausiids.

The prey items eaten by chicks did not differ significantly in size from those eaten by their accompanying adults (Table 5). Small unidentifiable food items were observed being fed to young murres by adults at sea on several occasions but no organisms of appropriate size were found in the analysis of stomach contents. As gauged by Sanger and Jones' (1984) Index of Relative Importance, Scorpaenidae are the most important food item for all groups followed by Engraulidae with other taxonomic groups of minor importance. Some differences among groups were noted (Table 4) with chicks feeding more on anchovies than did their accompanying adults or unaccompanied adults. No differences in prey size taken could be determined with the possible exception that unaccompanied adults may feed on smaller rockfish (Table 5).

Chicks at sea

I compared the occurrence of chicks within quarter-mile segments for the first 4 nautical miles offshore (west) and longshore (south) off the Yaquina Head breeding colony. These transects were run daily within one hour of each other. Although there were more adult–chick groups observed on the offshore transect than on the longshore one (156 vs. 102), a larger percentage and number of these were found within 1.8 NM of Yaquina Head on the offshore transect (Fig. 1), and I found more adult–chick groups at distances greater than 2 NM longshore than were found at these same distances offshore ($\chi^2 = 13.41$, $P < 0.005$).

Both the number and percentage of adults on the water that were part of adult–chick groupings increased following the first observation of chicks at sea (Table 2). At the same time, the number of murres/NM observed on the water remained relatively constant through the first two 2-week periods. The number of adults unaccompanied by chicks declined during this same time period,

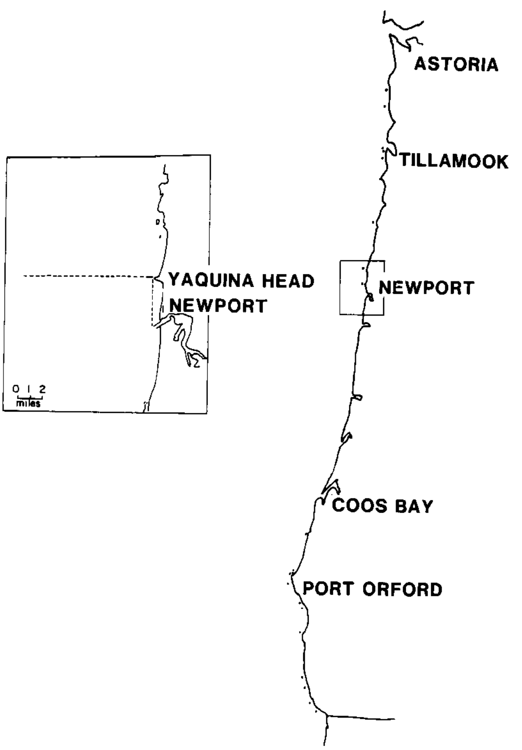

FIGURE 1. Study area in relation to other major breeding sites (designated by dots offshore) for Common Murres in Oregon. The dotted lines on the insert show the two major transect lines. The line running from the North Newport Jetty to Yaquina Head is the longshore transect and the line extending west from Yaquina Head depicts the offshore transect.

suggesting unaccompanied adults leave the area to forage in areas further from Yaquina Head.

Adults accompanied by chicks occurred significantly farther offshore (X̄ = 3.9 NM, SD =2.7, N = 551) than unaccompanied adults seen on the water (X̄ = 2.9, SD = 2.5, N = 453) for birds observed on transects run within 10 NM of the beach.

Eighty-two percent of the adult–chick groups (N = 167) I observed during transects run more than 40 NM offshore were found within 10 NM and 97.6% within 20 NM of the Newport Jetty (Fig. 2).

Adult–chick groups have been observed in Alsea Bay and in Siuslaw Bay 28.6, 15.4 and 29.8 NM south and 78.5 and 55.7 NM north of the nearest Common Murre colonies (Wayne Hoffman, pers. comm.). The greatest distance offshore I found a chick was 36 NM.

DISCUSSION

Chicks at sea

Common Murre chicks were most frequently found offshore with a single adult male. Like Varoujean et al. (1979) and others (Gaston and Nettleship 1981), I found that chicks are normally accompanied offshore by just one adult, a male. The number of adults accompanying a chick did not vary seasonally or yearly. This lack of variation is the same as found by Varoujean et al. (1979) and Birkhead (1976) for Common Murres and Harris and Birkhead (1985) for Thick-billed Murres. Storer (1952:141) reported for central California populations that "after the breeding season they are to be seen in family

TABLE 5. COMPARISON OF THE SIZE (CM FORK LENGTH FOR FISH TOTAL LENGTH FOR INVERTEBRATES) OF PREY ITEMS FOUND IN COMMON MURRE (*Uria aalge*) CHICKS, ACCOMPANYING ADULTS AND ADULT MURRES UNACCOMPANIED BY CHICKS COLLECTED AT THE SAME TIME JUNE–AUGUST (1970–1972) NEAR NEWPORT, OREGON

	Murre chicks		Accompanying adult		Unaccompanied adult	
Prey item	X̄ ± SE	N	X̄ ± SE	N	X̄ ± SE	N
Crustacea						
Mysids			1.3 ± 0.20	(13)	0.08[1]	(59)
Euphausiidae					0.68[1]	(550)
Thysanoessa spinifera					0.5 ± 0.04	(14)
Osteichthyes						
Clupeida			9.3	(2)		
Engraulidae	10.2 ± 1.5	(10)	10.6 ± 2.0	(3)	13.0	(2)
Osmeridae			6.0	(1)		
Scorpaenidae (except *Sebastes*)	6.1 ± 0.4	(11)	5.8 ± 0.6	(10)	5.5 ± 0.42	(19)
Sebastes	5.12 ± 0.7	(5)	5.7 ± 0.6	(17)	3.9 ± 0.2	(20)
Cottidae	5.4 ± 0.3	(5)				
Ammodytidae			9.2	(1)		
Anoplopomatidae					5.9	(1)
Unidentified fish		(1)				

[1] Average volume in cm^3.

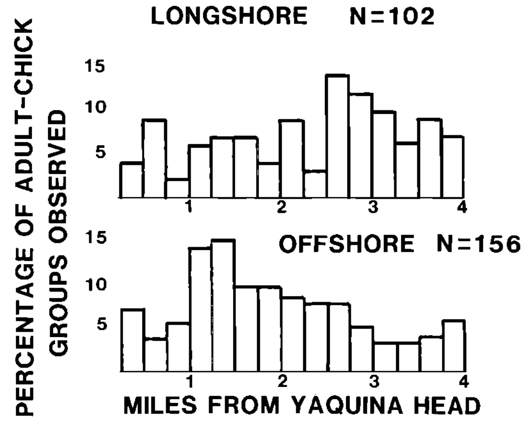

FIGURE 2. Occurrence of adult–chick groups observed during transects run alongshore and offshore of Yaquina Head.

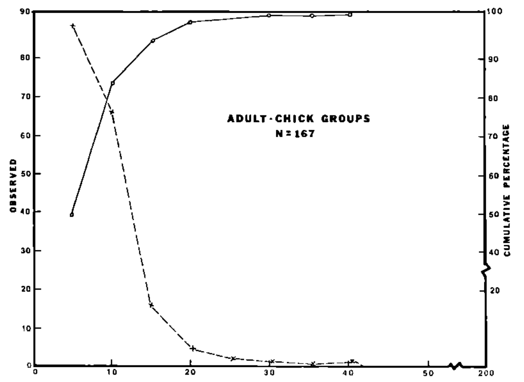

FIGURE 3. Number and distribution of Common Murres observed during transects extending at least 50 miles offshore of Oregon. Data are taken from six different cruises.

groups of three—two parents and one young—until about late August, after which time the young is usually convoyed by one parent." However, more recently he has indicated (pers. comm.) that the statement that two adults accompany a chick immediately after leaving the nest was based on statements in Bent (1919) and was not substantiated by his own field studies.

Uspenski (1958:54) indicates that one adult Thick-billed Murre of either sex usually accompanies a chick to sea. However, he also stated "that usually only one parent is engaged in finding food for the chick." He observed that in September and October flocks were observed in multiples of three "indicating that families (two adults and one young) have not broken up by that time.

The sighting of single chicks (less than ¾ adult size) probably resulted from the accompanying adult being submerged at the time of observation, although a small percentage of these might have been orphaned. The large percentage of unaccompanied murre chicks in 1969 may have been due to an increase in orphaned chicks. An alternative explanation is that, as a result of lower food availability, the adults were foraging a greater percentage of the time and were simply less visible. The percentage of birds collected with empty stomachs in 1971 was intermediate (48.4%) between the figures for 1969 (75.0%) and 1970 (26.9%). This may be indicative of a moderately poor food year. If so, this could explain the similarity in the nature of adult–chick groupings in 1969 and 1971.

Sex of accompanying adult

My finding that in 17 of 18 cases the male accompanied the chick offshore contradicts Tuck's (1961:164) statement that either sex may accompany the chick out to sea. However, Tuck (pers. comm.) indicated that, "of the 20 adults that I collected accompanying chicks, 16 or 17 were males." The only females collected were taken toward the end of the seagoing period and were accompanying late fledging young.

An advantage to having a single adult accompany a chick offshore is that it reduces the number of birds foraging in the immediate area of the breeding colony. These reductions in density could be achieved by a long as well as an offshore dispersal of adult–chick pairs.

I found no evidence to suggest seasonal or yearly variation in the number and sex of adults accompanying chicks at sea. If there is variation in the number and sex of adults accompanying chicks at sea and in other areas, then the question arises as to what factor or factors determine the number and sex of the accompanying adult(s). Food availability has been suggested as a key factor in the evolution of precociality in the alcids (Lack 1968). It could be postulated that two adults would accompany a chick offshore during poor food years to maximize chances of the young surviving. If this is so, then the number of adults accompanying a chick should vary with the availability of food. As stated earlier, I found no evidence for this in my study area nor in the literature.

Disperal from the breeding colony

The distribution of adult–chick groups at sea off Yaquina Head, Oregon, is primarily restricted to waters within 15 NM of the beach (85% of groups observed). The number of murres observed within 10 NM of the Yaquina Head breeding colony decreased 2 weeks after the first chick fledged. The dispersal appears to be more longshore rather than the offshore pattern suggested by Cody (1973:37). He argued that "the inshore zones are much more heavily fished than the offshore areas and thus the chicks could be moved to more profitable sites if food is equally available over larger and more distant areas." The water depth of Yaquina Head, Oregon, increases to 66 m at 5 NM, 80 m at 10 NM and 99 m at 15 NM. Additionally, the number of anchovy likely decreases with increasing distance offshore (Blaxter 1967).

The coastal area is where feeding opportunities might be expected to be the greatest. Anchovies are found in large numbers in shallow inshore waters (Blaxter 1967), and the water is shallow enough so that murres can feed on fish living at or immediately above the bottom, something they might not be able to do regularly in deeper water. Furthermore, the deeper the water, the greater the volume in which a school of fish and other prey can hide, and in deeper water a school might escape predation by swimming to depths beyond the diving capability of the murre. Studies of the distribution and abundance of murres and their principal prey species at sea in areas with different physical and biological resources are needed to determine if feeding opportunities are greater in coastal areas.

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MOVEMENTS OF ANCIENT MURRELET BROODS AWAY FROM A COLONY

DAVID C. DUNCAN AND ANTHONY J. GASTON

Abstract. Radio-tagged Ancient Murrelets (*Synthliboramphus antiquus*) were tracked by aircraft to monitor movements away from a colony. Family groups travelled 48 ± 8 (SE) km from the colony during the first day after departure, at an average speed of 2–3 km/h. Chicks catabolized 41% of their lipid reserves in the two days between hatching and departure from the colony. The remaining reserves can sustain chicks for <2 days more. The presence of some family groups in central Hecate Strait 2–4 days after departure shows that chicks must be being fed there.

Key Words: Ancient Murrelet; *Synthliboramphus antiquus*; energetics; parental behavior.

Alcids exhibit an array of chick-rearing modes, from feeding semi-precocial young at the nest site until fully grown to rearing precocial young completely at sea (Gaston 1985). The latter group is comprised of the *Synthliboramphus* murrelets. Because *Synthliboramphus* chicks go to sea within a few days of hatching (Sealy 1973), their ecology is almost unknown.

Ancient Murrelets (*S. antiquus*) are small precocial alcids that nest in burrows, often in mature forests, on islands in the North Pacific Ocean. Newly hatched chicks go to sea with their parents about two days after hatching (Sealy 1976). Parents lead their two chicks from the burrow at night, then generally fly to the sea and call, as the chicks run down to the shore to rejoin them (Jones et al. 1987a, b). Family groups of Ancient Murrelets appear to move rapidly offshore because they rarely are seen near colonies, and few have been observed at sea (Sealy and Campbell 1979, Gaston, pers. obs.). Sealy and Campbell (1979) considered the paucity of sightings of Ancient Murrelet broods puzzling in light of the large number of breeding birds (254,000 pairs in the Queen Charlotte Islands (QCI) (Vermeer and Lemon 1986)).

The study of animals at sea is difficult. Attempts to use radio telemetry on small seabirds have been hampered by difficulties in waterproofing and attaching small transmitters, and in tracking birds over large areas of water (Wanless et al. 1985), because studies have been restricted to tracking the birds from land (Harrison and Stoneburner 1981, Wanless et al. 1985, Croll et al. 1986, Anderson and Ricklefs 1987). We used small transmitters and fixed-wing aircraft to determine the movements of Ancient Murrelet broods away from a colony.

METHODS

Field work was conducted at a breeding colony on Reef Island, off the east coast of the QCI archipelago, and in Hecate Strait between the QCI and mainland British Columbia (Fig. 1). Transmitters were attached to Ancient Murrelet adults and chicks between 29 May and 6 June 1987. Two types of transmitters were used: RI-2 (2.0 g) for adults and BD-2 (0.8 g) for chicks (Holohil Systems Ltd., Woodlawn, Ontario, Canada).

Five adults whose young had hatched were removed from burrows during daylight and transmitters were glued to their lower backs using 5-min epoxy and then covered with waterproof tape (Superstik, Superior Insulating Tape Co., St. Louis, Missouri). Birds were then replaced in their burrows. Transmitters were also attached to two adults that were captured on the ground at night with a dipnet, while leading their chicks to the sea. Chicks were caught at night using funnel traps made of two 50-m-long fences of 0.5-m-high clear plastic sheeting positioned to guide departing chicks towards a catching point near shore. Sixteen chicks had transmitters glued to them and were released at the water's edge 10 min later. Only one transmitter was attached per batch of concurrently captured chicks to minimize the possibility of having more than one transmitter per family group. Some additional chicks were weighed and banded in their burrows to provide data on weight loss between hatching and departure.

Departures of families were monitored from the shore of the island with a hand-held Yagi antenna at approximately 15-min intervals for up to 4 h. Time of departure was noted, departure headings were estimated with a compass, and weather and sea conditions were estimated visually at Reef Island at midnight. Local wind speed and direction were obtained from Transport Canada at Sandspit Airport.

Aerial surveys were made from a Beaver aircraft with a Yagi antenna attached to each side of the plane, parallel to the wing. Surveys were conducted the day following departure of radio-marked birds and were concentrated in the area indicated by the birds' initial direction of departure. The area most intensively surveyed was between Sandspit and Reef Island, northeast across Hecate Strait to Banks Island. Locations of birds were plotted by triangulation from compass bearings on landmarks where possible, or by triangulation from bearings from radio beacons using an automatic direction finder (ADF). Surveys on subsequent days were conducted over central and northern portions of Hecate Strait, and were generally concentrated over an area indicated by extrapolation from the initial positions and directions of travel of the birds. These less frequent surveys covered an area due east from Reef Island

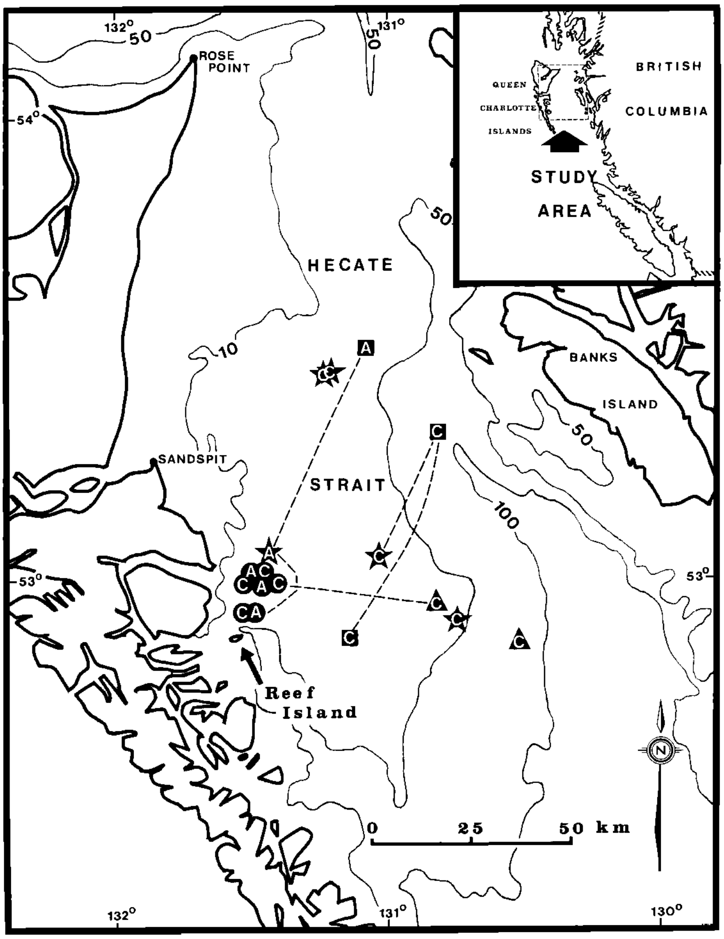

FIGURE 1. Bathymetric map (fathoms) of Hecate Strait, British Columbia showing the movements of radio-tagged Ancient Murrelet chicks (C) and adults (A) away from their breeding colony on Reef Island. Positions are 6–8 h (circles), 12–18 h (stars), 36–42 h (triangles), and 60–84 h (squares) after departure from the colony. Dashed lines connect positions of the same bird.

across Hecate Strait, north to Rose Point. Surveys were flown at an altitude of 90–180 m in an approximate grid pattern and extended virtually the entire width of Hecate Strait. The area where the surveys were conducted and over which birds potentially ranged was about 7500 km^2 (width of Hecate Strait × distance between Reef Island and halfway to northern tip of QCI). Twelve survey flights were made from May 29 to June 9. Detection distance of transmitters was 2–4 km as determined from time between radio contact and maximum signal strength, and from transmitters attached to pieces of wood floating at sea. The large area over which the birds ranged and small detection distance of transmitters, combined with presumed loss of some transmitters and mortality of chicks, resulted in few locations of radio-marked birds per flight, particularly of birds that had left the colony >1 day previously.

To determine energy reserves of chicks as they departed the colony, chicks were collected from the funnel traps in 1986. Yolk sacs of these chicks were excised and weighed, and all material was preserved in 9% formalin. Lipid was extracted from chicks and yolk sacs with petroleum ether in a Soxhlet apparatus. Energy reserves of these chicks were compared to those of newly hatched chicks (from Duncan and Gaston 1988). Lipid content is expressed as a lipid index (g lipid/g lean dry mass). Statistics are given as mean ± 1 SE.

RESULTS

Thirteen chicks captured in funnel traps had been weighed previously in their burrows. These chicks lost 5.1 ± 0.6 g during the 36 ± 3 h between weighings (N = 13). Because the chicks were 0–24 h old when first weighed, total weight loss between hatching and departure would be higher. Some weight loss was caused by catabolism of most of the yolk; yolk sacs of departing chicks were 0.6 ± 0.2 g (N = 10) compared to 3.4 g (N = 7) in newly hatched chicks (Duncan and Gaston 1988). Lipid from both the yolk sac and carcass was used during this time (Table 1); the lipid indices of chicks decreased from 0.71 to 0.41 between hatching and departure, representing a mean loss of 41% of their lipid.

We assume that the transmitters did not substantially interfere with the normal behavior of the birds and that radio-marked adults were accompanied by chicks. Observations of radio-marked chicks and adults leaving the colony supported this assumption with the following exception. One of the two adults captured above ground while accompanying chicks to the sea moved more rapidly at sea than the other birds and was observed twice from the aircraft, each time without chicks and in the company of 4–6 other adults (this was the only radio-marked individual observed from the air). This bird was excluded from all analyses.

All sixteen radio-tagged chicks left the island between 00:00–02:00. Signals from chicks were detected from shore for an average of 108 ± 12 min (N = 15) but those from adults (larger transmitters) were heard for 148 ± 24 min (N = 6). In all cases signal strength diminished within 30 min of chicks being released, indicating rapid movement away from the colony. All birds headed northeast, although it was difficult to determine direction because signal strength fluctuated, presumably because of obstruction from waves.

Wind was from the south on all dates when radio-marked birds departed from the colony. On 29 May, wind was from the southeast and increased from 20 km/h at 00:00 to 60 km/h by mid-afternoon. Birds located 6–8 h after leaving the colony that day (two chicks and one adult) were farther west than those located on other dates, probably due to the strong wind and consequent rough sea conditions.

Eleven birds (48%) were located from the air within 24 h of their leaving Reef Island. Mean distance from the colony 6–8 h after departure was 13 ± 2 km with an average speed of 1.9 ± 0.3 km/h (N = 7) (Figs. 1, 2). By 12–18 h after departure birds were 48 ± 8 km (N = 5) northeast of Reef Island, and were distributed over an area >1000 km². Average speed of the family groups at this time was 3.0 ± 0.4 km/h (N = 5).

Four birds located >24 h after they left the colony were at least 25 km from land, but were not much farther from the colony than those located after 12–18 h (Figs. 1, 2). No aggregations

TABLE 1. LIPID AND LEAN MASS (G) AND LIPID INDEX (G LIPID/G LEAN DRY MASS) OF CARCASSES, YOLK SACS, AND WHOLE BODIES OF ANCIENT MURRELET CHICKS AT HATCHING AND AT DEPARTURE FROM COLONY ($\bar{X}$ ± SE)

Status of chick	N	Carcass[1]			Yolk sac			Whole body
		Lipid	Lean	Lipid index	Lipid	Lean	Lipid index	Lipid index
Recently hatched[2]	8	2.96 ± 0.10	4.60 ± 0.07	0.64 ± 0.02	0.97 ± 0.08[3]	0.96 ± 0.09	1.03 ± 0.07	0.71 ± 0.02
Leaving colony	10	2.01 ± 0.15	5.18 ± 0.19	0.39 ± 0.02	0.31 ± 0.12[4]	0.25 ± 0.13	1.64 ± 0.49	0.41 ± 0.02

[1] Carcass = whole body (plucked) minus yolk sac.

[2] From Duncan and Gaston (1988).

[3] N = 7.

[4] N = 5; yolk sacs of the others were too small for analysis.

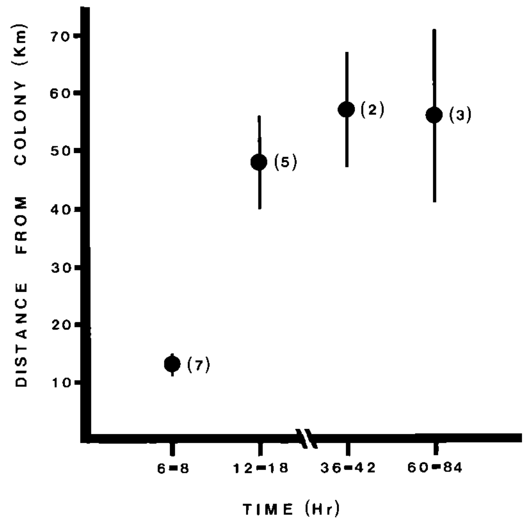

FIGURE 2. Mean (±SE) distances of radio-marked Ancient Murrelet family groups from Reef Island within 4 days of leaving the colony. Numbers in parentheses denote sample sizes.

of birds were observed, although two chicks were an estimated 500 m apart 12–18 h after departure (Fig. 1; northeast of Sandspit). The chicks differed in weight more than most siblings (Gaston, unpubl. data), suggesting that two family groups may have been travelling together. They may, however, have been siblings, despite attempts to mark only one member of a family group.

DISCUSSION

Ancient Murrelet chicks hatch with one of the highest lipid contents among birds (Duncan and Gaston 1988). However, they lose >5 g between hatching and leaving the colony (see also Sealy 1976, Vermeer and Lemon 1986), including 1.6 g of lipid. When the chicks go to sea, their lipid indices are 0.41. At indices of <0.20–0.30, lipids of migrating birds can only be used with a concurrent catabolism of non-fat tissue (Odum et al. 1964, Johnston 1968), and at 0.1–0.2, a chick is close to starving to death (Duncan 1988 and references within). An emaciated chick that was found dead at sea had a lipid index of 0.08. If the rate of lipid catabolism remained the same at sea as it was between hatching and colony departure, the lipid index of an unfed Ancient Murrelet chick would be 0.1 (i.e., starvation) about two days after leaving the colony. However, energy utilization is likely higher at sea because of increased costs of locomotion and of thermoregulation due to lower ambient air and water temperature (but see Eppley 1984). Thus, Ancient Murrelet chicks must probably be fed <2 days after leaving the colony.

The rapid attenuation of radio signals supports observations of family groups quickly leaving the vicinity of the island. Within 4 h after sunrise, Jones et al. (1987a) found some family groups swimming rapidly away from Reef Island, 4–12 km from the island, and Sealy (1976) reported that family groups from Langara Island in the QCI archipelago were >10 km from shore by daybreak. The rapid movement may be to reach areas of high food availability quickly, or to get away from land where avian predators (e.g., gulls) are more abundant, or both.

The rate of movement of family groups in the first 24 h after leaving the colony was 2–3 km/h, which is over two times greater than the theoretical maximum swimming speed of chicks (1.0–1.3 km/h; from Prange and Schmidt-Nielsen's (1970) equation). This suggests, assuming the theory is correct, that the chicks moved by running on the water (which they have been observed to do while departing from the island) or by moving with the currents.

Tidal flow apparently did not determine direction of travel because the direction of the tidal flow at night would have been reversed over the one-week span that birds departed; tidal flow generally runs north and south in Hecate Strait (Thomson 1981). Despite this, all family groups initially travelled northeast after leaving Reef Island. Also, family groups maintained this general heading for 12–18 h after leaving the colony even though the tidal current changed direction twice each day. Surface water flow in Hecate Strait is primarily due to wind-induced currents (Thomson 1981), and these probably influence the movements and survival of murrelet broods. For example, on May 29, the strong northeasterly wind and resulting rough sea conditions appeared to push birds to the west more than subsequent groups and may also have caused mortality of chicks. Three of the first four birds radio-tagged (three chicks and one adult) were located by aircraft early on that day, when they left Reef Island, but none was found subsequently. Because these were the first birds marked, they were available for the greatest number of searches and thus had the highest probability of being detected later.

Some family groups remained in central Hecate Strait for 2–4 days after leaving the colony despite the fact that they had the speed to move out of the study area within about two days. Although chicks must be fed during this time, it is unknown whether this is a brood-rearing area or merely a resting area. The initial northeastern heading suggests some family groups may have travelled to the north end of the QCI. Vermeer et al. (1985) recently observed Ancient Murrelet family groups over a seamount and along the edge of the continental shelf break >15 km off the northwest coast of the QCI. The water depth in those areas is 50–200 m, similar to that in which we found broods >24 h after leaving the colony (25–100 fathoms; Fig. 1). The shallow bank in northern Hecate Strait may make this area unfavorable and could be the reason no family groups were found there. It is not known if birds moved into southern Hecate Strait because surveys were not conducted south of Reef Island. Although Ancient Murrelet family groups appeared to be widely dispersed as suggested by Sealy and Campbell (1979), Vermeer et al.'s (1985) observations of aggregated groups shows how interpretation of spatial patterns is scale dependent (Hunt and Schneider 1987).

The use of radio telemetry to study small seabirds such as Ancient Murrelets is limited by the short transmission range of small radio transmitters and the wide dispersion of birds at sea. Surveys such as those of Vermeer et al. (1985) which census and document locations of birds at sea, combined with information on food habits and energy reserves of the chicks, are needed to further elucidate the chick-rearing ecology of Ancient Murrelets.

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Diets in Relation to Prey Resources

GELATINOUS ZOOPLANKTON IN THE DIET OF THE PARAKEET AUKLET: COMPARISONS WITH OTHER AUKLETS

NANCY M. HARRISON

Abstract. I studied the diet and foraging habits of the Parakeet Auklet (*Cyclorrhynchus psittacula*), Least Auklet (*Aethia pusilla*) and Crested Auklet (*A. cristatella*) in the northern Bering Sea from 1983 to 1986. Parakeet Auklets frequently fed on gelatinous zooplankton (e.g., jellyfish and ctenophores) and jellyfish symbionts such as hyperiid amphipods and fish larvae. In the Chirikov Basin 54% of the Parakeet Auklets collected (N = 13) had eaten jellyfish and 69% had eaten ctenophores (some birds with both prey); near St. Matthew Island 54% (N = 39) had eaten jellyfish, with no ctenophores in evidence. Euphausiids and other zooplankton, which live independently of jellyfish, were abundant at the latter site and were eaten by all three auklet species. I found greater dietary overlap between Parakeet Auklets and the *Aethia* species at St. Matthew Island than in the Chirikov Basin. The unique upturned bill of the Parakeet Auklet may be a specialization for handling slippery gelatinous zooplankton. In the Chirikov Basin Parakeet Auklets were more dispersed than were Least Auklets, which were usually aggregated. The dispersed foraging distribution of the Parakeet Auklet may be linked to its habit of feeding on jellyfish.

Key Words: Crested Auklet; Least Auklet; jellyfish; ctenophore; diet; Bering Sea.

Bédard (1969a) studied the feeding habits of the Parakeet Auklet (*Cyclorrhynchus psittacula*), the Least Auklet (*Aethia pusilla*), and the Crested Auklet (*A. cristatella*) on St. Lawrence Island in the Northern Bering Sea. He found very little dietary overlap among the three species. The Least and Crested Auklets were dependent on seasonally abundant zooplankton, copepods and euphausiids, respectively. Parakeet Auklets had a varied diet which included hyperiid amphipods, fish larvae and other large zooplankton; there was less temporal variation in their diet than in the diets of the *Aethia* species. All three species fed in the same areas at sea, and the low dietary overlap suggested there were fundamental differences in their foraging behavior.

Colony attendance patterns indicate that the Parakeet Auklets spend more time at sea than the *Aethia* auklets (Bédard 1969a, Manuwal and Manuwal 1979). Least and Crested auklets have activity patterns on the colony that suggest they feed after dawn and in the late afternoon (Sealy and Bédard 1973). The largest numbers of Parakeet Auklets occur on the colony at midday; they spend 60% more time at sea than the *Aethia* auklets (Bédard 1969a) and potentially feed at night as well as during the day (Bédard 1967, pers. obs.).

The auklets are in effect partitioning resources. The Least Auklet is smaller than the Crested and Parakeet auklets, and it consistently feeds on smaller prey. The Crested and Parakeet auklets, however, are of similar size and bill proportions, yet have completely different diets. Bédard (1969a) concluded that the differences in prey selection by these two species must result from differences in daily activity patterns, subtle differences in bill morphology and innate preferences for different zooplankton. It is difficult to infer how the auklets maintain their dietary specialties without an understanding of their foraging habitat, and the patterns in which they encounter their prey.

Birds living in terrestrial environments are often seen to feed in different microhabitats, the vegetation providing habitat structure that determines where they search for prey. In marine environments jellyfish potentially provide similar habitat structure (Hamner et al. 1975), offering surfaces for other creatures to sit upon and forests of tentacles to hide among, and they are ubiquitous and abundant.

I first noted Parakeet Auklets feeding on jellyfish at sea in the area of St. Matthew Island in 1983 (Harrison 1984); there are two reasons for suspecting that jellyfish are a frequent prey. First, Parakeet Auklets often have material in their stomachs that is amorphous, well digested, and difficult to identify (Bédard 1969a, pers. obs.). Second, many of the prey documented for the species (Bédard 1969a, Hunt et al. 1981) are jellyfish symbionts or parasites. Hyperiid amphipods are typically jellyfish associates (Harbison et al. 1977, Laval 1980) as are gadid fish larvae

(Mansueti 1963, Van Hyning and Cooney 1974). My observations were the first sign of the jellyfish host in their diet.

In this paper I assess the relative importance of jellyfish in the diet of the Parakeet Auklet. I address the following questions. To what extent do Parakeet Auklets eat jellyfish? Do crustaceans and fish associated with jellyfish constitute an important part of their diet? Do food habits vary geographically? Do jellyfish occur less in the diet of Parakeet Auklets from a site where more nutritious prey are abundant? How do the diets of Parakeet, Crested and Least Auklets differ? How are the distributions of Least and Parakeet Auklets affected by spatial patterns of prey availability?

METHODS

Collections

Foraging auklets were collected at sea during the breeding season (late June–August) from 1983 to 1986 in the waters surrounding St. Matthew Island and in the Chirikov Basin (Fig. 1). Small numbers of birds were collected from a number of sites, usually only one or two species represented in any single collection. Least Auklets were collected in the Chirikov Basin just north of Gambell, St. Lawrence Island, near the location of Bédard's study. Both *Aethia* species were collected north of Savoonga, St. Lawrence Island. Least and Parakeet auklets were collected in 1984 and 1985 at many positions along the "King Island transect" from east of King Island to a point 64 km due west (Fig. 1). Auklets were frequently collected from mixed-species feeding flocks in the St. Matthew area; in 1984 all St. Matthew collections were made on the east side of the island, where large aggregations of murres (*Uria* spp.) and auklets fed on euphausiids (Hunt et al. 1988). In 1985 and 1986 all collections were made in the Sarichef Strait area.

The proventriculus and gizzard were removed promptly after a bird was shot and the gular pouch was searched for prey. I found no difference between the contents of the proventriculus and the gular pouch (Harrison 1987) and combined the data for analysis.

Food samples were examined while fresh for the presence of fragile prey, such as jellyfish and ctenophores. The presence of ctenophores was confirmed by the identification of comb rows; nematocysts helped confirm the presence of jellyfish. Gut contents were preserved in 80% ethanol for later study.

All intact crustaceans and fish were tallied. When possible I measured the volume of each prey species or species group (e.g., Scyphomedusae). I calculated the frequency occurrence of prey among the samples (frequency occurrence = number of stomachs containing a given prey/number of stomachs examined × 100). Estimates of jellyfish are conservative because many samples had remnants of possible jellyfish tissue that could not be confirmed. The number of prey items is usually ambiguous in these samples because many prey are represented by fragments. I did not compare number, volumes or weights of prey, as these are likely to be biased by relative digestibility, especially for gelatinous zooplankton. However, to obtain some measure of the relative importance of prey, I used prey number and volume (for gelatinous zooplankton) to assess the importance of each prey in a given sample. I then made separate tallies of all prey in the stomachs, and assigned these to one, two or all three of the categories based on the following criteria:

1. Any identifiable prey type was tallied in the "all prey" frequency analysis.
2. Prey occupying at least one third of a sample's volume, or constituting at least one third of the number of prey items, was considered "significant prey."
3. Prey dominating a sample in volume or number by 10 fold was considered "dominant."

In comparing the diets of the auklets I used an overlap index (Horn 1966, Diamond 1983), "C," with values ranging from "0" for no overlap to "1" indicating complete overlap

$$C = \frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where s is the number of prey categories in the two bird species being compared, and category i is represented x times in species x and y times in species y. Although "1" indicates total overlap, the actual value calculated for a pair of samples depends on the number of prey categories (Diamond 1983). I did not include squid beaks, nereid beaks or fish bones when calculating overlap indices because they are retained an unknown time in the guts.

Using overlap indices is a problematical procedure because there is no theoretical statistical distribution that can be used to compare overlap measures. However, by taking random combinations of the data, a "random expectation" can be established. For example, to compare the diets of birds collected from a single feeding flock, I entered the prey of all individuals of each species pair (i.e., 6 Parakeet Auklets and 4 Least Auklets) into a Turbo Pascal program. The program shuffled the data into all possible permutations (a total of 10 birds redistributed into 210 possible combinations of 4 and 6), calculated overlap indices for each new set of 4 and 6 in turn (210 overlap values) and then determined the mean overlap and the standard deviation. The actual overlap between the two samples can then be compared to the calculated random expectation.

Overlap indices were also used to compare species using the full set of data. I did not run all possible combinations because of the very large numbers of permutations. After the program calculated 1000 overlap values for a species pair, the mean changed relatively little, and the standard deviation was nearly constant. Mean overlaps are presented based on 1000 permutations.

Plankton sampling

Acoustic data were collected by T. Cooney using a Biosonics high-frequency echosounder (200 kHz). Acoustic records showing plankton biomass, integrated with depth, are presented for the full water column

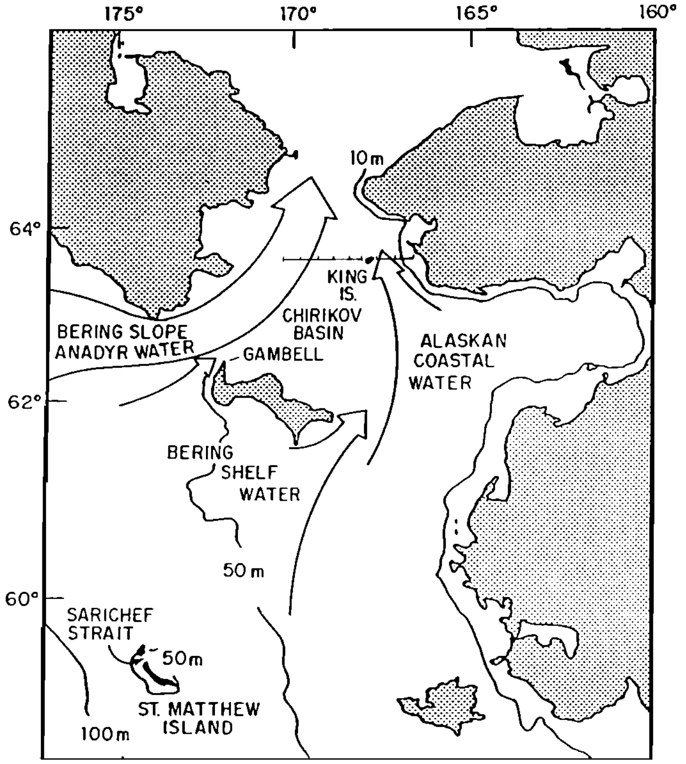

FIGURE 1. Location of the Chirikov Basin and St. Matthew Island in the northern Bering Sea, with transect shown extending east and west of King Island.

along two transects, one in the St. Matthew Island area, through the Sarichef Strait, and the second across the Chirikov Basin, west of King Island.

Plankton tows were made as part of a concurrent study (Hunt et al. 1990). A one-meter 505-micron mesh net was lowered to within 5 m of the bottom, then hauled vertically to the surface. Plankton were preserved in formalin, split into subsamples and counted in the laboratory. Gelatinous animals tend to be damaged or destroyed by nets, and no quantitative data are provided on their abundance.

Bird distributions

Numbers of Least Auklets and Parakeet Auklets were censused along a transect near King Island (Fig. 1), which extended 32 km due east of King Island to 64 km west. At 16 km intervals we made vertical plankton tows and measured physical properties of the water column (temperature, salinity and density with depth) using a CTD (Conductivity-Temperature-Depth probe). The transect was run 15 times during the four year study.

Continuous counts were made from the ship, the *R/V Alpha Helix,* while steaming between hydrographic stations. All birds were counted within a 90 degree arc from bow to beam to a distance of 300 m; only those auklets sitting on the water were used in the analysis of foraging dispersions.

I compared the distribution of Least and Parakeet auklets using Kolmogorov and Smirnov methods (Sokal and Rohlf 1981). I divided each continuous transect into 10 minute intervals, then established a frequency distribution based on the number of 10 minute observation blocks with 0 birds, 1 bird, 2 birds, etc. I compared each species to the expected cumulative frequency distribution for the Poisson distribution. If the frequency distribution was significantly different from the Poisson ($P < 0.05$) then I determined by inspection whether the birds were more clumped or more dispersed than random.

STUDY AREAS

The Chirikov Basin is the shallow (50 m) northern extreme of the Bering Sea. The western half has an oceanic fauna because of the influence of the Anadyr Current; the current passes from the deeper Bering Sea north through the Bering Strait (Coachman et al. 1975) (Fig. 1), carrying in large calanoid copepods and other oceanic zooplankton (Cooney and Coyle 1982). The plankton community changes across the basin, with a zooplankton community characteristic of coastal Alaskan waters in the east. The coastal community has a relatively low plankton biomass, and a high diversity of jellyfish, small fish and crab larvae (Cooney 1981). The highest biomass of plankton is in the central Chirikov Basin where the oceanic water and coastal water

TABLE 1. Frequency of Occurrence of Prey from Parakeet Auklets[1]

	St. Matthew Island				Chirikov Basin	
	1983	1984	1985	1986	1984	1985
No. samples	8	14	7	10	9	4
Gelatinous zooplankton						
Ctenophora					66	75
Scyphomedusae	75	43	43	60	56	50
Medusa associates						
Amphipoda						
Hyperia	38			10		
Hyperoche			43			
Unid. hyperiid					11	25
Gadid fish						
Theragra chalcogramma	25		100	40		
Unid. gadid larvae					33	
Free-swimming prey						
Pteropoda						
Limacina	25			20	33	50
Polychaeta						
Nereid beaks	25		57	80		
Copepoda						
Neocalanus plumchrus						25
N. cristatus					11	
Calanus marshallae			14			
Pseudocalanus elongatus			43			
Unid. copepod	13					
Amphipoda						
Parathemisto libellula	25		43	80	11	
Euphausiacea						
Thysanoessa raschii		64		60		

[1] For example, 75% of the 8 Parakeet Auklets collected in 1983 had Scyphomedusae in their stomachs, the remaining 25% without Scyphomedusae.

meet (Hunt et al. 1990); in these hydrographically structured areas there are high densities of large calanoid copepods (*Neocalanus plumchrus* and *N. cristatus*) and large numbers of larval shrimp and lithode crabs. Two species, frequently important prey for seabirds, also occur in these areas: the hyperiid *Parathemisto libellula,* a voracious predator on copepods, and euphausiid *Thysanoessa raschii* (Motoda and Minoda 1974).

St. Matthew Island is centrally located on the Bering Shelf in an area where there is a variety of zooplankton species from both northern and southern Bering Sea communities. Substituting for the large copepods of the Chirikov Basin is *Calanus marshallae,* which is the prey of carnivorous plankton such as walleye pollock larvae (*Theragra chalcogramma*) (Motoda and Minoda 1974).

The abundance of jellyfish and other gelatinous animals such as ctenophores is not discussed in the literature on the zooplankton of the region, most sampling based on net tows. However, their abundance is readily apparent. Divers suggest they are one of the dominant groups of the Bering Shelf community (Hamner 1982). Fishermen trawling for walleye pollock routinely complain about how jellyfish foul fishing nets.

The large medusae, *Chrysaora* (4–50 cm diameter bell) and the other common jellyfish of the Bering shelf community, *Cuspidella, Cyanea* and *Aequorea,* have benthic polyp stages that produce medusae asexually in the spring (Hamner 1982). The medusae are abundant in the midwater environment from spring through fall, when they develop gonads and become sexually mature. They produce planulae, which descend to spend the winter on the bottom.

RESULTS

Parakeet Auklets persistently fed on gelatinous animals such as jellyfish and ctenophores (Table 1). Comparisons of food samples with reference specimens confirm that the Scyphomedusae *Chrysaora* and *Cyanea* were among the auklet's prey; these are very large jellyfish (up to 50 cm diameter), which were abundant throughout the study area. The high occurrence of ctenophores (probably *Beroe*) in birds from the Chirikov Basin illustrates how generalized the Parakeet Auklet is in this behavior.

Many of the prey (Table 1) may have been ingested as a unit with medusae. The amphipods *Hyperia* and *Hyperoche* as well as gadid fish live in association with jellyfish (Van Hyning and Cooney 1974, Laval 1980). The pteropod *Li-*

TABLE 2. Frequency of Occurrence of Prey from Three Auklet Species from St. Matthew Island, for All Prey Occurring in Samples ("All"), Prey Occurring in Significant Numbers or Volumes ("Sig"), and Prey Dominating Samples ("Dom")[1]

	C. psittacula (N = 39)			*A. pusilla* (N = 58)			*A. cristatella* (N = 6)		
Taxon	All	Sig	Dom	All	Sig	Dom	All	Sig	Dom
Gelatinous zooplankton									
Scyphomedusae	54	38	13	5	0	0	17	0	0
Medusa associates									
Amphipoda									
Hyperia	10	5	0						
Hyperoche	8	3	0	5	0	0			
Unid. Hyperiidae				2	0	0			
Gadid fish									
Theragra chalcogramma	33	18	13	16	3	0	67	17	0
Theragra otolith	33			22			83		
Free-swimming prey									
Chaetognatha									
Sagitta				3	2	0			
Pteropoda									
Limacina	10	0	0	5	0	0			
Polychaeta									
Nereid beaks	36								
Copepoda									
Calanus marshallae	5	0	0	64	53	26			
Pseudocalanus elongatus	8	0	0						
Amphipoda-Hyperiidae									
Parathemisto libellula	33	18	3	36	7	2	67	0	0
Amphipoda-Gammaridae									
Protomedia				5	0	0			
Monoculodes				7	0	0			
Anonyx				2	0	0			
Pleustidae				3	0	0			
Unid. Gammeridae				5	0	0			
Unid. Amphipoda				9	5	2			
Euphausiacea									
Thysanoessa raschii	39	26	23	29	14	7	100	83	67
Decapoda									
Pandalidae larvae				3	0	0			
Hippolytidae larvae				16	5	2			
Crangodidae larvae				2	0	0			
Lithode crab larvae				22	2	0			
Brachyuran crab larvae				5	0	0			
Fish									
Ammodytes				3	0	0			

[1] For example, 54% of the 39 Parakeet Auklets collected near St. Matthew Island contained Scyphomedusae, the remaining 46% without Scyphomedusae. Of the same 39 birds, 38% had "significant" volumes of Scyphomedusae, the remaining 62% either had not eaten Scyphomedusae or only eaten a small amount. 13% of the 39 birds had Scyphomedusae dominating their stomach contents.

macina is the primary prey of the jellyfish *Chrysaora,* and it may have been ingested by the birds incidentally (Hamner 1982). Note the much lower occurrence of jellyfish associates among the prey of Parakeet Auklets from the Chirikov Basin, where they ate more ctenophores than jellyfish. *Beroe* does not typically have numerous associated fish and crustaceans as do jellyfish, and the birds with ctenophores in their crops tended to have little else.

All three auklet species fed both on jellyfish and jellyfish associates (Tables 2, 3). Parakeet Auklets more often had jellyfish associates in the "significant prey" category and the "dominant prey" category than did the other auklets. Very few symbiotic hyperiid amphipods were eaten by the *Aethia* auklets, although gadid fish larvae were frequently eaten. The contribution of jellyfish to the diet of the *Aethia* species was minor. On the other hand, jellyfish occurred more often

TABLE 3. FREQUENCY OF OCCURRENCE OF PREY FROM THREE AUKLET SPECIES FROM THE CHIRIKOV BASIN, FOR ALL PREY OCCURRING IN SAMPLES ("ALL"), PREY OCCURRING IN SIGNIFICANT NUMBERS OR VOLUMES ("SIG"), AND PREY DOMINATING SAMPLES ("DOM")[1]

	C. psittacula (N = 13)			*A. pusilla* (N = 83)			*A. cristatella* (N = 22)		
Taxon	All	Sig	Dom	All	Sig	Dom	All	Sig	Dom
Gelatinous zooplankton									
Ctenophora	69	54	38						
Scyphomedusae	54	38	15	5	2	2	23	10	5
Medusa associates									
Amphipoda									
Unid. Hyperiidae	23	0	0	2	0	0	5	0	0
Gadid fish									
Unid. Gadidae larvae	23	23	0	4	1	0	36	0	0
Theragra otolith				1					
Free-swimming prey									
Pteropoda									
Limacina	38	0	0						
Cephalopoda									
Squid beaks							5		
Polychaeta									
Nereid beaks				1					
Copepoda									
Neocalanus plumchrus	8	0	0	53	29	23	10	10	0
N. cristatus	3	8	8	64	29	7	14	5	0
Calanus marshallae				1	0	0			
Pseudocalanus elongatus				1	0	0			
Eucalanus bungii				11	1	0	5	0	0
Unid. Copepoda				11	2	2			
Amphipoda-Hyperiidae									
Parathemisto libellula	8	0	0	19	5	1	23	18	9
Amphipoda-Gammaridae									
Byblis				1	0	0			
Pleustidae				4	0	0			
Unid. Amphipoda				7	0	0			
Euphausiacea									
Euphausiid larvae				1	0	0			
Thysanoessa raschii				16	4	4	36	27	14
Decapoda									
Pandalidae larvae				39	22	7	23	14	5
Hippolytidae larvae				5	2	0			
Lithode crab larvae				8	1	0	5	0	0
Crab megalops				4	1	0			

[1] Explanation same as for Table 2.

in Parakeet Auklets than hyperiids or fish, suggesting the jellyfish frequently were ingested on their own.

Parakeet Auklets also fed on zooplankton that do not associate with jellyfish. Parakeet Auklets from the St. Matthew collections in 1984 were full of euphausiids (Table 1), as were all seabird species feeding in the area (Hunt et al. 1988). Most of the Parakeet Auklets collected in 1986 were part of mixed-species feeding flocks, and these birds had free-swimming prey such as euphausiids and the hyperiid amphipod *Parathemisto*.

Figure 2 compares auklet diets at St. Matthew Island, the Chirikov Basin and St. Lawrence Island; the information on the latter site is from Bédard (1969a). Bédard evaluated the relative importance of various prey by combining all samples from a given species and comparing the volume occupied by each prey. He calculated the volume using numerical data and estimated the volume that fresh, intact prey would occupy. Bédard's volumetric measure of prey importance is only roughly comparable to my measure based on the frequency occurrence of prey. Our data nonetheless permit comparison.

Bédard (1969a) did not identify jellyfish as a food of the Parakeet Auklet, although he observed ctenophores in their diet. While he did not separate free-swimming *Parathemisto* from

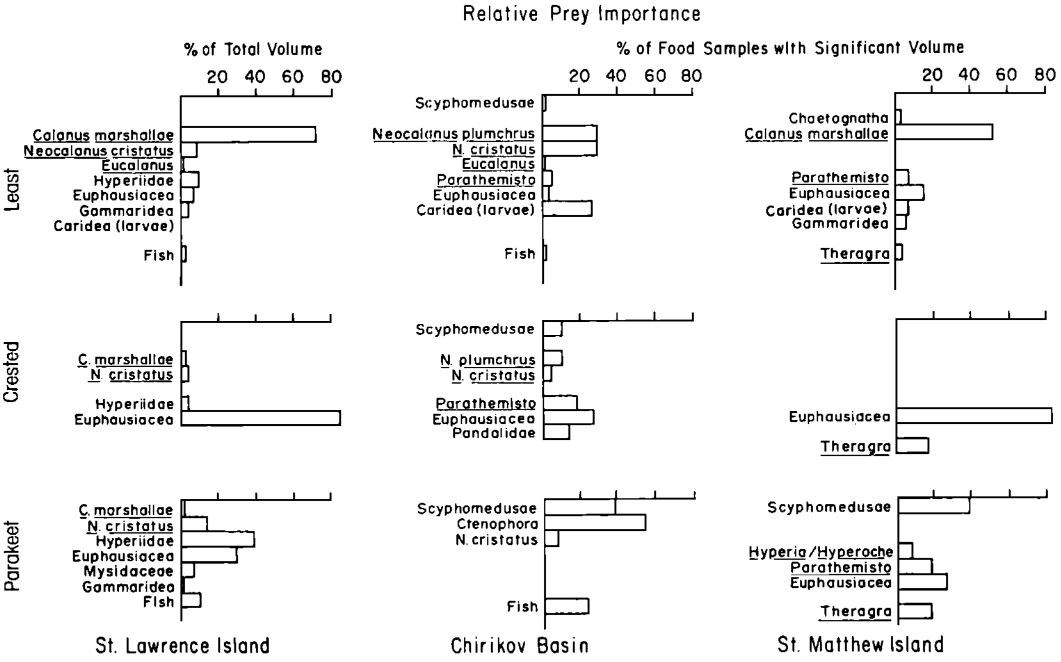

FIGURE 2. Diets of Parakeet, Crested and Least Auklets at three sites in the northern Bering Sea.

the parasitic hyperiid amphipods, combining them in the category Hyperiidae, he stated that *Parathemisto* was the most important constituent of the Parakeet Auklet's diet.

Bédard's (1969a) data for Least and Crested auklets were more similar to my data for these species at St. Matthew Island than in Chirikov Basin (Fig. 2). The Least and Crested auklets that I collected near Bédard's site both fed on *Neocalanus* copepods, whereas Bedard found Least Auklets feeding on *Calanus* and Crested Auklets feeding on euphausiids. Searing (1977) studied the *Aethia* on another St. Lawrence colony and his results were similar to mine. Given that *Calanus* is indicative of coastal influence and *Neocalanus* of the influence of the oceanic Anadyr Current, the changes in diet probably reflect a changing community and are linked to oceanographic variation.

There were marked differences in prey distributions at my two study sites. Figure 3 shows acoustic records for a transect across the Chirikov Basin, and another through the Sarichef Strait at St. Matthew Island. The mean biomass in the Chirikov Basin was 5.8 g/m^2; near St. Matthew Island it was 10.2 g/m^2. The variance to mean ratio for plankton biomass for the Chirikov Basin transect was 2.6, whereas the ratio along the St. Matthew transect was 21.2, indicating a much patchier biomass along the St. Matthew transect. Plankton tows indicated the patches of prey near St. Matthew were made up of euphausiids and hyperiid amphipods (*Parathemisto*).

There were differences between the two sites in the extent of dietary overlap among the auklets (Tables 4, 5). Only a few overlap values deviated significantly from the random expectation. There was relatively low overlap between the Parakeet

TABLE 4. DIETARY OVERLAP BETWEEN THREE AUKLET SPECIES IN THE CHIRIKOV BASIN

	"Sig. prey" category		"All prey" category	
	Actual overlap	Mean overlap (SD)[1]	Actual overlap	Mean overlap (SD)
Parakeet vs. Crested	0.13	0.50 (0.12)	0.36	0.51 (0.10)
Parakeet vs. Least	0.09	0.20 (0.07)	0.16	0.29 (0.06)
Crested vs. Least	0.52	0.50 (0.09)	0.53	0.65 (0.05)

[1] Mean overlap and standard deviation calculated from random permutations of data; see text.

Auklet and the *Aethia* auklets in the Chirikov Basin, and greater overlap at St. Matthew Island. The use of gelatinous prey by the Parakeet Auklet was most pronounced in the Chirikov Basin, where I calculated the lowest overlap values (Parakeet vs. Least 0.09, Parakeet vs. Crested 0.13). The Parakeet Auklets often captured locally abundant euphausiids and *Parathemisto* at St. Matthew Island, as did the Least and Crested auklets, and their diets were more similar. Least and Crested auklets differed more in their prey selection around St. Matthew Island where there were large patches of the preferred prey of each species, and less so in the Chirikov Basin. While some Crested Auklets fed on euphausiids, both *Aethia* species were eating mostly copepods in the Chirikov Basin; it is not clear whether this was due to a shortage of euphausiids or the abundance of large copepods.

The small scale distribution of prey is likely to affect the extent of dietary overlap between the three species. Table 6 describes the diet of auklets collected from a single feeding flock. The three species tended to have many of the same prey types in their stomachs. However, the various prey were represented in different proportions, resulting in distinct differences between auklet species in their prey selection; the differences are evident in the "significant prey" category. I found no overlap between the Crested Auklet and the other species in the "significant prey" category (Table 7). Least and Parakeet auklets had only slightly lower dietary overlap than would have occurred by chance. The Parakeet Auklets mostly ate *Parathemisto* and jellyfish (Table 6); the Least Auklets ate *Parathemisto* and copepods.

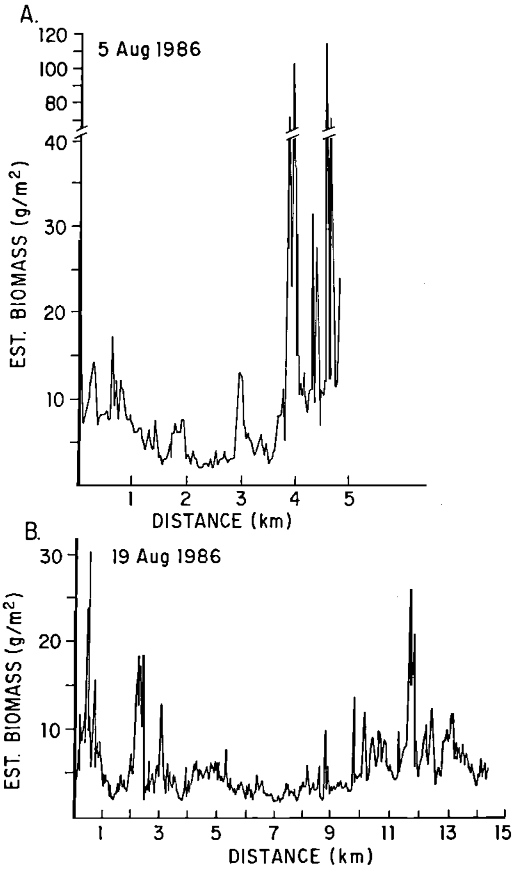

FIGURE 3. Acoustic records showing planktonic biomass along a transect through the Sarichef Strait, St. Matthew Island (A) and a transect west of King Island in the Chirikov Basin (B).

Least and Parakeet Auklets, while frequenting the same ocean habitat, behave differently. Parakeet Auklets were distributed randomly along the transect (Fig. 4) in a pattern that could not be differentiated from the Poisson distribution, while the Least Auklets were non-random, and clumped (K-S comparison to Poisson, P = 0.05). Least Auklets occurred in several patches between stations 5 and 7, an area with high densities of *Neocalanus copepods.* The eastern end of the transect (salinity 30–32‰) has lower plankton biomass than the oceanic western end (salinity 32–32.5‰). The Least Auklets were more restricted to the oceanic areas with high plankton biomass, whereas Parakeet Auklets were found in both habitats.

When all distributional data from the King Island area (15 transects) were compared to a Poisson distribution, Least Auklets were more aggregated than the random distribution on 14

TABLE 5. DIETARY OVERLAP BETWEEN THREE AUKLET SPECIES AT ST. MATTHEW ISLAND

	"Sig. prey" category		"All prey" category	
	Actual overlap	Mean overlap (SD)[1]	Actual overlap	Mean overlap (SD)
Parakeet vs. Crested	0.49	0.73 (0.11)	0.70	0.74 (0.09)
Parakeet vs. Least	0.18	0.24 (0.02)	0.49	0.47 (0.02)
Crested vs. Least	0.24	0.89 (0.13)	0.48	0.76 (0.07)

[1] Mean overlap and standard deviation calculated from random permutations of data; see text.

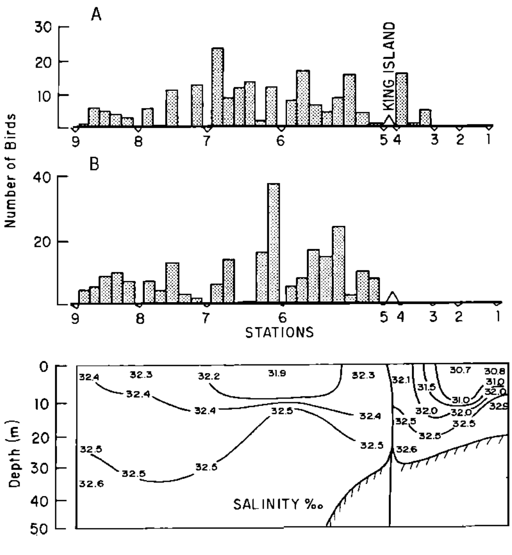

FIGURE 4. Distribution of Parakeet Auklets (A) and Least Auklets (B) relative to a salinity profile for the King Island transect.

of the 15 transects, and random on 1 of the 15 transects (K-S comparison to Poisson, P = 0.05). The Parakeet Auklets were aggregated on 6 of the 15 transects and random for the other 9.

DISCUSSION

Gelatinous zooplankton are an important part of the Parakeet Auklet's diet, and probably are a preferred food. The primary reason for feeding on jellyfish may be the high nutritive value of associated crustaceans and fish larvae; hyperiid amphipods and fish larvae are easily observed on and around jellyfish in the surface waters. All hyperiid amphipods are tied to jellyfish at some stage of their life cycle; some are specialized for a parasitic existence on jellyfish (Laval 1980). Fish larvae seek out the tentacles for protection (Dahl 1961), and association with jellyfish may be essential for the larval stages of many gadid species (Walford 1958). Many ctenophores and salps also often have hyperiid associates (Madin and Harbison 1977, Harbison et al. 1977).

Most seabirds in the Bering Sea feed on jellyfish (Harrison 1984). Gadid larvae together with small amounts of jellyfish are found in the guts of many alcids including Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*). In the Bering Sea only Northern Fulmars (*Fulmarus glacialis*) approach Parakeet Auklets in the frequency of jellyfish in their diet. Most of these species have eaten very little gelatinous tissue and probably are in pursuit of associated zooplankton. The quantities of gelatinous tissue in Parakeet Auklets, however, suggest that they are taking more than would be ingested incidentally while capturing associates. They also fed on a variety of ctenophore, which apparently had few associates, if any.

The Parakeet Auklet's bill is highly specialized and unusual in that the lower mandible is a narrow hook that curves up and around the blunt upper mandible. How Parakeet Auklets use this tool in capturing prey has long been disputed (Bent 1946). It has been suggested that the beak is a tool for picking crustaceans out of crevices, or prying open bivalves; given the pelagic distribution of Parakeet Auklets at sea, these explanations are unlikely.

In a study of bill structure in the Alcidae, Bédard (1969b) used bill width and tongue characteristics to place the Parakeet Auklet in an intermediate position between the plankton eating species and the puffins (which eat both plankton and fish). While this is consistent with the eclectic diet of the species, it does not explain the apparent scooping device for a lower mandible, which I suggest functions in either hooking gelatinous animals or picking zooplankton from medusae. Underwater observations of Parakeet

TABLE 6. FREQUENCY OF OCCURRENCE OF PREY FROM THREE AUKLET SPECIES IN THE SARICHEF STRAIT

	Parakeet (N = 6)		Least (N = 5)		Crested (N = 4)	
	All[1]	Sig[2]	All	Sig	All	Sig
Gelantinous zooplankton	83	50	0	0	25	0
Chaetognatha	0	0	20	0	0	0
Limacina (pteropod)	33	0	0	0	0	0
Calanus (copepod)	0	0	80	40	25	0
Parathemisto (hyperiid)	83	50	60	40	50	0
Thysanoessa (euphausiid)	33	0	20	0	100	100
Decapod larvae	0	0	20	0	0	0
Theragra (gadid fish)	17	0	20	0	25	0
Ammodytes (fish)	0	0	20	0	0	0

[1] "All prey" category.

[2] "Significant prey" category.

TABLE 7. Dietary Overlap between Auklets Collected in Sarichef Strait

	"Sig. prey" category		"All prey" category	
	Actual overlap	Mean overlap (SD)[1]	Actual overlap	Mean overlap (SD)
Parakeet vs. Crested	0	0.67 (0.23)	0.65	0.83 (0.08)
Parakeet vs. Least	0.44	0.68 (0.19)	0.42	0.76 (0.10)
Crested vs. Least	0	0.62 (0.21)	0.57	0.73 (0.11)

[1] Mean overlap and standard deviation calculated from random permutations of data; see text.

Auklets feeding on a variety of prey will be required to establish the merits of this peculiar bill.

A Parakeet Auklet has to eat a large quantity of jellyfish to derive the same net energy as from a meal of crustaceans (Table 8). Water content varies between 95–99% for both jellyfish and ctenophores (Curl 1962). It requires ten times the amount of gelatinous tissue to obtain the same amount of organic material as found in a hyperiid amphipod or euphausiid.

The frequency occurrence of prey in the Parakeet Auklet's diet appears to depend on the local relative abundance of food. In the St. Matthew Island area, where there were patches of euphausiids and other high quality prey, the Parakeet Auklet fed on a wide variety of animals; in the Chirikov Basin my small sample suggests a dependence on gelatinous animals.

The observations of prey taken by the three auklet species feeding together indicate the auklets are sensitive to fine-scale (10s to 100s of meters) patterns in prey distributions. Crested Auklets fed on euphausiids, whereas Parakeet Auklets from the same flock fed on jellyfish and *Parathemisto.* Parakeet Auklets may be feeding in a microhabitat surrounding and including jellyfish; they may not encounter many of the animals that dominate the diets of the *Aethia* species. The divergent diets of the auklets are probably related to their response to small-scale heterogeneity in their habitat.

Bédard (1969a) observed differences between the Parakeet Auklet and the *Aethia* species that appeared to be consequences of different foraging strategies. The *Aethia* species switched between zooplankton prey as they became sequentially abundant through the season; Parakeet Auklets maintained a constant diet. Least and Crested Auklets lost more weight during breeding (10–12%) than Parakeet Auklets (5.5%). Parakeet Auklets consistently had larger reserves of subcutaneous fat than the *Aethia* species; Crested Auklets, in particular, appear to experience extreme energetic stress during the breeding season. There is also more annual variation in breeding success in the *Aethia* species than in the Parakeet Auklet. Parakeet Auklets would appear to have a dependable supply of food.

TABLE 8. Prey Content for Selected Gelatinous Animals and Crustaceans[1]

	% water	% organic content	% ash	Energy (cal/ash free dry wt)
Cyanea (jellyfish)	95.4	1.7	2.9	5.5
Beroe (ctenophore)	95.3	1.4	3.3	4.0
Hyperoche (hyperiid)	80.0	16.7	3.3	6.4
Thysanoessa (euphausiid)	73.0	23.3	3.7	6.4

[1] Derived from Percy and Fife (1981) and Curl (1962).

The Parakeet Auklet may represent a species adapted for the capture of a widely dispersed prey, whereas the *Aethia* auklets appear to be adapted for tracking spatially and temporally patchy prey.

Parakeet Auklets occupy areas of the eastern Bering Sea where Least and Crested Auklets are absent (Bédard 1969a). The *Aethia* species are restricted to areas with high seasonal productivity. The Parakeet Auklet appears to find adequate conditions in less productive waters.

While the three auklets are seen feeding in the same marine habitats, they appear to be adapted for different prey distributions. The Parakeet Auklet is unusual among the Alcidae in feeding on a dispersed prey; it may be adapted for the use of a midwater microhabitat. The Parakeet Auklet's persistent use of jellyfish and associated animals may be the explanation for the many differences between it and the *Aethia* species.

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THE WINTER DIET OF THICK-BILLED MURRES IN COASTAL NEWFOUNDLAND WATERS

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Abstract. The diets of Thick-billed Murres wintering off Newfoundland were sampled by analyzing stomach contents of birds shot by hunters in 1984–1985 (N = 660) and 1985–1986 (N = 550). Fish, especially arctic cod (*Boreogadus saida*) with fewer capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.) and Atlantic cod (*Gadus morhua*), predominated in samples from November to December in northern zones. Crustaceans, particularly the euphausiids (*Thysanoessa* spp.), predominated from January to March as the murres gradually moved south. This switch in diet corresponded to a drop in surface temperature below 0°C as arctic pack ice moved into Newfoundland waters. We conclude that fish descended in the water column to reach warmer layers at a time when *Thysanoessa* migrated into coastal areas and swarmed near the surface, thereby reversing the relative availability of these prey for murres.

Key Words: euphausiid; murre; Newfoundland; diet; sea-surface temperature; food.

The summer diets of young and adult Thick-billed Murres (*Uria lomvia*) have been well described at colonies in the Canadian arctic and Labrador (e.g., Gaston 1985, Gaston and Noble 1985, Birkhead and Nettleship 1987). However, only Tuck (1961) and Gaston et al. (1983) have considered the diet of this species in winter in Newfoundland waters, from examinations based on limited stomach samples obtained from hunters.

Thick-billed Murres that breed in the eastern Canadian arctic and western Greenland move south in the fall with the Labrador current, which carries arctic water from western Baffin Bay and Hudson Strait along the coasts of Labrador and eastern Newfoundland to the Grand Banks. These birds reach northern Newfoundland in mid-October (Gaston 1980, pers. obs.), about two months ahead of the pack-ice. The murres remain as far north as they can find large patches of open water, but by March extensive ice keeps most birds southeast of the Avalon Peninsula (Gaston 1980). Smaller numbers winter along the south coast of the island, with a few in the Gulf of St. Lawrence.

Gaston (1980) calculated that about four million Thick-billed Murres from the Canadian arctic and western Greenland winter off Newfoundland. Based on the size of the annual harvest, we assume that about half of these birds spend part of that time in sheltered bays and coastal waters where Newfoundlanders traditionally hunt "turrs," the local name for murres (R. D. Elliot, unpubl.). The recovery of many harvested murres that had been banded in arctic colonies (Gaston 1980, R. D. Elliot and P. C. Ryan, pers. obs.) confirms that these are the same populations for which there is extensive information on summer diet (e.g., Gaston and Noble 1985). In addition to hunting pressure and disturbance, these wintering murres are subjected to many storms and rapidly-changing ice conditions that limit their movements and likely affect their feeding efficiency and requirements.

Both Thick-billed and Common murres (*Uria aalge*) are hunted legally in Newfoundland and Labrador, although most Common Murres move south of the island to winter offshore (Brown 1986). Thus, they are mainly taken early in the season, or along the south coast, and probably make up less than 5% of the total annual harvest (R. D. Elliot, unpubl.). The hunting season extends from September through March, although murres are usually present for only 1–3 months in any location, with most birds taken after November (Wendt and Cooch 1984). Murres are shot from open boats about 5–7 m long within 5–15 km of shore, when weather and ice conditions permit; 20–40 murres is a typical day's take for a crew of 2–3 hunters. Most birds are plucked and cleaned the day they are shot, giving us opportunities to collect stomach contents and data on species, age, and condition of the murres.

The objectives of this study were to determine the diets of Thick-billed Murres through the winter, in relation to surface water temperature, ice cover and geographic location, which are likely to influence the availability of prey. We compare the murres' winter and summer diets and review winter diets of potential competitors in Newfoundland waters. We also consider possible changes in murres' winter diet since the 1950s (Tuck 1961). Our results contribute new information on the wintering distribution of several species of non-commercial prey. Limitations imposed by reliance on hunters to provide stomach samples, and the lack of information on prey availability, are offset by the large numbers of samples obtained over five months of the fall and winter, from 1100 km of coast in the wintering range of this species.

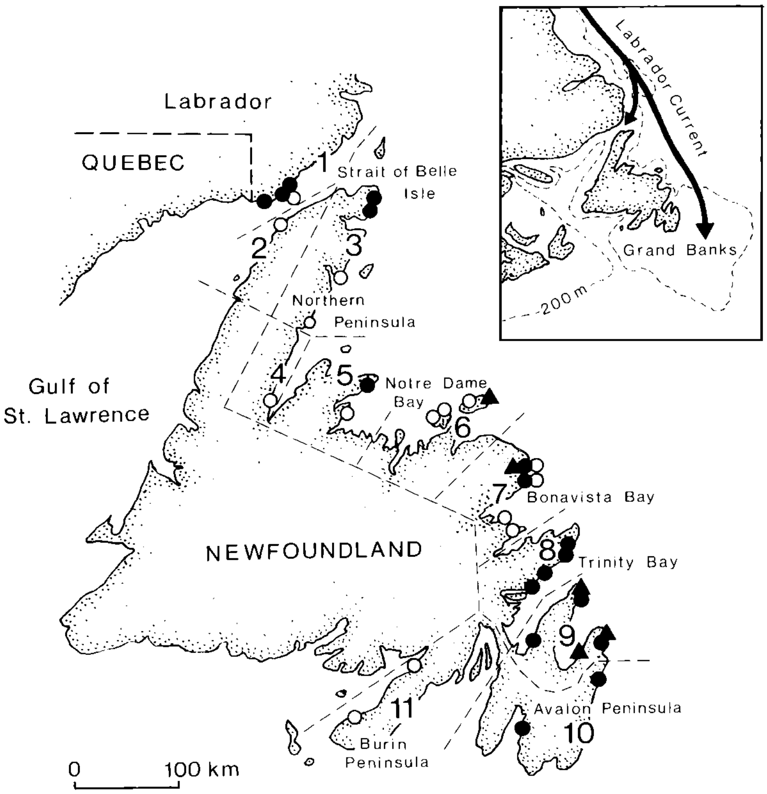

FIGURE 1. Map of the study area, showing murre survey zones and the locations where stomach samples were collected in early 1984 (▲), 1984–1985 (●), and 1985–1986 (○).

METHODS

Field Collections

Murres in this study were shot by hunters between 1 November and 31 March of 1984–1985 and 1985–1986, usually on the surface within 10 km of shore. It was not possible to collect foraging birds only, although most hunters believed that the birds were feeding when shot. Murres were kept cool until cleaned by hunters, usually within 6 h of shooting. For about half the samples we removed the stomachs (i.e., proventriculus and gizzard) and immediately froze them individually to avoid mixing or losing their contents. Stomachs from other samples were frozen by hunters for us, together with the other digestive organs, and were later thawed and separated in the lab.

We could not control or record the time between death and the freezing of the stomach, during which time digestion could still occur. Although this affects the numbers of organisms that could be identified and counted (see below), we do not believe that there was a systematic bias in the distribution of these elapsed times.

We tried to obtain at least 20 stomachs on each collection date. Thirty-five collections were made from 17 locations in 1984–1985, and 26 from 15 locations in 1985–1986 (Fig. 1). Details of collecting dates and locations have been deposited in the Atlantic Regional Library, Canadian Wildlife Service (Box 1590, Sackville, New Brunswick E0A 3C0). Samples were later grouped by month and by survey zone (Fig. 1) for analysis. Samples were also collected at five locations in Zones 7 and 9 in early 1984 while we developed our techniques, and these were analyzed in less detail.

Heads were collected from almost all birds sampled to identify the species of murre involved, but were grouped for each sample, rather than being kept with the correct stomach. Stomachs from known Common Murres were excluded from analysis, although others were included in some samples kept for us by hunters. Based on the identification of the heads with the samples, we estimate that 2–3% of the stomachs considered here were from Common Murres. An exception is a sample of 61 murres from Zone 11 taken on 12–13 February 1986, of which 20% were Common Murres.

Laboratory Analysis

After thawing, the contents of the proventriculus and gizzard were weighed, sorted, identified, and counted separately. Contents were separated initially into fish, crustacean, and squid remains and wet weight was measured for each group. Pebbles and other non-food items such as plastic were also weighed and counted.

Individual food items were identified to genus or species where possible, using reference samples collected during the surveys and standard keys. All fish material was well digested, and was identified by the otoliths present. Identifications were confirmed by personnel from the Northwest Atlantic Fisheries Centre (Department of Fisheries and Oceans) and the Biology Department, Memorial University of Newfoundland. Crustacean remains were preserved in 40% isopropyl alcohol, and fish otoliths and cephalopod beaks were washed in water, dried, and stored on acetate sheets.

The higher number of left or right sagittal otoliths was taken as the minimum number of fish present for species such as capelin (*Mallotus villosus*), where left and right otoliths could be separated. For other species, otoliths paired by size and differing in length by less than 5% were considered to be from the same individual (Gaston and Noble 1985). The numbers of pairs of eyes were counted for euphausiids, and the number of complete telsons enumerated for other crustaceans. We used the numbers of jaws divided by two for polychaete worms, and the greater number of upper or lower beak halves for squid.

DATA ANALYSIS AND INTERPRETATION

The effects of differential digestive rates on the interpretation of murre stomach content data have been discussed by Bradstreet (1980) and Gaston and Noble (1985). Prey tissue is digested very rapidly, with the exception of most bony or chitinous parts. Food remains from the main prey taxa encountered in our study are probably digested or evacuated in the following order: squid and fish flesh, crustaceans, fish otoliths, and squid beaks. Although the latter may remain in the gizzard for at least several weeks (Bradstreet 1980), most other items probably disappear within 24 hours (Uspenski 1956).

A crude estimate of the relative volumes of the major taxa consumed is given by the wet weight of the remains in the proventriculus. Gizzard contents were not included in these comparisons to reduce the error resulting from the more rapid digestion there of fish and squid. We presented our data in terms of: (1) the proportion by wet weight of fish, crustaceans and squid in the proventriculus; (2) the proportion of stomachs (proventriculus and gizzard) containing food in which each taxon was found; and (3) within fish and crustacea, the proportion of all individuals identified that were assigned to each taxon.

The categories of "other fish" and "other crustaceans" include taxa which were too digested to identify. Some of these would be taxa identified and recorded from other stomachs, and some may never have been identified. We assume that numbers involved were small enough to be of little consequence, with the possible exception of some unidentified gadoids (particularly *Gadus* and *Boreogadus*) grouped with "other fish."

Samples were compared on the basis of the murres' age composition, the proportion of ice cover, water temperature, survey zone and month. The proportion of birds 4–8 months old was calculated using a discriminant function based on four skull and bill measurements (Gaston 1984, Elliot and Gaston 1986). This proportion was derived from measurements of the overall sample of birds for which stomachs were analyzed. However, as the head and stomach from each individual were not usually kept together, we were unable to assign individual stomachs to a specific age category. Data for ice cover (expressed in tenths of the surface covered) were obtained from charts issued at 4-day intervals by the Atmospheric Environment Service, supplemented by hunter reports. Sea-surface temperatures were interpolated to the nearest 1°C from charts produced weekly by the Canadian Forces Meteorological Service.

RESULTS

Although a few stomachs from Common Murres were probably included in these analyses, their contents were generally similar to those from Thick-billed Murres. This similarity is apparent in the comparison of contents from the two species shot from the same flock in northern Bonavista Bay (Zone 7) on 12 December 1984 (Table 1).

TABLE 1. COMPARISON OF STOMACH CONTENTS OF COMMON AND THICK-BILLED MURRES FROM ONE FLOCK IN NORTH BONAVISTA BAY, 12 DECEMBER 1984

	Proportion by wet weight in proventriculus		Percent occurrence of taxa in stomachs containing food	
Prey species	Common	Thick-billed	Common	Thick-billed
Atlantic cod			0	3.4
Arctic cod			14.3	37.9
Capelin			100.0	58.6
Other fish			0	20.7
All fish	1.000	0.997	100.0	100.0
Hyperiid amphipods			0	3.4
Gammarid amphipods			0	3.4
All crustaceans	0.000	0.003	0	6.8
No. of stomachs containing food			7	29
No. of empty stomachs			2	12

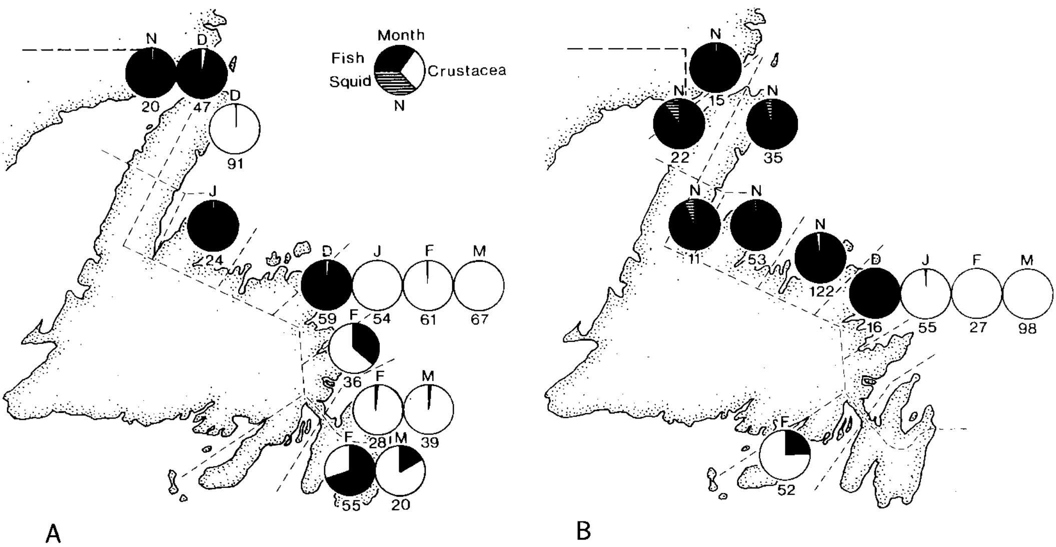

FIGURE 2. The proportions of major taxa in murre stomachs, by wet weight, month and survey zone. A, 1984–1985, and B, 1985–1986. The number of stomachs (N) is shown for each sample, and survey months are indicated as November (N), December (D), January (J), February (F), and March (M).

Overall Trends in Diet Composition

In 1984–1985 and 1985–1986 there was an overall trend for fish to predominate early in the season in samples in northern survey zones, when compared to the proportion of wet weight in the proventriculus (Figs. 2a,b). There was a marked shift to crustaceans after December in most southeastern zones in both years. Arctic squid (*Gonatus fabricii*) were only recorded regularly in northern survey zones early in 1985–1986 (Fig. 2b).

The increase in the proportion of crustaceans was related to increased ice cover and decreased surface water temperature. A step-wise multiple regression analysis of the factors in Tables 3 and 4, for both years considered together, showed that only the month of the sample and the amount of ice present significantly contributed to the regression relationship ($r^2 = 62.8\%$, $F = 20.40$, $P < 0.001$). The importance of sea-surface temperature is under-estimated in such a linear analysis, as it is related to the proportion of fish taken in a step function. Samples from water temperatures below and above 0°C have markedly different prey compositions (Fig. 3). Fish predominated in only two of the samples below 0°C, but in all from warmer surface waters.

TABLE 2. Percent Occurrence of Major Taxa in Murre Stomachs Containing Food in Early 1984

	Month		
	January	February	March
Zone	7	9	9
Gadidae	8.9	64.9	3.7
Capelin	2.2	5.4	34.3
Other fish	20.0	21.6	29.6
All fish	31.1	70.3	67.6
All crustaceans	84.4	45.9	45.4
Arctic squid	2.2	0	0.9
No. of stomachs containing food	45	37	108
No. of empty stomachs	5	0	66

All samples in north Bonavista Bay (Zone 7) included in Figures 2a,b were collected off the same 20-km stretch of coast near Wesleyville and Greenspond. In this zone, murres ate fish almost exclusively in December in both years, at sea-surface temperatures of about 2°C. They switched completely to crustaceans for the next three months when temperatures were below 0°C and pack-ice was usually present nearby (Tables 3, 4). Crustaceans also occurred in most stomachs there in January 1984 (Table 2) when surface temperatures were about −2°C. A similar difference between crustacea in December 1984, and fish in November 1985, off the eastern Northern Peninsula (Zone 3), again corresponded with lower water temperature and the presence of extensive ice in December (Tables 3, 4, Fig. 2). Similar trends were apparent when considering the percent occurrence of each prey taxon, or the proportion of stomachs from each sample containing food in which that taxon occurred (Tables 5, 6).

Among the fish recorded, Atlantic cod (*Gadus morhua*), arctic cod (*Boreogadus saida*), capelin, and sand lance (*Ammodytes* sp.) each predominated in samples from different zones (Figs. 4a,b). Samples in which crustaceans predominated showed less variation, with euphausiids (*Thysanoessa* spp.) being the most common in all but those from the Burin Peninsula in February 1986 (Zone 11, Tables 5, 6).

COMPARISON OF FISH SPECIES IN THE DIET

Individuals of all the major fish species were of similar size (5 to 15 cm) based on the size of otoliths, which enabled us to compare the approximate proportion each species represented of the total numbers of fish present in each sample (Figs. 4a,b).

Arctic cod was the most common species, being numerically dominant in both years at most sites on the northeast coast (Zones 2–6) where fish were the major prey by weight. Capelin dominated in samples from northern Bonavista Bay (Zone 7) in December of both years, off the southern Avalon Peninsula (Zone 10) in February 1985, and in the small sample from White Bay (Zone 4) in November 1985. Sand lance was most plentiful off southern Labrador (Zone 1) in December 1985, and Atlantic cod was the major fish species in the only sample from the southern Strait of Belle Isle in November 1985 (Fig. 4, Tables 5, 6).

Small numbers of other species were identified in addition to those listed in Tables 5 and 6. We recorded 67 sand lance (N = 21 stomachs), 16 rock cod (*Gadus ogac*) (N = 9), 6 silver hake (*Merluccius bilinearis*) (N = 6), 3 Greenland halibut (*Reinhardtius hippoglossoides*) (N = 3), and 2 redfish (*Sebastes* sp.) (N = 2). Apart from sand lance, which were mostly from Labrador samples, individuals of these species occurred sparingly in most samples where fish predominated.

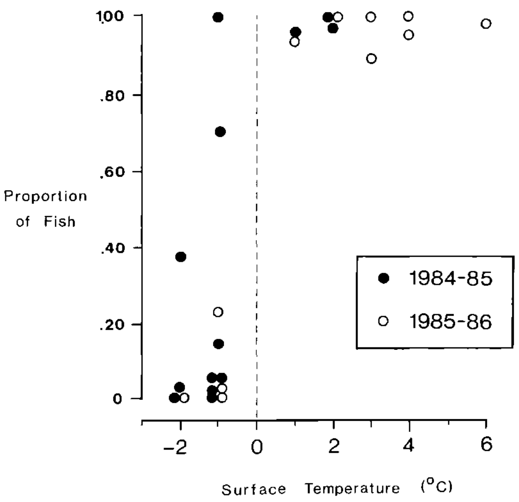

FIGURE 3. The relationship between sea-surface temperature and the proportion by wet weight of fish in the proventriculus.

There was no apparent relationship between the number of pebbles in stomachs and the month or location, or with the presence of fish in the stomach (Tables 5, 6). Pebbles may have been retained from the previous summer, when murres had fed on bottom-dwelling fish such as blennies (e.g., Gaston and Noble 1985). Most pebbles were also small enough (ca. 2–5 mm across) to have been present in the stomachs of the fish eaten by murres.

TABLE 3. THE PROPORTION OF FISH AND CRUSTACEANS BY WET WEIGHT IN PROVENTRICULUS IN RELATION TO ZONE, MONTH, ICE COVER, TEMPERATURE AND PROPORTION OF FIRST-YEAR MURRES, IN 1984–1985

Survey zone	Month	Sample size	Proportion of fish	Proportion of crustaceans	Ice cover (tenths)	Surface temp. (°C)	Proportion of first-years
1	Nov.	20	0.996	0.004	0	2	0.92
1	Dec.	35	0.963	0.037	0	1	0.86
3	Dec.	91	0.007	0.993	10	−1	0.78
5	Jan.	25	0.995	0.005	10	−1	0.15
7	Dec.	73	0.973	0.027	0	2	0.33
7	Jan.	58	0	1.000	7	−1	0.29
7	Feb.	61	0.009	0.991	10	−2	0.30
7	Mar.	102	0	1.000	9	−2	0.49
8	Feb.	37	0.372	0.628	9	−2	0.20
9	Feb.	41	0.032	0.968	1	−1	0.29
9	Mar.	40	0.031	0.969	9	−1	0.29
10	Feb.	57	0.703	0.297	8	−1	0.29
10	Mar.	20	0.155	0.845	6	−1	0.29

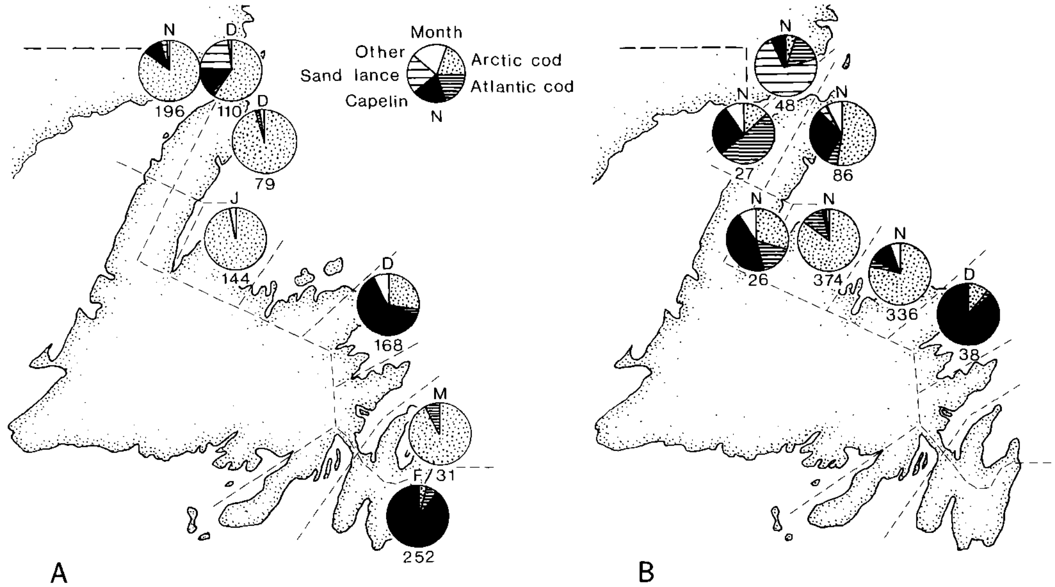

FIGURE 4. The proportion of all fish identified to species, by month and survey zone in (A) 1984–1985, and (B) 1985–1986, for samples in which at least 20 fish were identified. The number of fish (N) is shown for each sample, and survey months are indicated as November (N), December (D), January (J), February (F), and March (M).

COMPARISON OF CRUSTACEANS AND SQUID IN THE DIET

Comparisons of the relative importance of crustacean taxa by number are affected by differences in their biomass, ranging from relatively large shrimp such as *Pandalus borealis* to smaller euphausiids and amphipods such as *Parathemisto gaudichaudii.* However, this source of error is probably small, as euphausiids (*Thysanoessa* spp.) completely dominated all samples but one in which crustaceans predominated by weight, both by percent occurrence (Tables 5, 6) and by absolute number (Figs. 5a,b). The exception was the February sample from the south coast (Zone 11) where the hyperiid *P. gaudichaudii* predominated by weight and number.

Seven *Thysanoessa inermis,* 15 *T. raschii* and one *Meganyctiphanes norvegica* were positively identified to species in 1984–1985, and all of the several hundred euphausiids examined closely in 1985–1986 were *T. raschii.* The latter is assumed to have been the most abundant euphausiid taken in both years.

Of 1782 hyperiid amphipods identified to species, 1753 (98.4%) were *Parathemisto gaudi-*

TABLE 4. THE PROPORTION OF FISH, SQUID AND CRUSTACEANS BY WET WEIGHT IN PROVENTRICULUS IN RELATION TO ZONE, MONTH, ICE COVER, TEMPERATURE AND PROPORTION OF FIRST-YEAR MURRES, IN 1985–1986

Survey zone	Month	N	Fish[1]	Squid[1]	Crustaceans[1]	Ice cover (tenths)	Surface temp. (°C)	First-years[1]
1	Nov.	15	0.991	0	0.009	0	3	0.93
2	Nov.	22	0.889	0.111	0	0	3	0.91
3	Nov.	37	0.955	0.045	0	0	4	0.80
4	Nov.	12	0.941	0.051	0.008	0	1	0.89
5	Nov.	54	0.994	0.006	0	0	4	0.82
6	Nov.	130	0.980	0.001	0.019	0	6	0.95
7	Dec.	20	1.000	0	0	0	2	0.50
7	Jan.	58	0.012	0	0.988	8	−1	0.16
7	Feb.	27	0	0	1.000	9	−2	0.03
7	Mar.	115	0	0	1.000	9	−1	0.11
11	Feb.	60	0.238	0	0.762	0	−1	0.64

[1] Proportion.

TABLE 5. PERCENT OCCURRENCE OF MAJOR TAXA IN MURRE STOMACHS CONTAINING FOOD IN 1984–1985

	Month												
	Nov.	Dec.			Jan.		Feb.				Mar.		
Zone	1	1	3	7	5	7	7	8	9	10	7	9	10
Atlantic cod	0	3.7	1.1	10.2	0	0	1.6	0	0	9.1	0	5.1	5.0
Arctic cod	85.0	66.1	28.6	37.3	88.3	0	4.9	16.7	10.7	12.7	9.0	33.3	5.0
Capelin	65.0	29.6	0	59.3	0	0	0	8.3	3.6	43.6	0	0	10.0
Other fish	20.0	37.0	4.4	32.2	25.0	0	6.6	19.4	17.9	1.8	3.0	5.1	0
All fish	95.0	96.3	33.0	100.0	100.0	0	13.1	30.6	42.9	49.1	12.0	38.4	15.0
Euphausiids	5.0	14.8	96.7	1.7	4.2	100.0	100.0	80.6	39.3	69.1	85.1	92.3	80.0
Hyperiid amphipods	5.0	7.4	56.0	6.8	0	0	18.0	5.6	7.1	9.1	6.0	26.5	55.0
Gammarid amphipods	0	11.1	12.1	5.1	0	1.9	0	0	0	1.8	1.5	2.6	0
Decapods	10.0	3.7	4.4	0	0	0	0	5.6	7.1	1.8	0	0	5.0
Other crustaceans	0	7.4	0	0	4.2	0	0	2.6	3.6	0	0	0	15.0
All crustaceans	15.0	44.4	100.0	13.6	8.4	100.0	100.0	83.3	60.7	72.7	95.5	92.3	100.0
Polychaetes	0	0	2.2	0	0	0	0	0	0	0	1.5	0	0
Molluscs	0	3.7	1.1	0	0	0	1.6	2.8	7.1	0	1.5	0	0
Squid	0	7.4	4.4	1.7	4.2	0	0	5.6	0	0	0	0	0
No. of stomachs containing food	20	47	91	59	24	54	61	36	28	55	67	39	20
No. empty stomachs	0	8	0	14	1	4	0	1	13	2	35	1	0
% of stomachs containing pebbles	25.0	20.0	17.6	17.8	4.2	19.0	19.7	27.0	9.8	19.3	18.6	15.0	0

TABLE 6. Percent Occurrence of Major Taxa in Murre Stomachs Containing Food in 1985–1986

	Month										
	Nov.						Dec.	Jan.	Feb.		Mar.
Zone	1	2	3	4	5	6	7	7	7	11	7
Atlantic cod	26.7	45.5	0	18.2	50.9	9.0	6.3	29.1	3.7	7.7	10.2
Arctic cod	13.3	9.1	51.4	44.5	86.8	57.4	18.8	3.6	0	0	1.0
Capelin	20.0	18.2	31.4	54.5	9.4	18.0	87.5	3.6	0	0	0
Other fish	80.0	27.3	42.9	27.3	11.3	21.3	12.5	7.3	3.7	3.8	4.1
All fish	93.3	86.4	97.1	90.9	100.0	87.7	100.0	38.2	7.4	11.5	15.3
Euphausiids	6.7	0	0	0	0	0	0	32.7	92.6	1.9	96.9
Hyperiid amphipods	13.3	0	0	27.3	0	3.3	0	3.6	22.2	82.7	31.6
Gammarid amphipods	0	0	0	0	0	0	0	0	0	0	1.0
Decapods	0	0	2.9	0	0	0.8	0	3.6	0	3.8	1.0
Other crustaceans	6.7	4.5	5.7	0	0	0	0	41.8	0	11.5	0
All crustaceans	26.7	4.5	8.6	27.3	0	4.1	0	87.3	100.0	88.5	96.9
Polychaetes	0	0	0	0	0	0	0	0	0	1.9	0
Molluscs	0	4.5	0	0	0	0	0	0	0	0	2.0
Squid	13.3	77.3	74.3	72.7	64.2	40.2	25.0	0	0	0	0
No. of stomachs containing food	15	22	35	11	53	122	16	55	27	52	98
No. empty stomachs	0	0	2	1	1	8	4	3	0	8	17
% of stomachs containing pebbles	26.7	13.6	13.5	36.4	13.0	8.5	10.0	19.0	14.8	18.3	7.8

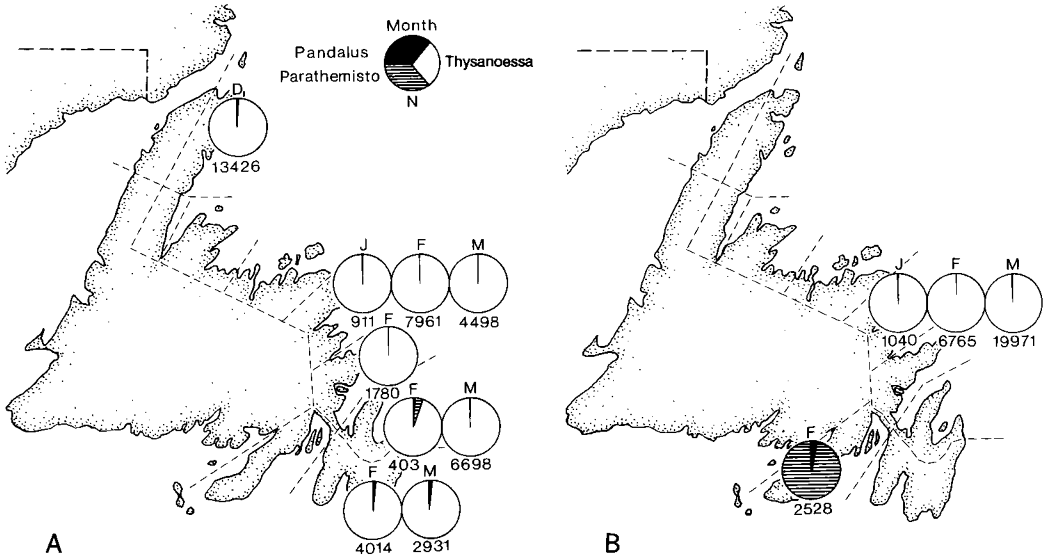

FIGURE 5. The proportion of all crustaceans identified to genus, by month and survey zone in (A) 1984–1985, and (B) 1985–1986, for samples in which at least 200 crustaceans were identified. The number of crustaceans (N) is shown for each sample, and survey months are indicated as December (D), January (J), February (F), and March (M).

chaudii (N = 15 stomachs) and 30 were *P. libellula* (N = 16). Twelve gammarid amphipods were keyed to species, including 2 *Gammarus wilkitzkii* (N = 1), 7 *G. locusta* (N = 7), 2 *Gammarellus angulosus* (N = 2) and 1 *Weyprechtia pinguis* (N = 1). Of 100 decapods identified, 94 were *Pandalus borealis* (N = 3), 5 were *P. montagui* (N = 3) and 1 was *Sabinea septemcarinata* (N = 1).

All of the 613 cephalopods identified by beaks in 149 stomachs were arctic squid. Most were recorded in 1985–1986 in November samples from southern Labrador and northern Newfoundland coasts (Zones 1–6, Tables 5, 6), at relatively warm surface temperatures of 1–6°C. Some beaks may have been retained in murres' stomachs for several weeks, and carried into these areas from farther north. The similar distribution of records of squid flesh in the proventriculus (Fig. 2), and the general absence of beaks from gizzards in samples collected farther south from January onwards in 1985–1986 (Tables 5, 6), suggest that retention times were short and that most squid were consumed in the zone in which they were recorded.

DISCUSSION

The diet of wintering Thick-billed Murres changed as they moved south along the Newfoundland coast ahead of advancing ice, and as water temperature decreased through the season at a single location. In both years, the diversity of the murres' diet declined markedly as surface temperatures dropped below 0°C, from a range of several important fish species to a single crustacean taxon, with a drop in the trophic level of their major prey. The records of Gaston et al. (1983) from the early 1980s fit well with the pattern recorded here; gadids, capelin and squid dominated the samples early in the winter, and euphausiids were most common later in the season.

The pattern of geographical and temporal change we recorded in coastal Newfoundland waters may not occur in murres wintering over the continental banks. Murres there concentrate at the shelf-breaks (Tuck 1961, Brown 1986), where upwelling conditions may make a different set of prey available (Ogi and Tsujita 1977).

ENVIRONMENTAL CONDITIONS AND PREY AVAILABILITY

The cold water and pack-ice carried south by the Labrador current influence the behavior and movements of the murres' winter prey as shown by differences in the birds' diet, both between years in one zone (e.g., Zone 2) and in one year through the season (e.g., Zone 6). The differing responses of prey to cold water and the presence of ice appear to be the main factors that affect their availability to murres.

Capelin

In summer capelin are the key forage fish for many vertebrate predators in Newfoundland waters, including fish (e.g., Reddin and Carscadden 1981, Akenhead et al. 1982), whales (Winters and Carscadden 1978), breeding alcids and visiting Greater Shearwaters (*Puffinus gravis*) (Brown and Nettleship 1984). Tuck (1961) also found that capelin predominated in winter murre diets in the early 1950s, occurring in over 90% of Thick-billed and Common murre stomach samples. Although the exact dates and locations of Tuck's samples are not known, it appears that capelin was a more important winter prey then, a conclusion also reached by Gaston et al. (1983) from fewer samples.

We doubt, however, that Tuck's (1961) samples were representative of the whole winter. Most capelin move well offshore as waters cool, or concentrate in deep inshore trenches in Trinity, Notre Dame and other bays (several of which were near some of our sampling sites), where they then occur in large inactive schools in cold water at depths of 140–200 m (Winters 1970). While these concentrations could be important prey for murres if within diving range, they were not heavily exploited during our study.

Capelin numbers vary markedly as a result of differential post-spawning survival of cohorts (Carscadden 1984, Leggett et al. 1984) and may be affected by commercial fishing. However, the commercial harvest has been low since 1979 (Carscadden 1984), and with high survival of the 1982 and 1983 cohorts (J. E. Carscadden, pers. comm.) appreciable numbers of 1½ to 3½ year-old capelin were probably available during our study. We conclude that capelin may be important prey early in the winter before they move to deeper water, and later in areas where birds are able to reach winter concentrations by diving deeply.

Arctic cod

The most important fish prey was the arctic cod, a small pelagic cold-water species often associated with near-shore environments and ice edges (Bradstreet 1982). It feeds on the same prey as the similarly-sized capelin (Lilly 1980) and is a major prey of breeding thick-bills in the arctic (e.g., Gaston et al. 1985); it also appears in the diet of Common Murre chicks in southern Labrador (Birkhead and Nettleship 1987). Tuck (1961) reported it as only an incidental prey item of murres wintering in Newfoundland waters. Gaston et al. (1983) found gadids, most of which were probably arctic cod, in 56% of stomachs from Twillingate (Zone 6) in November 1981, and 77% from Trinity Bay (Zone 9) in February 1983.

Arctic cod apparently spawn off Labrador in winter, with fry carried south in the Labrador Current, to remain in varying numbers off northern Newfoundland for one or more years. This probably reflects differences in year-class strength (W. H. Lear, pers. comm.). Arctic cod numbers appear to have increased in areas north of Bonavista Bay from the 1950s to the 1970s (Lear 1979), and were still quite high in late 1984 (Lear and Baird 1985). Most arctic cod have been recorded in concentrations at depths from 28–400 m, and at temperatures from −1.7 to 3.5°C (Lear 1979), although the murres we sampled fed on them in coastal waters at depths of less than 150 m.

Since arctic cod occasionally associate with ice in arctic waters, we doubt that their general absence from murre diets in late winter reflects a downward movement in the water column, out of the birds' diving range. Our small January 1985 sample in ice-covered Green Bay (Zone 5) was dominated by arctic cod, although this species is not common from Bonavista Bay (Zone 7) south (Lear and Baird 1985). The general lack of arctic cod in murre diets after January probably reflects the reduced overlap of areas occupied by the two species, as murres move south ahead of advancing ice.

Atlantic cod

Adult Atlantic cod are demersal fish that winter well offshore at depths of 200–600 m, at temperatures of 2–4°C (Lear 1984). However, many small cod of the size eaten by murres winter in coastal bays of eastern Newfoundland (Lear et al. 1980) frequented by murres. They may gradually become less available to murres as water temperatures drop through the winter, and they become less active and stay close to the bottom (Winters 1970). Atlantic cod was the dominant prey only in the southern Strait of Belle Isle (Zone 2) in November 1985, where surface temperatures were about 3°C, although they were still important later in the winter in southern zones at water temperatures close to 0°C.

Tuck (1961) reported Atlantic cod in about 4% of the stomachs of wintering Thick-billed and Common murres, similar to the overall proportion found in our study. Some of the gadids reported by Gaston et al. (1983) from Twillingate in November 1981, and Trinity Bay in February 1983, may have been Atlantic cod (see above).

Sand lance

Sand lance are important forage fish in areas where water is less than 90 m deep over a sandy bottom (Scott 1985). They are usually confined to cool waters in the range of −1 to 2°C (Winters 1983) and, unlike capelin, do not move to deeper water in winter. Spawning occurs from November to January (Winters 1983), and it seems likely that sand lance spend the winter in shallow water near, or buried in, the sandy bottom and are not available to murres in coastal areas after November.

Arctic squid

This pelagic species is widely distributed in arctic, low arctic and boreal waters (Wiborg 1979), and is a prey of minor importance for breeding Thick-billed Murres (e.g., Gaston 1985). It was found in low but regular numbers in coastal and offshore waters from southern Labrador to Bonavista Bay (Zones 1–6), by experimental trawls in November 1979, and November–December 1980 (E. G. Dawe, unpubl.). Arctic squid probably breed in April to June at one year of age (Wiborg 1979), so squid taken by murres in late fall were probably young-of-the-year about 2–5 cm in length.

All arctic squid that we recorded were from murres killed during November and December, in relatively warm waters above 0°C. This suggests that the availability of fish and squid, which often occurred together in murre stomachs, may both have been related to water temperature.

Like other squid species, numbers of arctic squid may vary from year to year, as they differed markedly between 1984–1985 and 1985–1986. We recorded very few in late 1984, although Gaston et al. (1983) found small squid, probably *Gonatus fabricii,* in all 16 murre stomachs from Zone 6 in November 1981. It was the most numerous item in their sample, but occurred in only 40% of stomachs we collected from Zone 6 in November 1985.

Euphausiids

The main euphausiids eaten by murres, *Thysanoessa raschii* and *T. inermis,* are abundant herbivorous crustaceans in arctic and northern boreal waters over the continental shelf of the North Atlantic. Surveys by Berkes (1976) and Sameoto (1976) over six years showed that both species were abundant in the Gulf of St. Lawrence most of the year, although they were not sampled when heavy ice was present from February to April. Both euphausiids were also found in fall and winter in the Bay of Fundy (Kulka et al. 1982), on the Scotian Shelf (Sameoto and Jaroszynski 1972), and off southeast Newfoundland (Lindley 1980). They normally descend to great depths each day; for example *T. raschii* usually concentrates in the upper 20 m at night, but reaches depths of 100–200 m by day (Berkes 1976).

In Nova Scotian waters, Sameoto and Jaroszynski (1972) found that *T. raschii* and *T. inermis* migrated from offshore areas farther than about 25 km from shore to within 3–5 km of the coast, in late winter and spring to spawn. *T. raschii* appeared inshore in large numbers in January and February, and *T. inermis* arrived about a month later. Many of these euphausiids did not undergo diel vertical migration, but remained near the surface during the day in pre-spawning swarming activities (D. D. Sameoto, pers. comm.).

We assume that similar pre-spawning movements take place off Newfoundland, where swarms of *Thysanoessa* in the upper layers of inshore waters during the day, beginning in January, would be particularly available to foraging murres. Fish are also probably less available after December because murres move south of the prey's range (e.g., arctic cod) or because the fish move into deeper water (e.g., capelin, Atlantic cod), and euphausiids then become the murres' main prey.

Hyperiid amphipods

The only other numerically-important crustaceans were the carnivorous hyperiids, *Parathemisto* spp. *P. gaudichaudi* has a more southerly distribution than the larger *P. libellula* (Shih et al. 1971), and was the dominant prey in the sample from the ice-free waters of Fortune Bay (Zone 11) in February 1986. Fish may not have been available in the upper sub-zero waters then, causing murres to prey on this locally-abundant crustacean which also migrates vertically each day.

COMPARISON WITH OTHER AREAS AND SEASONS

The diets of Thick-billed Murres collected at sea in the North Pacific Ocean have been dominated variously by squid (Sanger 1986), fish such as walleye pollock (*Theragra chalcogramma*; Ogi and Tsujita 1977), and crustaceans such as euphausiids (Ogi and Tsujita 1977) and amphipods (Ogi and Hamanaka 1982), the latter taken especially in deeper waters. Squid dominated a small sample (N = 8) from the west Gulf of Alaska in one of the few winter studies (Sanger 1986).

In the eastern Arctic, Thick-billed Murres fed mainly on arctic cod and a gammarid amphipod (*Onisimus litoralis*) in the Barrow Strait in June (Bradstreet 1980). Both fish and crustaceans also are taken by adults near arctic colonies in summer, with arctic cod usually predominating; sand lance and capelin are also important prey at some locations (Bradstreet and Brown 1985, Bradstreet and Gaston 1990).

Fish are usually fed to murre chicks at Canadian arctic colonies (Gaston 1985), and include the species eaten by adults along with several species of sculpins (Cottidae) and blennies (Blennioidea). Arctic cod are again usually the most important species numerically and by volume

(Bradstreet and Brown 1985). Most murres in our November and December samples were first-year birds, and their main prey species then were the same fish they were likely fed as chicks 3–4 months earlier. Thus there is considerable overlap in the diet of Thick-billed Murres in summer and winter, with arctic cod of major importance year-round except when murres are south of that prey species' range.

FACTORS AFFECTING PREY AVAILABILITY

Although arctic cod and euphausiids were the main prey items recorded, each of four fish species and two crustacean genera predominated in murre diets at different times in the two winters studied. These prey are all closely linked, either as potential competitors or predators, and declines in one species such as capelin may permit others such as sand lance to increase (Winters 1983).

Most pursuit-diving seabirds that may compete with murres for prey during the summer in Newfoundland (Winters and Carscadden 1978, Brown and Nettleship 1984) leave the area during the fall or occur in areas where competition with murres is minimal. For example, Black Guillemots (*Cepphus grylle*) winter in low numbers along the coast, and feed singly or in small groups much closer to shore, most likely on benthic fish (Bradstreet and Brown 1985). Dovekies (*Alle alle*), which probably feed on small crustaceans, including the euphausiids taken by murres (Bradstreet and Brown 1985), winter in high numbers well offshore (Brown 1986).

Harp seals are the only numerous marine mammals in coastal waters in late fall and winter. They reach Newfoundland waters later than Thick-billed Murres, with the arrival of pack ice in December and January, and remain until April or May.

Adult harp seals prey largely on arctic cod, capelin and shrimps (e.g., *Pandalus borealis*) (Sergeant 1973, 1976; Bowen 1985) in northern coastal areas (Zones 3–6) under the pack ice. These prey are inaccessible to murres that have moved farther south. Harp seal pups first feed independently in April on euphausiids *Thysanoessa* spp. and *P. borealis* (Sergeant 1976, Beddington and Williams 1980), while adults continue to eat fish with varying amounts of crustaceans (Bowen 1985). Thus, euphausiids are important to seals in early spring, when they may still be major prey of Thick-billed Murres.

The commercial fishery may have the greatest influence on numbers of prey such as shrimp, Atlantic cod and capelin. An intensive offshore capelin fishery in the 1970s was suspected of adversely affecting food availability and puffin chick survival (Brown and Nettleship 1984). The apparent shift away from capelin in the winter diet of murres since the 1950s (Tuck 1961), could also reflect effects of the fishery. However, the predator-prey dynamics of murre prey species are very complex, and capelin stocks may be as high now as they were 30 years ago (J. E. Carscadden, pers. comm.).

Prey populations may also be greatly affected by environmental variables, such as the effects of meteorological and hydrographic conditions on survival of larval capelin (Leggett et al. 1984), or the strength of the Labrador current on numbers of arctic cod. Because the availability of specific prey probably varies from year to year, we suspect that murres feed opportunistically on whichever of several prey taxa may be locally abundant in coastal waters. Variations in weather and ice conditions, and disturbance by hunters, which affect short-term feeding success, seem more likely to affect winter survival than more gradual changes in the abundance of specific prey.

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PHYSICAL AND BIOLOGICAL DETERMINANTS OF THE ABUNDANCE, DISTRIBUTION, AND DIET OF THE COMMON MURRE IN MONTEREY BAY, CALIFORNIA

DONALD A. CROLL

Abstract. Physical and biological factors affecting the diet, distribution, and abundance of the Common Murre (*Uria aalge*) in Monterey Bay, California were investigated from September 1981 through September 1983. Murre diet shifted both seasonally and annually, indicating an opportunistic feeding strategy. Highest abundance of murres was found during the summer period of late upwelling when murres exploit a dependable peak in prey availability (juvenile rockfish, *Sebastes* spp.) resulting from earlier upwelling episodes. Murres probably use this peak in food availability to feed dependent chicks at sea, replenish fat stores, and molt. During fall and winter productivity in Monterey Bay is low, and its importance to murres is reduced.

Distribution during summer when murre abundance is high is probably determined by local upwelling and current patterns. Densities were highest in the northern region of Monterey Bay, probably due to higher food availability. Water is advected from the southern to the northern portions of the Bay, carried by an eddy of the California Current. Upwelling is centered off of Point Pinos to the South. As recently upwelled, nutrient rich water is transported from south to north, it promotes increased phytoplankton production, which works its way to higher trophic levels as it is carried north. This results in higher prey availability in the north, and thus higher Common Murre density.

The primary effect of the 1982/1983 El Niño-Southern Oscillation phenomenon was a decrease in primary productivity that lead to a reduced availability of the normally dependable summer prey resources. As a consequence, murres which came into the Bay in June 1983 in large numbers quickly dispersed, resulting in low densities in July and August. Murres that were found in Monterey Bay at this time were thin and fed on a different array of prey items.

This study supports the hypothesis that concentrations of higher trophic level marine predators are concentrated "downstream" from upwelling centers. Peak abundance of murres in Monterey Bay occurred shortly after the seasonal peak in upwelling. During this peak abundance, murres were concentrated in the northern portion of the Bay (Soquel Cove) which is downstream of the upwelling center off of Point Pinos to the south.

Key Words: Seabird; murre; distribution; diet; Monterey Bay; El Niño.

The importance of food availability in the determination of seabird numbers has long been suggested but rarely documented quantitatively (e.g., Ashmole 1971, Shuntov 1972). The interrelation of breeding success, timing of breeding, and food availability has received considerable attention (e.g., Lack 1954, 1966, 1968), leading Ashmole (1971) to conclude that the location of breeding colonies may be determined in large part by the productivity of surrounding waters. For example, Anderson et al. (1982) found that Brown Pelican (*Pelecanus occidentalis*) reproductive output is closely related to local prey availability and abundance.

The role that food availability and productivity play in governing seabird distributions during nonbreeding seasons has not been determined clearly. Briggs et al. (1984) found that the distribution of phalaropes during the winter in the California Current was correlated with oceanographic "fronts." Haney (1987) found the nonbreeding seabirds he studied in the South Atlantic Bight off the southeastern United States were concentrated on the "crests" of internal waves, whereas Woodby (1984) found that the spring distribution of murres (*Uria* spp.) was only loosely correlated with prey patches in the southeastern Bering Sea. Brown (1980) suggested the characterization of nonbreeding seabird distribution on the basis of water types, while recognizing the importance of locally concentrated food. I used Brown's approach in analyzing the results of the present study.

The Common Murre (*Uria aalge*) is the most abundant breeding seabird along the coast of California (Briggs et al. 1983), typically arriving on central California colonies in February or March. Monterey Bay (Fig. 1) is approximately 32 km north of a small breeding colony of 2000–5000 birds at Hurricane Point, and approximately 160 km south of colonies on the Farallon Islands that number 60,000–100,000 birds (Sowls et al. 1980, Briggs et al. 1983). The first murres with dependent chicks normally appear in Monterey Bay in July (Alan Baldridge, Hopkins Marine Station, pers. comm.), but post breeding females, nonbreeders, and failed breeders may arrive earlier (pers. obs.). Although present in Monterey Bay throughout the year, murre abundance varies seasonally, apparently in concert with seasonal

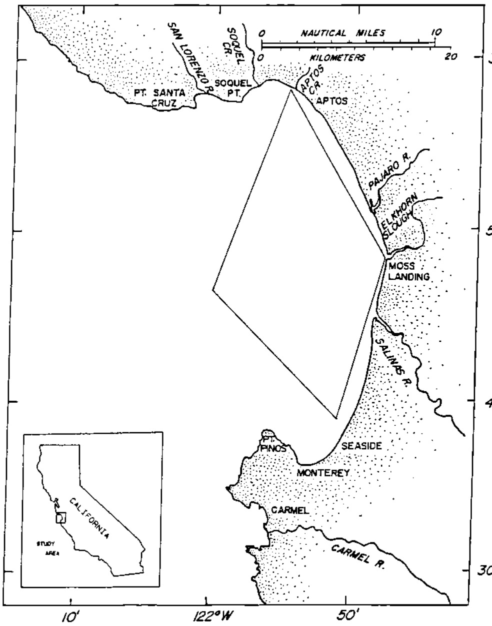

FIGURE 1. Monterey Bay, California study site. Transect route is indicated.

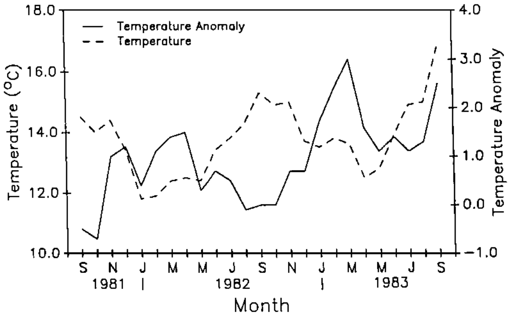

FIGURE 2. Monthly mean temperature and temperature anomaly for Monterey Bay, California. Temperature anomaly is the difference between the mean monthly temperature and the 30 year mean monthly temperature (Avers 1981, 1982, 1983).

changes in oceanographic conditions. In their large scale study of seabird distribution off Central California, Briggs et al. (1983) found significant seasonal changes in Common Murre distribution. However, the large scope of that study precluded the description of small scale distribution patterns in populations responding to local changes in currents and productivity.

Since nonbreeding seabirds are not tied to a colony site, their distribution should, to a large degree, be a reflection of prey distribution. The diet of the Common Murre in the northeastern Pacific has received considerable attention (see Ainley and Sanger 1979 for a review). Unfortunately, studies of the winter diet of the Common Murre suffer from low sample size, making both seasonal and interspecific comparisons difficult (e.g., Baltz and Morejohn 1977).

By coupling bimonthly shipboard transects with feeding data from Common Murres incidentally entangled in commercial gill nets, I sought answers to the following questions for Monterey Bay Common Murres: 1) are there major seasonal or yearly changes in the diet? 2) are there major seasonal or yearly changes in distribution and abundance? 3) how do observed changes reflect spatial and temporal differences in oceanographic conditions and biological productivity?

Normal oceanographic seasonal transitions within Monterey Bay have been described by several authors (Bolin and Abbott 1963, Abbott and Albee 1967, Broenkow and Smethie 1978, Shea and Broenkow 1982). Generally, the hydrographic cycle may be divided into three variable, overlapping seasons: 1) upwelling from February through August, which encompasses both the Common Murre breeding period in the spring (February through May) and postbreeding period in the summer (June through August); 2) the fall, when offshore California Current waters enter the coastal region from September through October; and 3) the winter, when the California Counter Current (Davidson Current) surfaces from November through January. For the present study I considered the oceanographic seasons of Monterey Bay as follows: February–May (early upwelling period), spring; June–August (late upwelling period), summer; September–October (oceanic period), fall; November–January (Davidson period), winter.

Beginning in fall, 1982 there was an increase in water temperature in Central California caused by a strong "El Niño," persisting through the end of this study (Fig. 2). This provided an opportunity to compare the feeding and distribution of Common Murres under different circumstances: a normal year (1981–1982) and an "El Niño" year (1982–1983).

METHODS

FEEDING

I examined the stomach contents of 238 murres incidentally entangled in commercial gill nets in Monterey Bay. One hundred ninety-nine samples were taken from June 1981 through August 1982, excluding November through January. In addition, 39 samples were taken June through August 1983. All individuals were caught within the Bay at depths ranging from 3 to 70 m. As the gill nets were set over a 24 hour period, exact time of capture could not be determined. Birds taken from the fishermen who were hauling in their nets were placed immediately on ice to retard digestive processes during transport to the laboratory. In the laboratory, the peritoneal cavity was opened and sex, length and width of gonads, and diameter of largest follicle in females were determined. The proventriculus and gizzard were removed and frozen for later analysis of their contents.

Fat analysis

As an objective index of the fat condition of each bird, I measured the thickness of the dermis at an incision made in the skin over the left part of the upper breast (over the furculum) to the nearest 0.5 mm. Chu (1984) found that this measurement is a reliable predictor of fat condition in shearwaters. Individuals collected in summer were separated by sex and breeding status. Nonbreeders were defined as those lacking a brood patch. In the fall (September–October), individuals were simply separated by sex.

All comparisons of fat thickness were made by analysis of variance or Student's t-test (Zar 1974). Multiple comparisons were made using the Student Newman Keuls (SNK) multiple comparisons test (Zar 1974).

Molt analysis

I evaluated the stage of molt for each individual. Body molt was scored as present when new pinfeathers were found over approximately 10% or more of the breast area. Wing molt was recorded if one primary was missing with a pinfeather coming in to replace it, or if two or more primaries were missing on both wings.

Stomach analysis

The contents of the proventriculus and gizzard were sorted to the lowest determinable taxonomic category. The volume of each category was then measured by displacement of water in a graduated cylinder. Cephalopod beaks and fish otoliths were washed, and then identified by comparison with reference collections at Moss Landing Marine Laboratories, and pictorial guides (Fitch 1964, 1966; Iverson and Pinkas 1971; Morrow 1977). The minimum number of fish represented by otoliths was taken to be the greatest number of left or right sagittae; the minimum number of individual cephalopods was taken to be the greatest number of upper or lower beak halves (Baltz and Morejohn 1977).

Data analysis

To describe the seasonal importance of each prey species, I calculated percent composition of prey by number (%N), volume (%V), and frequency of occurrence (%FO). Using these values, I then calculated an Index of relative importance (IRI) developed by Pinkas et al. (1971) to avoid biases in assessing prey importance indicated by the above categories. This index is calculated for each prey category as:

$$(\%N_i + \%V_i)\,(\%FO_i) = IRI_i$$

Diversity indices

Green (1979) and Hurlbert (1971) suggest that simple indices such as the number of prey species (S) is a biologically meaningful measure that is a less ambiguous and better measure of biological change with respect to its relationship to environmental change than the more complex diversity indices. Accordingly, I calculated the simpler values: number of species (which is the number of species found in each stomach averaged over the sampling period), and percent dominance for each season. The percent dominance of prey species in the diet was calculated as follows:

$$D = \sum_{i=1}^{s} (n_i/N)^2$$

where Σ = total number of prey species eaten, n_i = number of individuals of prey species, i, present in sample, and N = total number of individuals in sample.

This value was then averaged over all stomachs for the sampling period. Dominance values range from 0 to 1. A dominance value of 1 indicates a sample with only one prey species.

Overlap indices

I used the percent similarity index (PSI) (Saunders 1960) to measure dietary overlap by season and year. It is calculated by summing the smallest percent by number of each prey species within the seasons or years under comparison:

$$PSI = \sum_{i=1}^{s} \min \%N_i$$

There are no statistical tests for computing significant overlap; I follow Silver (1975) in using 80%. I used chi-square analysis of the raw numerical prey data to compare yearly and seasonal murre diets. Prey observed in less than 10 stomachs were lumped as "other fish." I computed the G-statistic for significance testing (Sokal and Rohlf 1981).

TRANSECT

Thirty-five strip transects were surveyed within Monterey Bay from September 1981 through September 1983, using methods similar to those described by Briggs and Hunt (1981), except that the zone distances were modified to 200 m. These transects occurred approximately bimonthly, conditions permitting. To facilitate seasonal comparisons of relative densities, the ship ran an identical rectangular course for each census (Fig. 1) at a constant speed of 18.5 km/hr. Course was selected to sample adequately both the inshore region of the Bay, and the offshore canyon slope.

Two observers sat 3 m above the water line and recorded murres observed between 0 and 90 degrees to port and starboard of the bow. To minimize variation due to observer bias, the same observers made almost all surveys. In addition to number of individuals, the following data were taken: 1) distance from the ship, visually estimated and coded as Zone 1, 0–50 m from the ship or Zone 2, 51–200 m from the ship; 2) time of observation; 3) behavior of bird (flying, sitting on water surface, or following the ship); 4) sea condition (Beaufort scale), glare, percent cloud cover, precipitation, and a subjective evaluation of sighting conditions were recorded each hour or as conditions changed; the transect was terminated if sea state was greater than Beaufort 3, or subjective sighting conditions were poor; 5) boat speed, location, and time were logged every 15 min and at course changes to ensure that the ship followed the designated track for placement of sightings along the track line; 6) during the late upwelling period, Common Murre chick/adult pairs were noted.

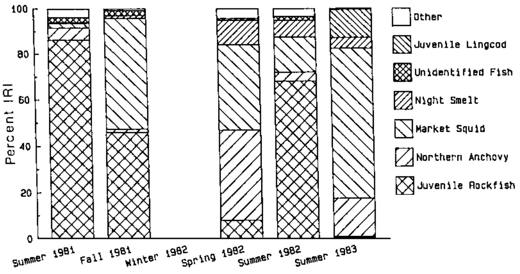

FIGURE 3. Seasonal diet of Monterey Bay Common Murres. Importance of prey species represented by percent index of relative importance (see text for explanation). ND = data not available for this season.

The transect was broken into 3 km segments for analysis. For each segment a density was calculated (number of murres per 3 km × 0.2 km segment) to be used as a discrete sample for statistical comparisons. Because variances were proportional to the means, samples were transformed by a square-root transformation for statistical testing. Comparisons between density values for each season were made by analysis of variance (Zar 1974). The data were subdivided into two depth categories: offshore (waters deeper than 40 m), and inshore (waters ≤40 m deep). The Monterey submarine canyon axis was chosen as the north–south dividing line. Therefore, comparisons within each season were made with respect to: north bay, inshore; north bay, offshore; south bay, inshore; and south bay, offshore. Comparisons between locations were made with one-way ANOVA or Student's t-test (Zar 1974).

Sea-surface temperature was measured by aircraft within four days of transect date using a radiation thermometer (Barnes PRT-5) mounted through the aircraft floor (see Briggs et al. 1981 for system description). Isotherms were plotted from aircraft data and then superimposed on transect data. Chlorophyll-a was measured by the Coastal Zone Color Scanning satellite (CZCS-Nimbus 7; see Gordon et al. 1980 for system description) within two days of transect date. Relative chlorophyll values are derived for each km^2. The satellite-derived chlorophyll values for the center of each discrete transect segment were used for data analysis. Depth was taken as the depth at the center of each discrete transect segment. Distance from nearest point of land was taken from the center of each discrete transect segment.

RESULTS

FEEDING

Percent IRI values show that the diet of Common Murres in Monterey Bay is dominated by juvenile rockfish (*Sebastes* spp.), market squid (*Loligo opalescens*), northern anchovy (*Engraulis mordax*), and night smelt (*Spirinchus starksi*) (Fig. 3). The importance of each of these species changed seasonally (Fig. 3). Juvenile rockfish (primarily *Sebastes jordani*) dominated during summer 1981 (% IRI = 83.5), then became less important during the 1981 fall period (% IRI = 45.5), when market squid became much more important (% IRI = 48.0). By winter, 1982 juvenile rockfish % IRI had dropped to a low of 8.0 and market squid to 36.9, while northern anchovy dominated (% IRI = 38.5), and night smelt increased to 10.7%. The diet of the Common Murre was different each season (G = 198.465, $P < .001$), and subdivision of the chi-square showed that each season was different from both the previous and subsequent season.

Diets in the summers of 1981, 1982, and 1983 were significantly different (G = 198.7, $P < .001$) (Fig. 3). As in 1981, the diet in 1982 was dominated by juvenile rockfish (% IRI = 66.8); however, in 1982 market squid and night smelt were much more important. There was also a significant difference (G = 67.26, $P < .001$) in summer diets in 1981 and 1982.

In the summer of 1983 the murres' diet changed dramatically, and differed significantly from 1981 (G = 444.08, $P < .001$) and 1982 (G = 274.8, $P < .001$). Juvenile rockfish were not important in 1983 and were replaced by market squid as the important food item, followed by northern anchovy. Also, a new species became important, juvenile ling cod (*Ophiodon elongatus*). Table 1 reveals that there was no seasonal difference either in the number of prey species per stomach (Kruskall Wallis; H = 9.452, $P > .05$) or in dominance values (Arcsine transform ANOVA; F = 1.289, $P > .05$). Therefore, individuals at any one time only fed upon one or two prey types. Within year overlap comparisons from June 1981 through May 1982 (Table 2) revealed that there were notable seasonal shifts in diet.

Results of between-year overlap comparisons from the summers of 1981, 1982, and 1983 (Table 2) show that overlap was high (PSI = 77.6) for 1981 vs. 1982, whereas it was low between 1981 vs. 1983 (PSI = 25.6) and 1982 vs. 1983 (PSI = 9.5). Thus in 1983 murres preyed upon a much different array of prey than in the previous two years.

FAT ANALYSIS

Summer fat indices did not differ between 1981 and 1982 for each breeding or sex category (Student's t-test, $P < .05$). Therefore, the indices for each category were combined for analysis. Mean (±SD) summer indices for each category were: nonbreeding female 3.3 mm (±1.0), N = 37; postbreeding female 2.1 mm (±0.9), N = 48; nonbreeding male 3.5 mm (±0.9), N = 69; postbreeding male 3.0 mm (±1.0), N = 50. Mean values for the four categories were significantly different (one way ANOVA; F = 22.04, $P < .001$), and female postbreeders were significantly leaner than all other categories (SNK; q = 11.14;

TABLE 1. NUMBER OF SPECIES PER STOMACH AND SPECIES DOMINANCE VALUES FOR MONTEREY BAY COMMON MURRES

Season	Number species/ stomach	Dominance
Summer 1981	1.63	0.72
Fall 1981	1.13	0.75
Spring 1982	1.80	0.53
Summer 1982	1.47	0.68
Summer 1983	1.59	0.67

TABLE 2. COMPARISONS OF MONTEREY BAY COMMON MURRE DIET BY SEASON AND YEAR (AS MEASURED BY PERCENT SIMILARITY INDEX)

Comparison	PSI
Summer 1981 vs. Fall 1981	53.18
Fall 1981 vs. Spring 1982	49.74
Spring 1982 vs. Summer 1982	37.50
Summer 1981 vs. Summer 1982	77.61
Summer 1981 vs. Summer 1983	9.46
Summer 1982 vs. Summer 1983	25.60

$P < .001$). No difference was found between the remaining three categories (SNK; $P > .05$). Therefore, summer postbreeding females were leaner than all other birds, which in turn exhibited no important differences in fat indices.

Fall fat indices of males did not differ from females ($t = 1.54$, $P > .05$), and the combined mean fat value was 3.9 mm (±1.0), $N = 42$.

Summer 1983 fat values did not differ significantly among the breeding/sex categories, in contrast to the situation in 1981 and 1982 (one way ANOVA; $F = 2.592$, $P > .05$). Therefore, the 1983 fat values were combined (combined mean 2.6 [±0.9], $N = 34$) and compared with 1981–1982 values. The 1983 summer birds were significantly fatter than 1981–1982 summer postbreeding females (Student's t-test; $P > .05$), but significantly leaner than all other 1981–1982 summer categories (one way ANOVA; $P > .05$).

MOLT

Body molt began in early July and finished by early November. Body molt occurred gradually over an extended period, while wing molt was rapid; all primaries were lost simultaneously.

Comparison of the number of postbreeding (as indicated by brood patches) vs. nonbreeding Common Murres molting in July shows that nonbreeding birds begin their molt sooner than postbreeding birds (G test; $G = 7.38$, $P < .01$).

TRANSECT

Seasonal abundance: September 1981–August 1982

In Monterey Bay, Common Murres were most abundant during the summer and fall (Fig. 4). Beginning in September 1981, population densities declined and remained low through the winter (Fig. 4). Density increased abruptly in March 1982, suggesting a strong northward migratory pulse, since 12.6% ($N = 144$) of all murres sighted were actively flying to the north, whereas 85.0% ($N = 1057$) were sitting on the water, and the remainder (2.4%, $N = 39$) flew in directions other than north. Moreover, numbers rapidly dropped again in April and remained low until July. Murre numbers then increased and peaked in late August. Thirty-two percent of all murres observed during summer 1982 were adult/chick pairs. The remarkably high mean density (169.2 birds/km^2) for late August was due primarily to a feeding flock comprised of over 3000 individuals in the northern, inshore region.

Areal utilization: September 1981–August 1982

Not all areas of Monterey Bay were equally important to Common Murres. In fall 1981 and summer 1982, the greatest concentrations were found in the northern inshore regions of the bay (Fig. 5) (Table 3). During other seasons the four areas were used equally (Table 3). However, numbers increased sharply during March in the offshore regions of the bay due to the migration pulse mentioned above.

Environmental correlates: September 1981–August 1982

A correlation matrix from environmental measurements along the transect line on 22 September 1981 and 30 August 1982, when murre densities were high, showed that densities were positively correlated with temperature, but not with distance from land or depth of water (Table 4; critical $r_{(.05,21)} = 0.413$). While chlorophyll was negatively correlated with both depth and distance from land, temperature was not correlated with either parameter. Although positively correlated in 1981, chlorophyll and temperature were not correlated in 1982. Murre density was highly correlated with chlorophyll in 1981 but not in 1982 (Table 4).

Seasonal abundance: September 1982–September 1983

From September 1982 through May 1983 (fall–spring) murre abundance was similar to that of the previous year (Fig. 4). However, the influx observed during the spring 1982 was not duplicated in 1983. In 1983 there were marked differences in murre abundances during the summer months. There was a rapid, large buildup in June, followed by an exodus in July. Numbers

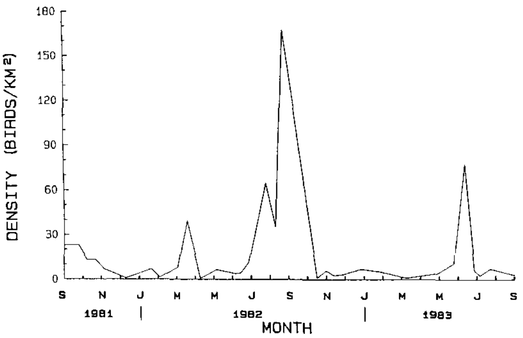

FIGURE 4. Common Murre densities in Monterey Bay from bimonthly transects.

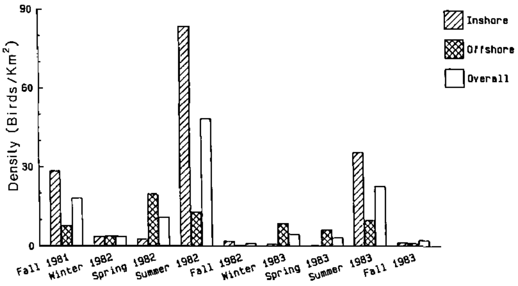

FIGURE 5. Areal distribution of Monterey Bay Common Murres. Depths greater than 40 meters considered offshore.

throughout the rest of the summer remained at low levels, similar to those in winter.

Areal utilization: September 1982–August 1983

Unlike in 1981, murres did not utilize the various regions of Monterey Bay differently during the fall period (Fig. 5). In the winter and spring of 1983, density was significantly higher in the offshore regions. These differences were not observed the previous year. Differences in areal utilization from the previous year were also evident during the summer. Similarly to summer 1982, murres were concentrated in the northern inshore region during summer 1983.

DISCUSSION

Throughout the year murres in Monterey Bay preyed upon groups that form large surface schools as adults (market squid, northern anchovy, night smelt), or have schooling juvenile forms (rockfish). The importance of the various species in the diet changed from season to season and from year to year. The widest variety of important prey species (% IRI values greater than 5) is taken by murres in the spring, whereas in summer murres appear to depend mainly on juvenile rockfish. As a population, the murres fed on a wide range of prey items, but the number of different prey species found in each individual bird was low. Evidently individual murres feed opportunistically, and since most of the prey species form large, monospecific schools (Frey 1971), an individual gut will show high dominance of a few species.

TABLE 3. ANOVA COMPARISONS OF SEASONAL MONTEREY BAY COMMON MURRE DENSITIES (BIRDS/KM²) BY AREA

Season	F	Error df	Significance
Fall 1981[a]	7.02	100	$P < 0.01$
Winter 1982	1.38	106	N.S.
Spring 1982	2.39	126	N.S.
Summer 1982[a]	5.11	152	$P < 0.01$
Fall 1982	1.85	22	N.S.
Winter 1983[b]	15.78	100	$P < 0.01$
Spring 1983[b]	12.52	94	$P < 0.01$
Summer 1983[a]	3.10	126	$P < 0.05$

[a] Student Newman Keuls multiple comparisons found Common Murre density was significantly higher in the northern inshore area; no significant difference between other areas.

[b] Student Newman Keuls multiple comparisons found Common Murre density was significantly higher in the offshore area; no significant difference between north-south densities.

Because wintering seabirds are not tied to breeding colonies, they are able to exploit ephemeral prey patches. Accordingly, one may expect winter seabird distribution and abundance to be adjusted rapidly as prey availability changes. The primary reason for an overwintering seabird to be found at sea is to exploit food resources dependably available there. Thus, differential seasonal abundance of wintering seabirds should be a reflection of differential seasonal availability of prey within a particular area.

The seasonal abundance of murres in Monterey Bay was greatest in the summer. Abundance then dropped rapidly during the fall, and remained low during the winter and spring (breeding) seasons. Their absence during the breeding season indicates that Monterey Bay is not an important area to breeders. However, it is used by adults with dependent chicks, molting nonbreeders, and lean, molting postbreeding females as a feeding area beginning in July. Braune and Gaskin (1982) speculated that the build-up of postbreeding larids off Deer Island, New Brunswick, indicated the importance of the area as a reliable food source for the replenishment of energy reserves lost during breeding, and as a feeding area to meet the energetic demands of molting. Monterey Bay probably serves a similar function for Common Murres.

TABLE 4. CORRELATION MATRICES OF COMMON MURRE DENSITIES AND ENVIRONMENTAL PARAMETERS DURING SUMMER 1981 AND 1982 IN MONTEREY BAY

	Depth	Distance	Temperature	Chlorophyll
Murre density	−0.291[a]	−0.378	0.442	0.622
	−0.303[b]	−0.348	0.594	0.202
Depth		0.832	−0.381	−0.515
		0.832	−0.281	−0.544
Distance			−0.270	−0.736
			−0.264	−0.783
Temperature				0.565
				0.361

[a] Transect date: 22 September 1981.

[b] Transect date: 30 August 1982.

The productivity of the waters of Monterey Bay has been studied intensively, mostly through the efforts of the California Cooperative Oceanic Fisheries Investigations program (e.g., Bolin and Abbott 1963, Broenkow and Smethie 1978, Garrison 1979, Shea and Broenkow 1982). Garrison (1979) found that phytoplankton standing stocks peaked during the spring and summer upwelling period between February and June and dropped to their lowest levels during winter. One would expect to first see an increase in grazers, followed by an increase in higher-level zooplankton feeders resulting from this increase in phytoplankton standing stocks. Anchovy, which feed directly on phytoplankton as well as on zooplankton, form large surface schools between April and June off California (Frey 1971). Cailliet et al. (1979) found that northern anchovy had the highest relative abundance of all shoaling prey groups collected in midwater trawls in February in Monterey Bay. It appears they are available to murres between February and June, when the anchovy possibly take advantage of the increase in phytoplankton standing stocks. Indeed, the northern anchovy was the most important prey of murres at this time.

The murre diet was dominated by juvenile rockfish during the summer, which Cailliet et al. (1979) found to be the most abundant prey taxa in shallow water in Monterey Bay during this period. Juvenile rockfish feed primarily on small crustaceans (Todd Anderson, Moss Landing Marine Laboratories, pers. comm.) and probably come into the bay during the summer to take advantage of high zooplankton numbers which result from the earlier phytoplankton increases. These observations best support the hypothesis that Common Murres in Monterey Bay exploited a seasonal peak in prey availability produced by earlier upwelling episodes.

Juvenile rockfish abundance probably drops off beginning some time in the fall, as juvenile rockfish begin to switch to rock substrate habitats offshore (Anderson 1984). This coincides with a reduction of primary productivity in the bay (Bolin and Abbott 1963). At this time murre abundance also drops and those that remain begin to feed upon market squid. However, squid availability is reduced at this time as well (Cailliet et al. 1979). Thus, Common Murres disperse out of Monterey Bay some time during the fall, when primary productivity has dropped considerably (Bolin and Abbott 1963), and prey availability has presumably decreased as well. Evidence suggests that at this time murres may be concentrating in the offshore shelf waters (Briggs et al. 1983).

Differential utilization of various habitats by seabirds has been discussed on both large and small scales (see Hunt and Schneider 1987 for a review). During the summer, murres concentrate in the shallow, northern portions of the bay. Correlation analysis from this time period revealed that murres concentrated in the warmer regions of the bay that were shallow and close to shore; chlorophyll was relatively unimportant in explaining variability in murre density. Thus, within the small-scale area of Monterey Bay during the summer period, murres appeared to select a particular set of environmental parameters.

How do these observations reflect the small scale processes occurring in Monterey Bay? Broenkow and Smethie (1978) found that upwelling occurs predominantly south of Monterey Bay. Nutrient-rich upwelled waters are advected into the Bay from the south by an eddy of the California Current and penetrate northward. Lasley (1977) found a net northerly inshore flow of water from Point Pinos towards Point Santa Cruz. Lasley (1977) also found that as water flowed to the north, chlorophyll levels decreased from a maximum off Point Pinos to a minimum in the northern bay, nutrient levels decreased, while temperature and oxygen levels increased. He believed low chlorophyll-to-phaeophyton ratios in the central and northern bay indicated substantial zooplankton grazing, whereas high ratios in the southern bay suggested little grazing. As water moves to the north, the biomass of higher trophic levels increases. As a result, a relatively higher abundance of species feeding upon zooplankters (i.e., juvenile rockfish) in the northern regions of the bay is expected. It appears that murres are concentrated in the warmer, low chlorophyll waters some distance away from the source of upwelling. This distance allows time for the effects of increased primary production to work its way up the food chain as the water is transported from the upwelling center.

Briggs et al. (1984) concluded similarly from a study of phalarope feeding in the California Current. They found that phalaropes fed upon zooplankton that was concentrated in convergences offshore. Phalarope distribution was correlated negatively with chlorophyll concentration. In their view, the best possible feeding conditions for phalaropes probably occurred "downstream" from an active upwelling center, where productivity resulting from upwelling has had time to work its way up the food chain. In their study of the relationship of seabird distribution to the hydrography of California, Briggs and Chu (1987:295) stated that "for fish and squid and their predators as well, optimal combinations of substrate, circulation, and feeding conditions are met downstream from major upwellings in less turbulent waters." Indeed, zooplankton and phytoplankton stocks were inversely related at smaller scales (Hunt and Schneider 1987). This may explain the relatively poor correlations of higher-trophic-level seabirds with oceanographic indicators of primary productivity such as low water temperature, high nutrient levels, and high chlorophyll concentration.

In winter 1982/1983, the effects of an El Niño-Southern Oscillation (ENSO) were first measured in the California Current off California (Reed 1983). These included anomalously high sea surface temperatures, high sea levels, and a deepening of the thermocline from about 30 m to 60–70 m in 1983 (McClain 1983). McGowan (1985) found zooplankton levels were down to record lows from previous 30 year median values. The 1982/1983 ENSO probably had two possible effects in the Central California region: 1) the onshore transport of warm, low-salinity water from the California Current (Simpson 1984) resulted in a downward tilt of the coastal thermocline; and 2) the poleward propagation of a baroclinic wave created at the equator resulted in an anomalous isotherm deepening off California and enhancement of the Davidson Current during winter 1982/1983, creating record high sea levels (McClain 1983). Whatever the cause, warm oceanic waters intruded into Monterey Bay (Fig. 2), effectively capping the usual nutrient upwelling. Anomalous observations of warm water species from the south (e.g., pelagic red crabs, *Pleuroncodes planipes*; California barracudas, *Sphyraena argentea*; and common dolphins, *Delphinus delphis*) increased (Alan Baldridge, Hopkins Marine Station, pers. comm.), while productivity decreased.

Concurrently, on the Farallon Islands off San Francisco, reproduction of seabird species dependent on seasonal upwelling was severely depressed (Boekelheide 1984). Common Murre egg production fell to 49% of the previous year, and the fledging rate of murres dropped from a normal mean of 0.7 to 0.9 chicks per pair to less than 0.05 per pair (Boekelheide 1984). Juvenile rockfish, which are normally the dominant prey delivered to chicks, were delivered in only 17.8% of the feeds in 1983 compared to 64.7% in 1982 (Boekelheide 1984).

There were also changes in murre distribution in Monterey Bay. Significantly more murres were found in the offshore regions in spring 1983. Maximum mean abundance in June increased well above the maximum mean density seen the previous year (from 4 birds/km^2 in 1982 to 88 birds/km^2 in 1983). This increase probably included failed breeders (out of 16 females examined, ova with yolk were found in 3 females, and eggs with complete shells were found in 2 females, pers. obs.). Evidence of widespread breeding failure was indicated by the absence of dependent chicks. Murre numbers then declined rapidly so that by late July the mean density was only 3 birds/km^2 (compared to 65 birds/km^2 in 1982).

Fat indices and diet of Common Murres in Monterey Bay also differed markedly during summer 1983. Murres examined were significantly leaner than those examined in 1981 and 1982, with the exception of the postbreeding females. Juvenile rockfish were the most important prey item to murres during the summer in 1981 and 1982, but in 1983 few juvenile rockfish were taken. Instead, market squid dominated the diet, followed by northern anchovy. Lea and Van Tresca (1984) found reduced rockfish reproductive output in both 1982 and 1983, and McClain (1983) observed lower market squid abundance in Monterey Bay in 1983. A prey species never seen in previous years, juvenile ling cod (*Ophiodon elongatus*), became the third most important prey item in 1983. Juvenile ling cod are widely dispersed on the sandy bottom (Frey 1971). This change in Common Murre diet to include a nonshoaling prey species in significant numbers is especially interesting, since it would require a coincidental change in the normal foraging behavior.

Therefore, as a result of the 1982/1983 ENSO, a large number of lean Common Murres entered Monterey Bay in June 1983. No chicks were found in the bay in 1983. The normally reliable juvenile rockfish resource probably was not available, resulting in a change in diet from that observed in the previous years. With low food availability, the murres quickly moved out of the bay, creating densities in July that are normally observed during the fall and winter seasons of low productivity.

During normal hydrographic years in Monterey Bay, Common Murres exploit a dependable seasonal peak in prey availability resulting from an earlier upwelling episode. Murres use this peak in food availability during the summer to feed dependent chicks, replenish fat stores, and molt. Murre diet and abundance change seasonally in response to changing local productivity. During the summer, when murre densities are highest, murres concentrate in the northern part of Monterey Bay. As advected water is transported from the southern to northern portions of the bay in an eddy of the California Current, the effects of increased production due to offshore upwelling results in a concomitant increase in higher trophic level productivity. This results in higher prey availability in the northern areas, leading to higher Common Murre abundance. The 1982/1983 ENSO resulted in depressed productivity, and ultimately decreased murre abundance in Monterey Bay.

This study indicates the importance of recognizing the temporal lag in productivity that results from increased nutrient availability after a physical event such as coastal upwelling. Biological benefits from increased nutrient availability are separated in time from the physical events that initiated them. Ocean currents translate this temporal separation into a spatial separation. Thus, distributions of higher trophic level organisms such as seabirds will be spatially separated from the physical indicators of primary productivity and nutrient availability.

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Auks in Peril

DECLINE OF THE COMMON MURRE IN CENTRAL CALIFORNIA, 1980–1986

JEAN E. TAKEKAWA, HARRY R. CARTER, AND THOMAS E. HARVEY

Abstract. Aerial surveys of 13 Common Murre (*Uria aalge*) colonies were conducted in California in 1985 and 1986. Breeding population estimates for eight colonies in central California and five colonies in northern California were compared with estimates determined in 1980–1982. The central California population declined 52.6% within 4–6 years, from 229,080 in 1980–1982 to 108,530 in 1986. The northern California population remained relatively unchanged during the same period; combined totals at four colonies declined 5.4% from 118,080 in 1979–1982 to 111,730 in 1986. Population decline in central California was caused by high mortality from an intensive nearshore gill-net fishery, compounded by that from oil spills and a severe El Niño-Southern Oscillation event in 1982–1983. Individual colonies declined 45.8–100% and the most severe declines occurred at colonies located nearest to areas of highest gill-net fishing mortality.

Key Words: Aerial surveys; Alcidae; Common Murre; El Niño; oil spill; gill-net fishery; *Uria aalge*.

In 1979 and 1980, over 360,000 Common Murres (*Uria aalge*) nested in colonies distributed between Castle Rock, Del Norte County, in northern California and Hurricane Point Rocks, Monterey County, in central California (Sowls et al. 1980). Eight colonies in central California (about 30% of the state population) occurred south of Point Reyes (37°59′N, 123°59′W), whereas 12 northern California colonies (about 70% of the state population) occurred north of Cape Vizcaino (39°43′N, 123°49′W) (Fig. 1). We think there is little immigration or emigration between populations in central and northern California because they are separated by a distance of about 200–250 km, and in both areas birds remain near breeding colonies throughout the year (Storer 1952; DeGange and Sowls 1981; Ainley and Boekelheide 1990).

While murre numbers have increased at some colonies throughout this century (Osborne and Reynolds 1971, Osborne 1972, Sowls et al. 1980), increases in Farallon Island colonies in central California followed a severe historical population decline due to human occupation, egging, and chronic oil pollution in the Gulf of the Farallones. An estimated population of 400,000 birds in the mid-1800s fell to a few thousand birds in the mid-1900s (reviewed in Ainley and Lewis 1974). Partial protection was afforded colonies in 1909 when North Farallon (Fig. 1) and West End islands (Fig. 2) were established as the Farallon National Wildlife Refuge (NWR), under the jurisdiction of the U.S. Fish and Wildlife Service (USFWS). Egging stopped around the turn of the century and Dawson (1923) reported as many as 20,000 murres in 1911. However, mortalities caused by oil pollution from ship bilge discharges and oil spills continued to occur in the area (Palmer 1921, Moffitt and Orr 1938, Houldson 1952) and only a few hundreds to thousands of murres were reported from the 1920s to 1950s (e.g., Chaney 1924).

Additional protection was established in 1969 when Southeast Farallon Island (SEFI) and neighboring islets (Fig. 2) were included within the Farallon NWR. Since 1967 Point Reyes Bird Observatory (PRBO) has conducted research on the Farallon Islands, and since 1971 PRBO personnel have resided on the refuge through a cooperative agreement with USFWS, providing wardens for the first time on the islands and monitoring marine bird populations. Between 1959 and 1972 the murre population grew from about 6000 to 22,000 birds, despite the major 1971 San Francisco oil spill when thousands were killed (Smail et al. 1972, Ainley and Lewis 1974). In 1974 North Farallon and West End islands were designated as Wilderness Areas. This protection and lessened oil pollution allowed the breeding population to increase through the 1970s and early 1980s (DeSante and Ainley 1980; Ainley and Boekelheide 1990). By 1980, the South Farallon Islands (including West End Island, SEFI, and neighboring islets) supported the second largest murre colony in California (about 17% of the state population). The largest was at Castle Rock in northern California (Sowls et al. 1980), which was designated a NWR in 1980. There is little historical information on murre colonies in northern California, but numbers also increased there through the 1970s (Osborne 1972, Sowls et al. 1980). In southern California, murres for-

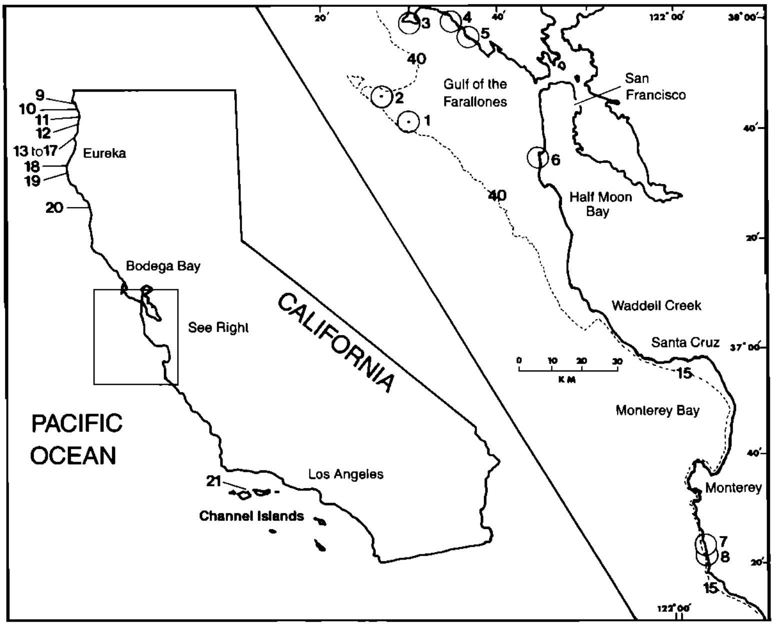

FIGURE 1. Locations of 21 Common Murre colonies in California (from Sowls et al. 1980). Central California colonies (inset): 1, South Farallon Islands; 2, North Farallon Islands; 3, Point Reyes; 4, Point Resistance; 5, Double Point Rocks; 6, Devil's Slide Rock; 7, Castle Rocks; 8, Hurricane Point Rocks. Northern California colonies (left): 9, Castle Rock; 10, Sister Rocks; 11, False Klamath Rock; 12, Redding Rock; 13, White Rock; 14, Green Rock; 15, Flatiron Rock; 16, Blank Rock; 17, Pilot Rock; 18, False Cape Rocks; 19, Steamboat Rock; 20, Cape Vizcaino. Southern California colonies (left): 21, Prince Island. The 40 and 15 fathom contours (inset) are indicated by the dashed line north and south of Waddell Creek, respectively.

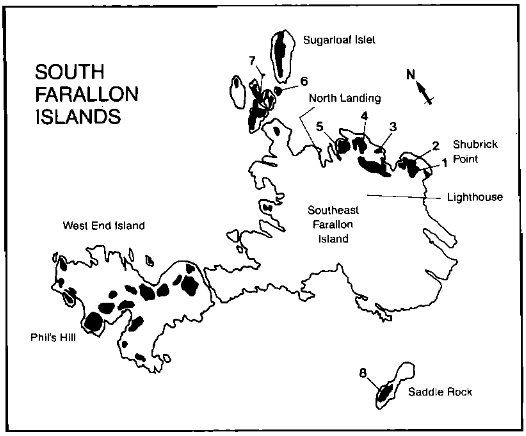

FIGURE 2. Map of the South Farallon Islands, San Francisco County. Common Murre nesting areas in 1986 are darkened. Numbered plots were used to monitor murres and to provide correction factors: 1, Upper Shubrick Point; 2, Lower Shubrick Point; 3, Cove Point; 4, Tower Point; 5, North Landing; 6, Chocolate Chip Islet; 7, Finger Rock; 8, Saddle Rock.

merly bred at Prince Island, but have been absent since the early 1900s (Hunt et al. 1979, Sowls et al. 1980).

After 1979 a decline in the numbers of murres breeding at the Farallon Islands occurred following heavy mortality of murres from gill-net fishing, two major oil spills, and the effects of the intense 1982–1983 El Niño-Southern Oscillation event (ENSO) (Carter 1986; Atkins and Heneman 1987; Ford et al. 1987; Page et al. 1990; Ainley and Boekelheide 1990). ENSO causes reduced ocean productivity, thereby affecting seabird reproduction. However, gill-net mortality was of special concern, because it was restricted to the smaller central California population and thousands of murres were being killed (California Department of Fish and Game [CDFG] 1981, 1987; Atkins and Heneman 1987; Stenzel et al. 1988; CDFG, unpubl. data).

Declines were first detected at the Farallon Islands in 1984. Other colonies had not been censused since 1982 and their status was unknown. In 1985 and 1986, USFWS and PRBO conducted aerial surveys to refine breeding popu-

FIGURE 3. Rock #4 subcolony at Point Reyes, 1986, showing the high resolution and clarity of slides used to count murres.

lation estimates at the Farallon Islands and determine the status of other colonies. In this paper, we compare our results to earlier population estimates to determine the extent of decline of the central California murre population between 1980 and 1986, and evaluate causes for this decline. We discuss several procedural inconsistencies that made it difficult to determine trends at some colonies, recognition of which should assist in interpreting past and future trends.

METHODS

AERIAL SURVEYS

In 1985, aerial surveys were conducted at five colonies in central California (South and North Farallon islands, Point Reyes, Point Resistance, and Double Point Rocks) and at Castle Rock in northern California. Surveys in 1986 covered all eight central California colonies (adding Devil's Slide, Castle, and Hurricane Point rocks) and five major colonies in northern California (Castle, False Klamath, Redding, Green, and Flatiron rocks), north of Eureka (Fig. 1). In both years, colonies in central California were surveyed on two days (30 May and 12 June 1985, 4 and 5 June 1986), whereas northern California colonies were surveyed on one day (5 June 1985, 19 June 1986). Surveys were flown at 50–90 knots (depending on wind speed) from a single engine, wing-over Cessna 150 or 182 aircraft at altitudes of 120–150 m in northern California. A quieter twin engine, wing-over Partanavia aircraft was used at altitudes of 150–200 m in central California, where murres were more sensitive to disturbance by aircraft, particularly at the South Farallon Islands. All surveys were flown without flushing birds.

Colonies were photographed by two photographers, each using a 35 mm camera set at rapid shutter speeds (1/500 or 1/1000 secs), a 300 mm telephoto lens, and color slide film (ASA 400). Overview photos were also taken using a 50 mm lens and color slide film (ASA 64). We attempted to pass directly overhead to minimize oblique photographs; however, when surveying the South Farallon Islands, passes were flown farther off the island due to steep topography and to prevent disturbance. At Point Reyes, high winds and steep topography made full coverage difficult.

Slides of the highest quality (Fig. 3) were projected onto white paper and areas to be counted were demarcated using landmarks or colony outlines. Slides were scrutinized by several observers who dotted each bird with a felt tip pen and later tallied dots with a hand-held counter. All slides and counting sheets were archived at the San Francisco Bay NWR office.

Aerial survey results were compared to similar surveys conducted in 1979 and 1980 by Sowls et al. (1980) and in 1980 and 1982 by Briggs et al. (1983). Data from 1981 surveys by Briggs et al. (1983) were excluded due to lower photo quality (K. T. Briggs, pers. comm.). In both previous studies, birds had been counted individually. However, in large colonies or when individual birds could not be distinguished in slides, they were counted in blocks of 10, 50, or 100 by Sowls et al. (1980) and in blocks of 100 by Briggs et al. (1983). Our slides were generally of larger scale, higher resolution, and greater clarity, so that we were able to count birds individually and achieve a higher degree of accuracy.

GROUND AND BOAT SURVEYS

Colonies on the South Farallon Islands were surveyed by PRBO using ground and boat counts in 1972, 1979–1982, and 1984–1986 (Ainley and Lewis 1974; Ainley and Boekelheide, 1990; PRBO, unpubl. data). Birds on SEFI were counted mainly from several ac-

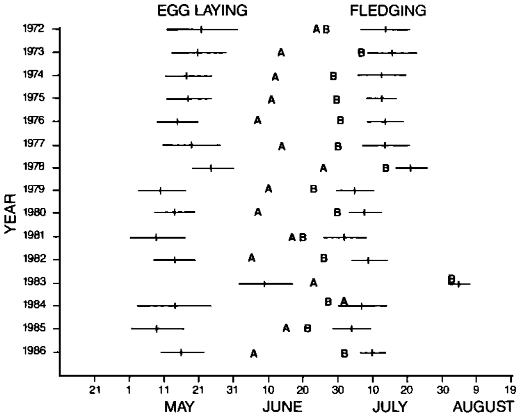

FIGURE 4. Annual variation in mean (±SD) egg-laying and fledging dates of Common Murres in the Upper Shubrick Point plot, SEFI. Symbols A and B refer to last egg laid and first chick fledged, respectively. Data are from Ainley and Boekelheide (1990) and PRBO (unpubl. data).

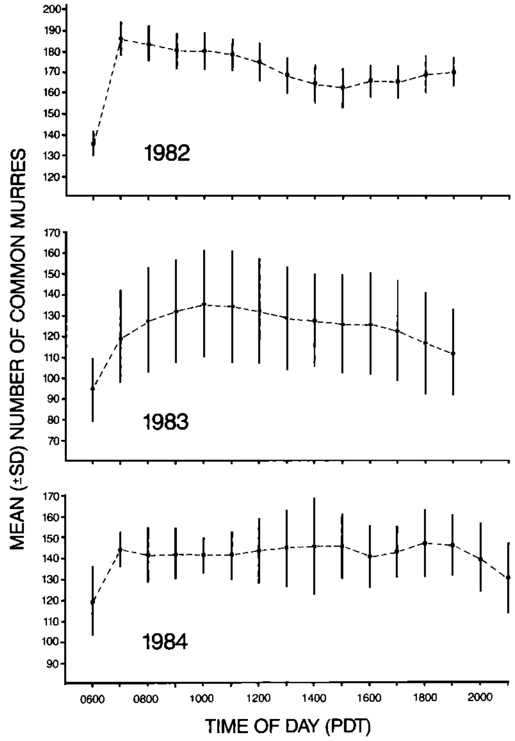

FIGURE 5. Mean (±SD) numbers of Common Murres in the Upper Shubrick Point plot at hourly intervals throughout the day during the census period in 1982, 1983, and 1984. Data are from L. B. Spear (unpubl. data) and PRBO (unpubl. data).

cessible vantage points on the island, whereas those on neighboring islets and West End Island were counted mainly from a small boat. Murres were counted individually in small colonies and in blocks of 10, 50, or 100 in larger or very dense colonies.

PRBO recognized several potential sources of counting error (primarily for boat surveys) including environmental conditions, visibility, and observer experience. Hence, we initiated aerial surveys in 1985 to estimate populations more accurately on West End Island and elsewhere. Murres on SEFI continued to be surveyed mainly by ground counts due to their accessibility and the greater accuracy of these counts.

CENSUS PERIOD

Aerial surveys were conducted between the end of egg laying and the start of fledging as determined at the South Farallon Islands. Murre numbers are high and least variable during this period (Birkhead 1978, Slater 1980, Gaston and Nettleship 1981), although Hatch and Hatch (1989) found a wider window. We based census dates on information from South Farallon Islands, where timing and success of breeding have been monitored in the Upper Shubrick Point plot (Fig. 2) since 1972 (data from Ainley and Boekelheide, 1990; PRBO, unpubl. data). Breeding phenology in northern California appears to be similar to that in central California (Sowls et al. 1980).

There is much annual variation in breeding phenology on South Farallon Islands (Fig. 4). Egg laying was protracted; on average, only 16.2 ± 10.4 days (N = 15 years, R = 0–41 days) occurred between dates when the last egg was laid (excluding replacement eggs) and the first chick fledged. We attempted to conduct aerial surveys of the Farallon Islands near the date when the last egg was expected to be laid. Other colonies were surveyed as soon as possible thereafter. Boat and ground surveys at South Farallon Islands were conducted slightly later, usually in early to mid-June when egg laying was completed, except in 1984 when rough weather and prolonged egg laying (Fig. 4) delayed the census until 1 July.

TIME OF CENSUS

Surveys were conducted during mid-day when numbers of murres attending colonies are usually high and least variable (Birkhead 1978, Birkhead and Nettleship 1980). Although diurnal patterns of attendance have been found to vary between colonies (Gaston and Nettleship 1981, Piatt and McLagan 1987), it generally has been assumed that year-to-year patterns are similar at specific colonies (see Birkhead and Nettleship 1980).

To determine the time of day when murre numbers were most constant at SEFI, we examined counts made in the Upper Shubrick Point plot from 1982 to 1984 (Fig. 5) between when the last egg was laid (excluding replacements) and the first chick fledged (6–29 June 1982, N = 10 days; 24 June–22 July 1983, N = 25 days). In 1984 we widened this window of time (27 May–10 July, N = 10 days) when the first chick fledged before the last egg was laid. Diurnal attendance patterns varied widely between years (Fig. 5). In 1983 and 1984, greater coefficients of variation (CV) occurred around hourly means, averaging 0.19 ± 0.01 (SD; R = 0.16–0.21; N = 14 means from 06:00–19:00 [PDT]) and

TABLE 1. NUMBERS OF COMMON MURRES IN THE UPPER SHUBRICK POINT PLOT ON SEFI USED TO CALCULATE THE K CORRECTION FACTOR AND BREEDER : NON-BREEDER RATIO (BNR), 1980–1986

Year	Date	No. birds per site in plot[1]		K	BNR
		TB	TNB		
1986	3 Jun	1.03 (119)[2]	1.71 (7)	1.76	19.83
	4 Jun	1.02 (117)	1.50 (6)	1.83	26.00
	5 Jun	1.03 (118)	1.83 (6)	1.77	21.45
	mean	1.03	1.68	1.79	22.43
1985	19 Jun	1.08 (121)	2.50 (8)	1.60	12.10
	21 Jun	1.07 (121)	2.63 (8)	1.61	11.52
	mean	1.08	2.57	1.61	11.81
1984	1 Jul	1.17 (86)	1.52 (33)	1.14	3.44
1981	8–9 Jun	1.14 (155)	—	1.66	31.00
1980	7 Jun	1.17 (150)	—	1.64	42.86

[1] Total breeders (TB) includes failed breeders; total non-breeders per non-breeding site (TNB).

[2] The number of sites are indicated within parentheses.

0.10 ± 0.03 (R = 0.06–0.16), respectively. The CV was lower in 1982, averaging 0.05 ± 0.01 (R = 0.04–0.06). These values were within the range of those found by Lloyd (1975) and Gaston and Nettleship (1981). Only in 1984 did CV vary slightly with time of day.

Diurnal attendance patterns in 1982 and 1983 may have been influenced by the intense 1982–1983 ENSO (Ainley and Boekelheide 1990). We conducted hourly counts of murres in the Upper Shubrick Point plot on 13 and 29 June 1985 and 1 and 17 June 1986. Murre numbers most closely approximated the diurnal pattern of attendance exhibited in 1984 (Fig. 5) and we suspect that in most years, murre numbers are consistent throughout mid-day. Therefore, we conducted aerial surveys of the South Farallon Islands between 10:00–12:00 when murre numbers there should be high and least variable. Other colonies were surveyed between 10:00–14:00 to provide sufficient time to survey several colonies in a day and to minimize effects of any diurnal variation. Previous surveys were also conducted in mid-day (Sowls et al. 1980), although Briggs et al. (1983) used a wider window of time (09:00–17:00).

K CORRECTION FACTOR

Birkhead and Nettleship (1980) and Gaston and Nettleship (1981) used the K correction factor to convert total counts of birds into estimates of breeding pairs as follows:

$$K(t_1) = n_e/n_t(t_1) \qquad (1)$$

where: n_e = number of first eggs laid in a plot and $n_t(t_1)$ = total number of birds present in a plot at time t_1. We used a slight variation of K to convert total counts of birds into estimates of total numbers of breeding birds as follows:

$$K(t_1) = n_s(2)/n_t(t_1) \qquad (2)$$

where: n_s = number of egg-laying sites for first eggs in the Upper Shubrick Point plot on the census day (multiplied by two breeding birds per site). Since some sites were partially obscured in some years (R. J. Boekelheide, pers. comm.), only those sites fully visible on the census day were used. In 1981 and 1986, the last egg (excluding replacements) was laid a few days after the census date (see Fig. 4). Although these factors slightly biased our calculation of K, overall error probably remained within about 5% (see Gaston et al. 1983).

K varied between 1.14–1.79 during the 5 years examined (Table 1). In 1984, K was very low (1.14) due to larger-than-normal numbers of non-breeding birds and sites and a sharp decrease in the number of breeding sites in the plot. In the remaining years (1980, 1981, 1985, and 1986), K varied little between days and years (R = 1.60–1.83). We averaged these annual K values to derive a mean (±SD) K-value of 1.68 ± 0.08 (N = 4 years) and applied it to all aerial counts by Sowls et al. (1980), Briggs et al. (1983), and this study, except for Farallon Islands counts. Thus, atypical breeding years such as 1983 and 1984 were not used to develop the mean K value and, coincidentally, aerial surveys were not conducted in those years. This mean K value was very close to the value of 1.67 that Sowls et al. (1980) and Briggs et al. (1983) used to adjust their counts (Ainley and Boekelheide 1990). K values specific to each year were used to adjust counts at the South and North Farallon islands, except for 1982 when K was not determined; here the 1981 K value was substituted because these years seemed similar. All breeding population estimates were then rounded to the nearest 10.

South and North Farallon islands aerial survey counts were further refined with a ground truthing correction factor determined each year on SEFI. Breeder : non-breeder ratios and minimal non-breeding population estimates were also determined at the South Farallon Islands (see Appendix).

RESULTS

CENTRAL CALIFORNIA POPULATION TRENDS

The total breeding population in central California declined 52.6%, from 229,080 in 1980–1982 to 108,530 in 1986 (Table 2). Progressive declines were striking when colonies were compared in slides taken from 1979–1980 through 1986 (Figs. 6 and 7). Individual colonies decreased 45.8–100%.

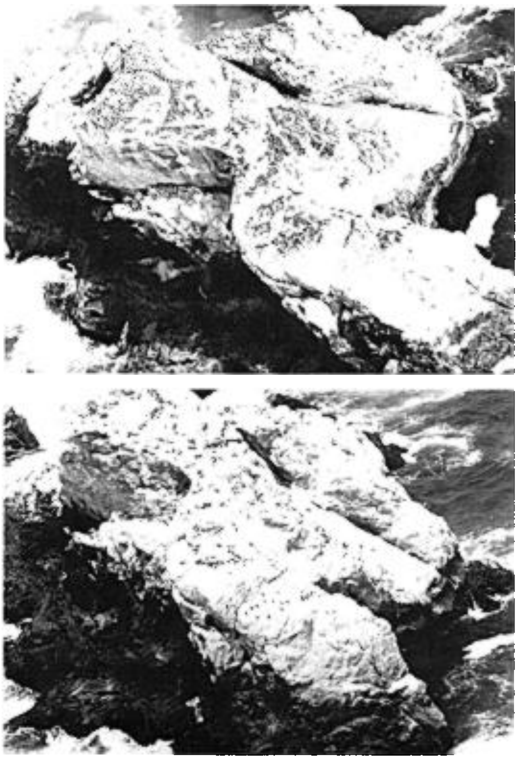

FIGURE 6. Common Murres on the south island at the North Farallon Islands in 1982 (top) and following a 55.4% decline in 1986 (bottom).

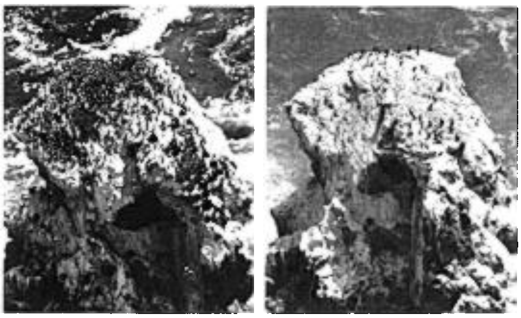

FIGURE 7. Common Murres on Devil's Slide Rock in 1982 (left) and after the colony disappeared in 1986 (right). Fewer than 100 murres were present on 5 June 1986, and none on 4 June.

Farallon Islands

The breeding population peaked at 102,110 birds in 1982 on the South Farallon Islands (Briggs et al. 1983), followed by a 46.8% decline with only 54,370 birds remaining in 1985 (Table 2). Numbers were similar in 1986, with a decline of 45.6% since 1982.

Boat and ground survey results also peaked in 1982 (Fig. 8) and declines of similar magnitudes occurred between 1982 and 1985 (55.4%) and 1982 and 1986 (53.6%) (see Ainley and Boekelheide 1990). However, when results were compared to 1980–1982 aerial survey results for the South Farallon Islands (Briggs et al. 1983), it became clear that combined ground and boat surveys greatly underestimated murre numbers; even so, trends from both methods were similar, indicating that they provided an effective population index.

Plots can sometimes reflect direction of change in colony numbers (e.g., Harris et al. 1983, Mudge 1988). The Upper Shubrick Point plot confirmed trends for the whole colony, but the degree of change may not have been representative because the plot was one of the few areas on the South Farallon Islands where murres bred in 1983 (H. R. Carter, pers. obs.). In 1980 and 1981, similar numbers of egg-laying sites (145 and 146) were recorded, but by 1983 eggs were laid at only about 52% of 84 known-individual sites that had been monitored the previous year (Kaza and Boekelheide 1984; PRBO, unpubl. data). By 1984, there was only 52.7% of the 1981 total. While changes in numbers of egg-laying sites in 1983 reflected depressed breeding activity, many breeding birds were still present. For example, about 90% of known-individuals that bred in the plot in 1982 were observed sometime in 1983 (PRBO, unpubl. data). Thus, population decline began in 1983 but major mortality may not have occurred until after the breeding season.

Numbers at the North Farallon Islands peaked at 51,540 in 1980 but declined 55.6% to 22,900 by 1986 (Fig. 6, Table 2). The total Farallon Island murre population declined 48.9%, from 153,560 in 1980–1982 to 78,470 in 1986.

Nearshore central California

Both Sowls et al. (1980) and Briggs et al. (1983) surveyed colonies at Point Resistance, Double Point, Castle, and Hurricane Point rocks in 1980. We used the higher totals, mainly of Sowls et al. (1980), as the more accurate representation of peak breeding populations because their 12 June survey occurred within the optimum survey period at South Farallon Islands in 1980, whereas Briggs et al. (1983) surveyed later on 1–2 July. In 1986, slides of Castle and Hurricane Point rocks could not be easily separated, so these colony totals were combined. At Double Point Rocks, a small natural arch fell into the ocean sometime between 1982 and 1985 and breeding habitat for less than 5% of the population was lost.

Populations at nearshore colonies in central California declined more severely, and in most cases, began to decline earlier than populations at the South and North Farallon islands. All colonies peaked in 1980 and declined through 1986, except for Point Reyes, which peaked in 1982 (Table 2). Sharpest declines occurred at colonies located between Point Reyes and Devil's Slide Rock. In fact, the Devil's Slide Rock colony had disappeared by 1986, after peaking at almost 3000 birds in 1980 (Fig. 7). Small subcolonies of murres breeding on the mainland at Point Reyes and Castle Rocks also declined and even disappeared at Castle Rocks. The total for all six colonies decreased by 60.1%, from a peak of 75,430 in 1980–1982 to 30,060 in 1986.

NORTHERN CALIFORNIA POPULATION TRENDS

Populations in northern California remained relatively unchanged between 1979 and 1986 (Fig. 9, Table 3). Large colonies at False Klamath and Flatiron rocks decreased 9.7% between 1982 to 1986 but increased 13.0% between 1979 and 1986, respectively. We discount trends at large colonies that changed ≤10% because of counting error, single censuses, and differences in survey methods. Thus, these colonies were considered relatively unchanged from 1979 to 1986 and appeared similar in slides (Fig. 9; Sowls et al. 1980). Declines of 40% or more were obvious when we compared slides for different periods (see Figs. 6 and 7).

At Castle Rock, Briggs et al. (1983) estimated 143,220 birds in 1982, compared to our estimate of 100,570 birds in 1986 (Table 3). However, a change was not discernible in slides and may be at least partly due to inaccurate block counting by Briggs et al. (1983). The estimate of 126,750 by Sowls et al. (1980) could not be used for comparison due to their late survey date (mid-July).

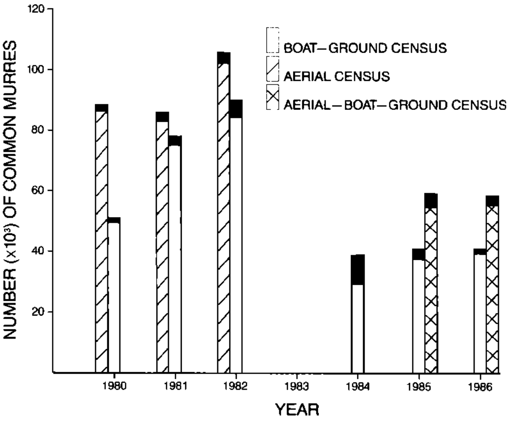

FIGURE 8. Estimates of the total numbers of Common Murres on the South Farallon Islands from 1980–1986 using various methods. Minimal estimates of the numbers of non-breeding birds (NB) are indicated by the darkened portion of each bar.

Both Sowls et al. (1980) and Briggs et al. (1983) surveyed Green and Redding rocks in 1980, on 9 July and 2 July, respectively, producing widely disparate estimates (Table 3). Sowls et al. (1980) surveyed at the time of peak fledging in 1980 at the South Farallon Islands (Fig. 4) and after the highest ground counts were obtained during periodic counts at Green Rock (DeGange and Sowls 1980). By this late date, large chicks may have

TABLE 2. ESTIMATES OF COMMON MURRE BREEDING POPULATIONS DETERMINED FROM AERIAL SURVEYS AT ALL COLONIES IN CENTRAL CALIFORNIA, 1979–1986

Colony							% change: peak (1980 or 1982) to 1986 (see text)
No.	Name	1979	1980	1982	1985	1986	
1	S. Farallon Is.	—	86,140^b	102,110^b	54,370	55,570	−45.6
2	N. Farallon Is.	—	51,540^b	51,320^b	29,940	22,900	−55.6
3	Pt. Reyes	16,600^a	22,550^b	44,250^b	15,380^c	20,590	−53.5
4	Pt. Resistance	—	7360^b 7540^a	6890^b	3790	3030	−59.8
5	Double Pt. Rks.	—	14,870^b 13,080^a	11,930^b	5680	3280	−77.9
6	Devil's Slide Rk.	2310^a	2940^b	2570^b	—	0	−100.0
7	Castle Rks.	—	1340^b 3520^a	1860^b	—		
8	Hurricane Pt. Rks.	—	1920^b 2310^a	1710^b	—	3160^d	−45.8

[a] Source: Sowls et al. (1980).
[b] Source: Briggs et al. (1983).
[c] Minimal number due to incomplete coverage.
[d] Castle Rocks and Hurricane Point Rocks combined (see text).

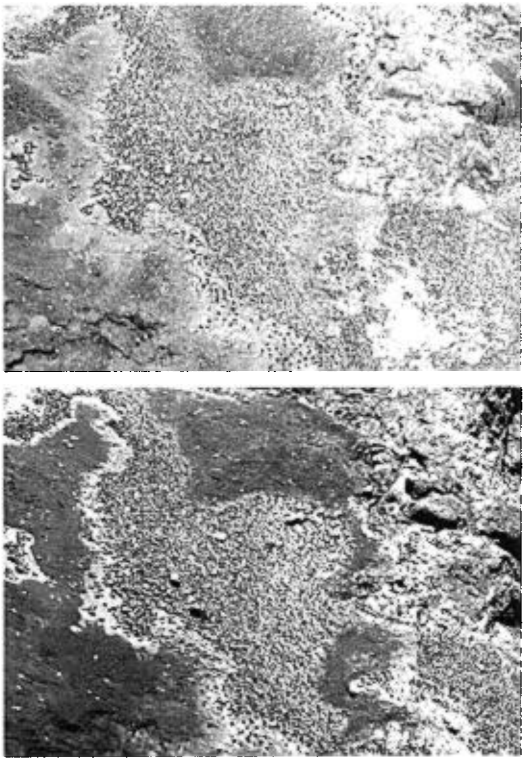

FIGURE 9. Subcolony of Common Murres on Castle Rock in northern California in 1982 (top) and in 1986 (bottom). This colony appeared similar in extent and density, indicating little change.

been indistinguishable from adults in slides, partly accounting for the higher estimate. Differences between 1980 survey results at Redding Rock were not as great, but Sowls et al. (1980) again produced a higher population estimate (19%). For these reasons, we compared our results to 1980 or 1982 data from Briggs et al. (1983) (Table 3).

The combined population for False Klamath, Redding, Flatiron, and Green rocks decreased 5.4% from 118,080 in 1979–1982 to 111,730 in 1986, a difference that could not be assessed by our methods.

DISCUSSION

IMPLICATIONS FOR FARALLON ISLANDS POPULATIONS

As reflected for the whole colony (Table 2) in aerial surveys, breeding populations were similar in the Shubrick Point plot in 1985 and 1986. Numbers of egg-laying sites equaled 78.1% and 77.7% of the 1981 total, respectively. This increase over 1984 reflected a change in population structure, which can be best understood by combining non-breeding and breeding sites. Non-breeding sites were not observed in 1980–1982, but in 1984 33 non-breeding sites made up 30% of the total. In 1985 and 1986 non-breeding sites comprised 9.5% (12 sites) and 5.1% (6 sites) of the totals, respectively. Thus, when all sites in 1984, 1985, and 1986 were compared to the 1981 total, proportions were similar (75.3%, 86.3%, and 80.8%, respectively). Thus, the increase in the breeding population from 1984 through 1986 in the plot reflected a decrease in an inflated non-breeding population. However, in 1986 the minimal non-breeding population size (NB) was 2480 birds, or 4.3% of the total breeding and non-breeding population of 58,050 birds (see Appendix). This proportion was still slightly higher than in 1982 (3.1%; N = 3290 birds) suggesting that by 1986 population structure may not have returned to pre-1983 conditions.

Declines probably were buffered by recruitment in 1983–1986 of strong year classes of young birds produced during 1979–1981 (Ainley and Boekelheide 1990). Common Murres in the North Atlantic Ocean breed for the first time when 4 to 6 years old (reviewed by Hudson 1985). However, the stormy fall and winter of 1982–1983 may have led to higher mortality of hatching year

TABLE 3. ESTIMATES OF COMMON MURRE BREEDING POPULATIONS DETERMINED FROM AERIAL SURVEYS AT FIVE COLONIES IN NORTHERN CALIFORNIA, 1979–1986

Colony						
No.	Name	1979	1980	1982	1986	% change: peak (1979–1982) to 1986 (see text)
9	Castle Rk.	126,750^{a}	132,590^{b}	143,220^{b}	100,570	see text
11	False Klamath Rk.	26,660^{a}	37,820^{b}	53,430^{b}	48,320	−9.6
12	Redding Rk.	—	1730^{b} 2110^{a}	1180^{b}	1310	−24.3
14	Green Rk.	—	28,490^{b} 53,330^{a}	38,780^{b}	34,820	−10.2
15	Flatiron Rk.	24,140^{a}	17,810^{b}	18,070^{b}	27,280	+13.0

[1] Symbols as in Table 4.

(HY) birds from 1982, almost no chicks were raised to nest leaving in 1983, and lowered population size and poor breeding success led to a weak 1984 year class (Ainley and Boekelheide 1990; PRBO, unpubl. data). Thus, recovery will be further delayed due to much lower recruitment.

CAUSES FOR DECLINE OF THE CENTRAL CALIFORNIA MURRE POPULATION

Between 1979 and 1986, three sources of mortality (excluding usual levels of natural mortality) affected Common Murres in central California: ENSO in 1982–1983, oil spills, and gill-net fishing (Carter 1986). Comparing patterns of colony decline with other studies of these specific mortalities provided a rare opportunity to assess how, when, and why the murre population in central California declined so rapidly and drastically; to what degree different sources of mortality were responsible for the decline; and why decline is expected to continue for at least several years.

El Niño-Southern Oscillation 1982–1983

ENSO first began to affect seabirds at the South Farallon Islands prior to the murre fledging period in June 1982, but did not affect fledging success that year (Ainley and Boekelheide 1990). During the fall and winter of 1982–1983 murres exhibited much lower winter attendance of this colony than usual (Kaza and Boekelheide 1984) and egg laying in 1983 was delayed (Fig. 4) and reduced. It appeared that many birds moved into inshore waters to feed and the few birds that bred in 1983 foraged at great distances from the colony (Kaza and Boekelheide 1984).

Although ENSO occurred in the period when the major population decline occurred at the South Farallon Islands, additional evidence suggests that ENSO mortality was not focused on breeding adults. While the 1982–1983 ENSO event affected seabird reproduction in central and northern California, and Oregon (Hodder and Graybill 1985), large declines were not found at northern California colonies surveyed between 1982 and 1986 (Table 3). However, ENSO may have affected future recovery of the central California population by causing minimal reproduction in 1983 and lower survival to breeding of pre-breeders.

Oil pollution

Two major and several smaller oil spills caused mortality of Common Murres in central California between 1979 and 1986. In November 1984, the *Puerto Rican* oil spill spread across the outer shelf of the Gulf of the Farallones (Herz and Kopec 1985, PRBO 1985) killing an estimated 1500–2000 murres (Dobbin et al. 1986; R. G. Ford and G. W. Page, unpubl. data). In February 1986, the *Apex Houston* oil spill occurred between San Francisco and the Monterey Peninsula, killing 7500 murres or more (Page et al. 1990). Despite significant chronic oiling problems during the 1979–1986 period (see Stenzel et al. 1988), we have no estimate of numbers affected.

The *Puerto Rican* spill occurred before the main arrival of migrant murres that winter in central California but breed farther north; thus, mortality was focused on the resident central California population. Although the *Apex Houston* spill and chronic oiling (Stenzel et al. 1988) affected both central California and other breeding populations, effects on northern California colonies may be limited because murres appear to be year-round residents there (DeGange and Sowls 1981). Little information is available on the age and sex classes of murres affected by these oil spills. In the *Apex Houston* spill, both first-year (FY) and after-first-year (AFY) murres were killed and no evidence of sex-biased mortality was found. Of 164 birds examined, 54.9% were male (H. R. Carter, unpubl. data).

By assuming that 50% of 7500 murres killed by the *Apex Houston* spill and a projected minimum of 500 birds from chronic oiling were from the central California population, and that 50% of these and of murres killed by the *Puerto Rican* spill were breeding adults, we estimate that 3000 breeding adults were killed by oil spills in central California from 1979–1986. This corresponded to 2.5% of the 120,550 murres lost from the central California breeding population from 1980–1982 to 1986.

Gill-net fishing

Gill-net fishing for California halibut (*Paralichthys californicus*) and starry flounder (*Platichthys stellatus*) has occurred in central California since at least the 1930s. In the late 1970s, the number of gill-net fishermen increased by as much as 400–500% in some areas (Atkins and Heneman 1987) and a new white croaker (*Genyonemous lineatus*) fishery began in Monterey Bay, using long monofilament nets. Fishing effort intensified and the halibut fishery gradually shifted from using twine to monofilament nets, all of which resulted in a much higher catch of nontarget species, especially seabirds (CDFG 1981, 1987; Atkins and Heneman 1987).

From 1979 to 1982 fishing effort was concentrated in Monterey Bay. By 1980 it was evident that large numbers of murres and other seabirds were being killed in gill nets (CDFG 1981, Stenzel et al. 1988). In late 1982, CDFG established the Central California Gill and Trammel Net

TABLE 4. NUMBERS OF COMMON MURRES CAUGHT PER GILL NET MONITORED IN CENTRAL CALIFORNIA FROM 1980–1986 DURING THE CALIFORNIA DEPARTMENT OF FISH AND GAME MONITORING PROGRAM (P. W. WILD AND C. W. HAUGEN, UNPUBL. DATA). EACH NET WAS MONITORED FOR ONE SET

Period	N Murres	No. Murres caught per net				
		Monterey Bay[1]	Half Moon Bay	San Francisco	Bodega Bay	Total
Jun–Nov 1980	123	3.4 (36)[2]	—[3]	—	—	3.4 (36)
Dec–Mar 1980–1981	1	1.0 (1)	—	—	—	1.0 (1)
Apr–Nov 1981	365	6.0 (61)	—	—	—	6.0 (61)
Dec–Mar 1981–1982	1	0.1 (11)	—	—	—	0.1 (11)
Apr–Nov 1982	94	2.2 (42)	—	—	—	2.2 (42)
Dec–Mar 1982–1983	—	—	—	—	—	—
Apr–Nov 1983	1156	6.8 (16)	23.1 (31)	2.7 (87)	2.3 (43)	6.5 (177)
Dec–Mar 1983–1984	1	0.0 (9)	0.0 (5)	0.0 (2)	0.1 (10)	<0.1 (26)
Apr–Nov 1984	498	0.1 (148)	1.6 (72)	1.2 (109)	1.6 (149)	1.0 (478)
Dec–Mar 1984–1985	5	0.5 (10)	0.0 (8)	0.0 (6)	—	0.2 (24)
Apr–Nov 1985	962	0.1 (67)	1.3 (83)	3.2 (168)	2.9 (108)	2.3 (426)
Dec–Mar 1985–1986	5	—	0.0 (6)	—	0.1 (41)	0.1 (41)
Apr–Nov 1986	950	0.1 (50)	5.5 (82)	1.5 (252)	1.0 (121)	1.9 (505)
		(N = 715)[4]	(N = 1389)	(N = 1274)	(N = 776)	(N = 4161)

[1] Monterey Bay area includes areas off Santa Cruz, Moss Landing, and Monterey; Half Moon Bay area includes the area between Pigeon Point and Mussel Rock; San Francisco area includes the area between Mussel Rock and Point Reyes; and Bodega Bay area includes the area between Point Reyes and the Russian River.

[2] Number of nets in parentheses.

[3] Dash indicates that no nets were monitored.

[4] Total number of murres observed in gill nets per fishing area.

Program to monitor bycatch (catch of nontarget species). Following a northward shift in fishing effort, this program was extended in 1983 to the Gulf of the Farallones and Bodega Bay areas. Nearshore gill-net fishing was concentrated from Half Moon Bay to Bodega Bay from 1983 to 1986.

Estimates of seabirds killed in gill-net fisheries were: 1) in Monterey Bay, 19,800 birds in 1980 and 1981 combined; and 2) in the Gulf of the Farallones and Bodega Bay areas, 30,000, 7000, 8000, and 5000 birds in 1983, 1984, 1985, and 1986, respectively (CDFG 1981, 1987; see Atkins and Heneman 1987). As 50–97% were Common Murres, over 60,000 murres were netted between 1980 and 1986 (CDFG 1981, 1987). However, mortality was not estimated in Monterey Bay in 1979 or 1982–1987, nor in the Gulf of the Farallones and Bodega Bay prior to 1983 or in 1987, despite known mortality based on beached birds and the gill-net monitoring program (Table 4). An additional 10,000–15,000 murres probably were killed (P. W. Wild, pers. comm.), for a rough total of 70,000–75,000 from 1979–1987.

Gill-net fishing in central California occurred primarily from May to October, with highest fishing effort and seabird mortality occurring from June through September. Murres on South Farallon Islands usually rear nestlings in June, when large numbers of nonbreeders also attend the colony. Feeding murres often aggregate on the outer also frequent nearshore waters to a variable degree (Briggs et al. 1987; Ainley and Boekelheide 1990; Briggs et al. 1988). In July, murres leave the Farallon Islands and many move into nearshore waters. Murres at nearshore colonies in central California appear to remain in nearshore waters through the breeding season and nearer to colonies in June and early July (PRBO, unpubl. data). The loss of 70,000–75,000 murres can be attributed to the consistent spatial and temporal overlap of large numbers of feeding murres and high gill-net fishing effort in nearshore waters in Monterey Bay, the Gulf of the Farallones, and the Bodega Bay area from 1980 to 1986 (Table 4). Similar conditions have led to high mortalities of murres and other alcids in other nearshore gill-net fisheries (e.g., Carter and Sealy 1984, Piatt et al. 1984).

Little data are available regarding age and sex classes of murres killed in nets. In Monterey Bay, both adults and subadults were killed in nets and of 20 adults and 35 subadults examined from May to October 1982, 85.0% and 62.9% were male, respectively (D. A. Croll, unpubl. data). On 21 August 1984, 78% of 37 murres recovered at Point Reyes National Seashore in Marin County were male (R. J. Boekelheide, unpubl. data). The killing of breeding males, which raise chicks at sea, undoubtedly resulted in the death of dependent chicks. This, in association with high chick production by peak populations of murres, probably resulted in higher median numbers of dead HY murres on Monterey Bay beaches in 1980–1982 (see Stenzel et al. 1988).

By assuming that 75% of the 70,000 murres netted in the 1980–1986 survey period (excluding 5000 murres killed in 1979 and 1986 before and after surveys) either were or soon would have been breeding adults, we accounted roughly for 40–45% of the 120,550 murres lost from the central California population from 1980–1982 to 1986 (Table 2). We attribute gill-net mortality to most of this decline.

COLONY DECLINES

There was a strong connection between areas and periods of gill-net fishing mortality and individual colony declines in central California. Colonies at the South and North Farallon islands and Point Reyes were unchanged or continued to increase from 1980 to 1982 (Table 2). However, colonies at Castle and Hurricane Point rocks declined by 47.2% and 26.0%, respectively. Degree of decline was related to proximity to Monterey Bay, where heavy mortality occurred in 1980 and 1981 (Fig. 1, Table 4). Mortality was greatly reduced in Monterey Bay after 1982–1983, and overall decline from 1980 to 1986 for these two colonies was not as severe (45.8%) as at most other colonies in central California.

From 1982 to 1985, declines occurred at Double Point Rocks, Point Resistance, and South and North Farallon islands, of 52.4%, 49.7%, 46.8%, and 41.7%, respectively (Table 2). These declines reflected high gill-net fishing mortality in the Gulf of the Farallones in 1982 through 1984 (CDFG 1987). The largest decline occurred at Double Point Rocks, which was closest to fishing areas off the Golden Gate and southern Marin County. Declines continued from 1985 to 1986 at Double Point Rocks (42.3%), North Farallon Islands (23.5%), and Point Resistance (20.1%), all near San Francisco and Bodega Bay, where fishing mortality persisted. In this period the Devil's Slide Rock colony disappeared. We associate this with high fishing effort within 1–2 km of the colony. Between 6 and 10 August 1983, 918 murres washed ashore a few kilometers north of Devil's Slide Rock (Stenzel et al. 1988). If all were local breeders, 35% or more of this colony could have been killed in a single event.

Less severe overall declines (50–60%) at Point Resistance, Point Reyes, and North Farallon Islands corresponded with intermediate-sized colonies located farther from gill-net fishing areas. A smaller relative decline at South Farallon Islands may reflect wide dispersal of murres into nearshore waters, but the 46,540 birds lost from this colony almost equaled the total lost from all other central California colonies combined.

SOLUTIONS FOR GILL-NET FISHING MORTALITY

Species of seabirds killed in gill nets from 1980–1987 included: Common, Pacific, and Red-throated loons (*Gavia immer, G. arctica, G. stellata*), Western and Clark's grebes (*Aechmophorus occidentalis, A. clarkii*), Sooty Shearwater (*Puffinus griseus*), Brandt's and Pelagic cormorants (*Phalacrocorax penicillatus, P. pelagicus*), White-winged and Surf Scoters (*Melanitta fusca, M. perspicillata*), Common Murre, Pigeon Guillemot (*Cepphus columba*), and Marbled Murrelet (*Brachyramphus marmoratus*) (CDFG 1981, 1987; Carter and Erickson 1988). Common Murres accounted for about 50–97% of the mortality during 1980–1986.

In 1982, State Senate Bill (SB) 1475 imposed a permanent ban on gill-net fishing in waters 10 fathoms (18.3 m) or shallower in most of Monterey Bay; the ban was extended to 15 fathoms (27.5 m) in 1984 (Fig. 1). Temporary seasonal closures (May–October) were imposed by CDFG during 1982–1984 in a patchwork pattern to exclude areas of highest seabird and marine mammal mortality. Even so, murre bycatch remained relatively high through 1986 (Table 4). In 1986 and 1987, CDFG, with a cooperative group of gill-net and other fishermen, state and federal agencies (including USFWS) and lawmakers, and private research and environmental groups (including PRBO), attempted to develop a long-term solution to the seabird and marine mammal mortality caused by gill-net fishing. Survey data presented in this report showed that the central California murre population could not sustain continued mortality and that continued existence of individual colonies was threatened.

In September 1987, SB 40 was passed, containing much stronger regulations. Gill-net fishing was prohibited year-round in waters north of Point Reyes, in waters 40 fathoms (73 m) or shallower between Point Reyes and Waddell Creek, and within 3 miles of the Farallon Islands and Noonday Rock (just northwest of the Farallon Islands). Area closures were selected to eliminate murre mortality; over 99% of murre mortality observed in nets by CDFG had occurred in waters less than 40 fathoms (73 m) in depth (P. W. Wild, pers. comm.).

These regulations resulted in virtual elimination of the nearshore halibut, shark, and white croaker fisheries north of Monterey Bay, but allowed the offshore rockfish fishery (which caused very low levels of seabird mortality) to continue. In Monterey Bay some gill-net fishing has continued outside 15 fathoms with virtually no seabird mortality (P. W. Wild, pers. comm.). A research advisory committee was formed to investigate and monitor the use of alternative fishing gear.

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APPENDIX

GROUND TRUTHING CORRECTION FACTOR

Aerial counts of murres have been criticized for underestimating actual numbers present, depending on the nature of background habitat, bird activity, and observation distance (but see Gaston and Nettleship 1981). Birkhead and Nettleship (1980) suggested that murres can be counted readily from aerial photographs if the colony is neither indented greatly nor varies greatly in height such that all areas can be seen in photographs.

At all colonies surveyed in California (except parts of SEFI) the vast majority of murres nested in large colonies on gentle slopes and flat areas at the base of slopes or on rounded hilltops. In these habitats, murres were easily photographed and counted. However, to account for birds obscured in tightly-packed groups and those hidden by small rocks and ledges, we determined a ground truthing correction factor (G) on South Farallon Islands, which we applied to aerial survey data from West End and North Farallon islands.

In 1985, we established seven additional plots on SEFI, including one at Tower Point (Fig. 2). Ground counts were conducted at all plots between 11:00–13:00 on 10–15 days between 30 May and 23 June, including the 12 June census day (Table A-1). We compared numbers from the Tower Point and Upper Shubrick Point plots with the mean of 10 counts of the best aerial photographs of these plots. Two versions of G were derived as follows:

$$G_1 = a/g_d \qquad (3)$$

and

$$G_2 = a/g_p \qquad (4)$$

where: a = mean count of birds from aerial photo; g_d = mean count from ground censuses on the census day; and g_p = mean count from ground censuses over the census period. We used G_1 values of 0.764 and 0.917 to adjust numbers of birds counted in aerial photographs, because G_1 minimized possible bias due to daily variation in numbers. G_2 could be used as an alternative when g_d cannot be determined.

The same method was used in 1986 with four plots, but since the aerial survey required two days to complete due to fog, we used either (or both) 4 and 5 June ground counts to derive G_1 values (Table A-1). The Tower Point plot (which was photographed on both days) yielded similar ground counts but quite different means of photo counts, probably a result of differing aerial viewing conditions. Also, in all four plots, mean G_1 values exceeded 1.0 (R = 0.775–1.278) which should have been impossible (disregarding counting error), since all birds were visible from the ground in plots.

TABLE A-1. Numbers of Common Murres Counted in Plots on SEFI, Used to Calculate Ground Truthing Correction Factors (G) in 1985 and 1986

Plot	Date	Ground count Mean ± SD (N)	Min	Max	Aerial photo count Mean ± SD (N)	G
1985						
Tower Point	30 May–23 Jun	502.1 ± 79.5 (10)	390	635	375.2 (1)	0.747
	12 Jun	491.0 (1)	—	—	375.2 ± 35.4 (10)	0.764
Upper Shubrick	30 May–21 Jun	154.7 ± 9.7 (15)	134	163	138.4 (1)	0.895
Point	12 Jun	151.0 (2)	149	153	138.4 ± 11.8 (10)	0.917
1986						
Tower Point	28 May–24 Jun	214.6 ± 11.3 (10)	190	244	206.7 (2)	0.963
	4 Jun	225.8 ± 8.7 (5)	218	240	175.1 ± 7.7 (10)	0.775
	5 Jun	224.7 ± 6.3 (6)	215	232	238.2 ± 9.1 (10)	1.060
Cove Point	28 May–24 Jun	159.2 ± 9.7 (10)	141	176	176.5 (1)	1.109
	5 Jun	154.8 ± 3.1 (6)	152	160	176.5 ± 18.5 (10)	1.140
Upper Shubrick	28 May–17 Jun	136.1 ± 5.0 (12)	128	143	135.9 (1)	0.999
Point	5 Jun	131.9 ± 1.6 (7)	129	134	135.9 ± 5.0 (10)	1.030
Lower Shubrick	4 Jun–5 Jun	23.7 (2)	21	27	30.3 (1)	1.278
Point	4 Jun	25.3 ± 1.3 (4)	24	27	30.3 ± 3.4 (10)	1.198

However, it was not possible to synchronize individual ground counts with individual aerial photographs, because the plane made several passes over a period of about 0.5–2.0 h. G_2 values also exceeded 1.0 (R = 0.963–1.109) in 1986.

To get an overall G_1 value for each year, we categorized plots based on numbers of birds, and calculated mean G_1 values of 0.841 and 1.067 for 1985 and 1986, respectively (Table A-2). The large difference presumably resulted mainly from the lower altitude aerial photographs in 1986, which made it easier to distinguish individual birds. In fact, the 1986 value was so close to 1.0 that we felt it was appropriate to apply a G_1 value of 1.0, especially given the small amount of inherent error in the method that resulted in values over 1.0.

Breeder : Non-breeder Ratio

On the census day at the Farallon Islands, we also determined the number of non-breeding sites (i.e., consistently occupied sites where eggs were never observed), numbers of birds attending these sites, and the numbers of "other" birds (i.e., not associated with a specific site) in the Upper Shubrick Point plot (Table 1). All of these birds were considered to be non-breeders even though at some sites eggs may have been laid and lost between site checks (see Gaston et al. 1983) and some may have been off-duty mates. To examine relative differences in the numbers of non-breeding birds between years, we calculated a breeder : non-breeder ratio (BNR) as follows:

$$BNR = n_s(2)/n_{nb}(t_1) \qquad (5)$$

where: n_s = total number of non-breeding birds in a plot at time t_1 on the census day. This index does not take into account numbers of non-breeding birds that visit the colony but were absent during the census or younger non-breeding birds that are not yet visiting the colony. BNR varied greatly between years (R = 3.44–42.86).

Breeding and Minimal Non-breeding Population Estimates

To estimate numbers of breeding birds (B) at a colony, we used the following formula:

$$B = N_{ap}(K)/G_1 \qquad (6)$$

where: N_{ap} = number of birds counted from aerial photos; K = number of breeding birds/bird counted; and G_1 = ground truthing correction factor. In 1985 and 1986, we added the number of birds counted on SEFI and neighboring islets from boat and ground counts (multiplied by K) to that derived using Equation 6 for West End Island to derive an overall breeding popu-

TABLE A-2. Summary of Ground Truthing Correction Factors (G_1) Used in 1985 and 1986

No. birds per plot	1985 No. plots	G_1	Range	1986 No. plots	G_1	Range
1–99	1	0.917	0.905–0.929	1	1.198	1.122–1.263
100–199	—	—	—	2	1.085	1.030–1.140
200–299	—	—	—	2	0.918	0.775–1.060
500–599	1	0.764	—	—	—	—
Mean	2	0.841	0.764–0.929	3	1.067	0.775–1.263

lation estimate for South Farallon Islands. To estimate minimal numbers of non-breeding birds (NB) at South Farallon Islands, we used the following formula:

$$NB = B/BNR + C \qquad (7)$$

where: C = direct count of birds in non-breeding "clubs" from boat and ground counts. These clubs were excluded from boat and ground counts when determining B.

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NUMBERS OF SEABIRDS KILLED OR DEBILITATED IN THE 1986 *APEX HOUSTON* OIL SPILL IN CENTRAL CALIFORNIA

GARY W. PAGE, HARRY R. CARTER, AND R. GLENN FORD

Abstract. We developed models describing carcass deposition on beaches and carcass loss at sea in order to estimate the number of birds killed by the February 1986 *Apex Houston* oil spill along the central California coast. A carcass deposition model was used to estimate the total number of beached carcasses by integrating single censuses of dead birds on 51 beaches at the time of the spill, estimated daily proportions of total numbers of carcasses depositing on shore, and a daily rate of beached carcass persistence. A carcass trajectory model was used to estimate the number of birds killed by oil that did not reach shore by integrating simulated slicks arising along the path of the *Apex Houston,* the distribution and abundance of birds at sea, and a daily at-sea carcass loss rate.

The *Apex Houston* spill killed thousands of seabirds along the central California coast. At least 3364 debilitated live oiled birds, primarily Common Murres (*Uria aalge*), were collected from beaches for cleaning and rehabilitation. An estimated additional 5880 dead oiled birds, primarily Common Murres and Rhinoceros Auklets (*Cerorhinca monocerata*), washed ashore. Only 87.1% of 7488 Common Murres, 78.6% of 1566 Rhinoceros Auklets, and 82.8% of 169 Cassin's Auklets (*Ptychoramphus aleuticus*) debilitated or killed by oil were determined to have reached shore. Overall, at least 10,577 birds of 26 species were debilitated or killed including in addition to the above: 276 loons (*Gavia* spp.), 115 small grebes, 468 *Aechmophorus* grebes, 19 unidentified grebes, 283 scoters (*Melanitta* spp.), 37 auklets or murrelets, and 156 birds that were unidentified or of other taxa. Limitations of the models are discussed and future research for refining them is suggested.

Key Words: Seabirds; oil spill; California, *Apex Houston*; Common Murre; Rhinoceros Auklet; Cassin's Auklet.

Despite extensive documentation of large seabird mortalities during marine oil spills (reviews in Stowe 1982, Evans and Nettleship 1985), little has been published on methods of estimating the extent of mortality. Reported numbers of casualties have tended to be guesses, usually simple multiples of the number of carcasses or debilitated birds, or both, found along shorelines (e.g., Greenwood and Keddie 1968, Hope Jones et al. 1970, Bibby and Lloyd 1977, Heubeck and Richardson 1980). More accurate estimates are required for examining the short- and long-term impacts of oil spill mortality on seabirds or preparing the damage assessments used to recover costs from the party responsible for the spill (Dunnet 1987, Ford et al. 1987).

We developed new methods for estimating seabird mortality from a spill of San Joaquin Valley Crude oil, which caused thousands of birds to beach suddenly in February 1986 along the central California coast. The California Regional Water Quality Control Board (CRWQCB) concluded that the tank barge *Apex Houston* probably was the source of the spill. After being towed from the Shell Oil refinery at Martinez, California, to Long Beach, California, between 28 January and 1 February, the *Apex Houston* was missing 616 barrels (25,800 gallons) of oil, had lost a hatch cover, and had visible signs of oil outflow near the hatch opening (CRWQCB 1986).

We developed a model that used tallies of live birds taken to rehabilitation centers and carcass counts on beaches to estimate the number of oiled birds that beached along 355 km of shoreline between Salmon Creek, Sonoma County, and Point Lobos, Monterey County. By subdividing the bird tallies for six coastal regions (Fig. 1), we accounted for differences in beached bird deposition in relation to distance from the spill and variation in the distribution of birds at sea. An aerial census of birds at sea was used in an oil and carcass trajectory model to estimate the number of dead oiled birds that never reached shore. Our methods can be applied elsewhere to alcids and other diving marine birds that tend to be heavily affected by marine oil spills.

METHODS

Point Reyes Bird Observatory (PRBO) is experienced in conducting beached bird censuses (Page et al. 1982, Stenzel et al. 1988) and has estimated the mortality of seabirds in two oil spills—the 1971 San Francisco oil spill (Smail et al. 1972) and the 1984 *Puerto Rican* oil spill (PRBO 1985). Oiled birds from the *Apex Houston* spill first came ashore on 1 February. PRBO began beached bird censuses in Marin County on 3 and 4 February, expanding coverage southwards on 5 February after learning that government agencies were not counting dead birds. The late start, due to our lack of knowledge of the incident, and a limited availability of personnel created three major problems: 1) due to the long length of coastline with oiled birds, we could only cover a sample of beaches and extrapolate for uncovered areas; 2) since we could cover most beaches only once, it was necessary to estimate the numbers of birds beaching before and after censuses began; and 3) the public had removed most live oiled birds from beaches before we could count them.

Rehabilitation center data

Live oiled birds were recovered from beaches and taken to collection centers for further transport to rehabilitation centers or were transported directly to rehabilitation centers during a large scale rescue effort by government agencies, private organizations, and concerned individuals. Not all collection centers kept complete records. Rehabilitation centers usually made an accession record which included all or part of: date, number of birds of each species, presence or absence of oil, and location found (Carter et al. 1987). We used the accession records of rehabilitation centers to determine the number of live oiled birds removed from beaches, substituting collection center records for incomplete rehabilitation center records when necessary and possible. Despite laborious comparisons, we probably missed hundreds of birds that had been sent to rehabilitation centers. Incomplete records permitted the breakdown of total birds either by taxa or by date and recovery area, but not by all three variables simultaneously.

Beached bird censuses

PRBO conducted 86 carcass counts on 51 beach segments from Point Reyes, Marin County, to Del Monte, Monterey County, between 2 and 11 February 1986. The number of birds of each species with and without oiled plumage, the degree of carcass decomposition, date, beach length, and beach type were recorded for each census. Carcasses were marked or removed to prevent them from being recounted on future censuses. Beaches were typed as: 1) *dune,* sandy with a dune backshore; 2) *bluff,* sandy with a cliff or bluff backshore; 3) *pocket,* short sandy beach at a river or creek mouth; 4) *rocky,* rock or cobble beach with a cliff or bluff backshore; and 5) *protected harbor,* one beach (Princeton Harbor) largely cut off from the ocean by breakwaters.

Once beached, carcasses remain visible for varying amounts of time depending on decomposition, scavenging, burial in sand, and whether or not they are washed back out to sea (Tanis and Morzer-Bruijns 1962, Alexandersen and Lamberg 1971). On 6, 7, and 8 February, the daily rate of carcass persistence was measured on 6.8 km of shoreline at Half Moon Bay and on 5.7 km of shoreline from Pomponio State Beach to north of San Gregorio State Beach. The toes of carcasses were clipped in different patterns to separate birds by date and beach section and carcasses were left where found.

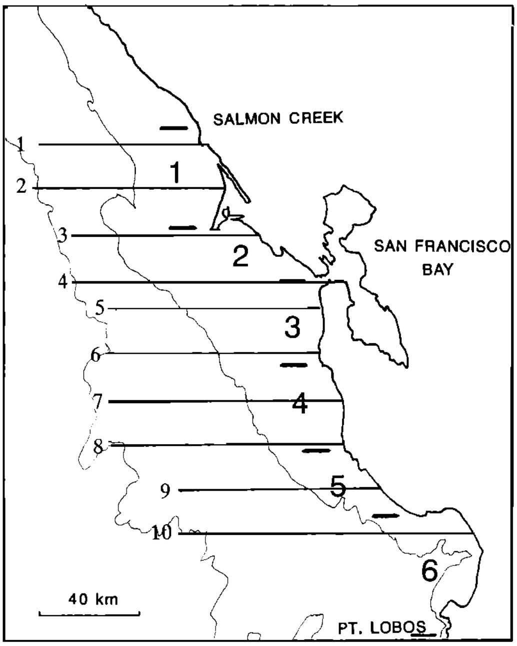

FIGURE 1. Six regions on the central California coast where live and dead oiled birds beached during the *Apex Houston* oil spill, and ten transect lines flown on the 5 February 1986 aerial survey of birds at sea. The 200 m and 3000 m depth contour lines are also shown.

Survey of birds at sea

One aerial survey was conducted on 5 February 1986 by the University of California, Santa Cruz, using census protocols developed by Briggs et al. (1985a, b; 1987) for marine birds over the California outer continental shelf. All seabirds within 50 m were recorded along 10 predetermined east-west transects between Bodega and Monterey bays (Fig. 1) during flights at an altitude of 65 m and a speed of 165–185 km/hr. Sightings were converted to densities (birds/km^2) by transect and water depth. Shelf waters were <200 m and slope waters 200 to 3000 m deep. Shelf waters were further divided into inner and outer sections by the 100 m depth contour. A total of 40.9 km^2 was surveyed.

RESULTS

NUMBERS OF OILED BIRDS FOUND ON BEACHES

At least 3858 live oiled birds were sent to rehabilitation centers between 1 February and 31 March (Page and Carter 1986). Live bird beachings peaked between 1–8 February when 3364 birds (or 87.2%) were recovered (Fig. 2). Common Murres (*Uria aalge*) accounted for 86.9% of the total recoveries and over 73% of the recoveries in each region (Tables 1, 2).

The pattern of live bird beachings varied among coastal regions (Fig. 2). Although substantial numbers of birds had been recovered from all regions by 3 February, peak numbers occurred on 3 February in regions 1 to 3, on 4 February in regions 4 and 6, and on 6 February in region 5. In regions 1 to 4, numbers exhibited a sharp peak whereas in regions 5 and 6, they built up and declined more gradually.

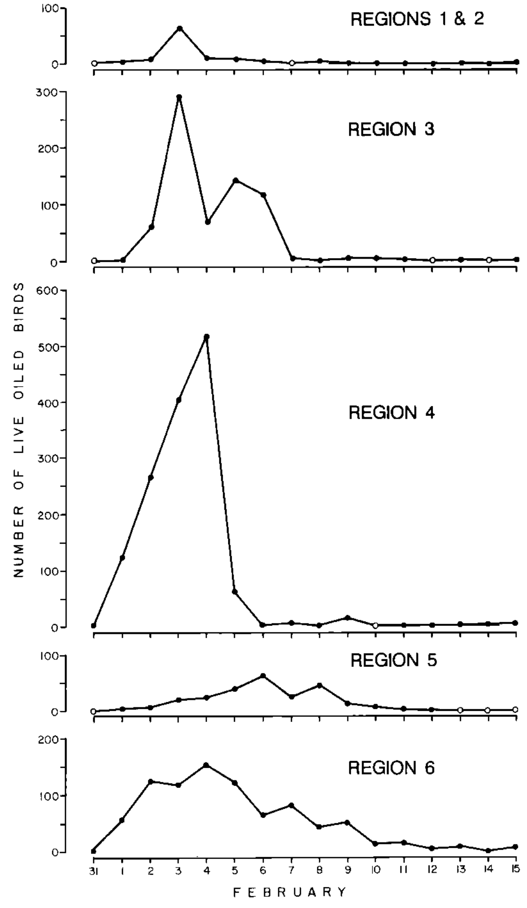

FIGURE 2. Numbers of live oiled birds sent to rehabilitation centers from six coastal regions between 1 and 15 February 1986. Open dots refer to zero counts.

In all, 834 oiled bird carcasses were found on 86 censuses of 51 beach segments between 2 and 11 February (Table 1). Common Murres again accounted for the majority (66.4%) of the oiled carcasses. However, carcasses contained a much higher proportion (15.7%) of Rhinoceros Auklets (*Cerorhinca monocerata*) than did live oiled birds (0.9%).

CARCASS PERSISTENCE

Daily carcass persistence on beaches was determined regardless of when carcasses were deposited. On the day following marking, 69.1% (N = 97) and 72.0% (N = 93) of the carcasses were found on the two beaches. From the second to third day, carcass persistence was 38.1% (N = 97) and 57.2% (N = 138), respectively. Carcass persistence may vary with species, beach type, tide, and time since beaching (Page et al. 1982).

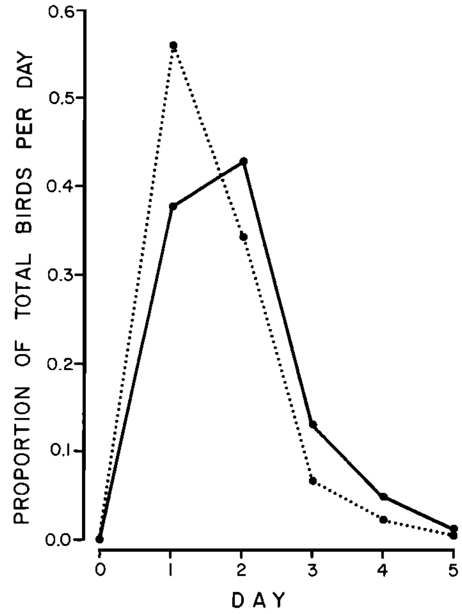

FIGURE 3. Proportions of total live (dotted line) and dead (solid line) oiled birds that reached shore in the Bodega Bay area between 10 November (day 1) and 14 November (day 5), during the 1984 *Puerto Rican* oil spill (N = 298 live and 399 dead oiled birds; PRBO 1985, unpubl. data).

However, our data were insufficient to obtain separate values for any of these categories so we used the mean value of 59.1% (SE = 7.7%, N = 4) in subsequent calculations.

BEACHED BIRD MODEL

We extrapolated for the number of carcasses that washed ashore on a beach over the spill period from the equation:

$$N_t = \frac{O_d}{\sum_{i=1}^{d} S^{d-i} P_i}$$

where:

N_t = total number of carcasses that actually washed onto a beach during the t days of the spill period. In the *Apex Houston* spill, this period was limited to the eight-day peak period of live oiled bird beachings.

O_d = observed number of birds on day d on a single census of a beach.

d = number of days that oiled birds have been depositing on the beach.

S = average daily persistence or survival of carcasses.

TABLE 1. Species Composition of Live Oiled Birds Taken to Rehabilitation Centers from 1–8 February 1986 and Dead Oiled Birds Found on Beaches from 2–11 February 1986 during the *Apex Houston* Oil Spill. Dashes indicate zeros

	Live oiled		Dead oiled	
Species	No.	%	No.	%
Common Loon (*Gavia immer*)	27	0.8	—	—
Pacific Loon (*G. arctica*)	25	0.7	7	0.8
Red-throated Loon (*G. stellata*)	18	0.5	6	0.7
Unidentified loon	58	1.7	4	0.5
Aechmophorus grebes	155	4.6	48	5.8
Horned Grebe (*Podiceps auritus*)	3	<0.1	—	—
Eared Grebe (*P. nigricollis*)	2	<0.1	11	1.3
Pied-billed Grebe (*Podilymbus podiceps*)	4	0.1	—	—
Unidentified grebe	19	0.6	—	—
Northern Fulmar (*Fulmarus glacialis*)	1	<0.1	4	0.5
Brandt's Cormorant (*Phalacrocorax penicillatus*)	4	0.1	2	0.2
Unidentified cormorant	3	<0.1	—	—
Black Scoter (*Melanitta nigra*)	—	—	3	0.4
White-winged Scoter (*M. fusca*)	19	0.6	17	2.0
Surf Scoter (*M. perspicillata*)	20	0.6	10	1.2
Unidentified scoter	22	0.7	—	—
Unidentified duck	5	0.1	—	—
Unidentified plover	—	—	1	0.1
Red Phalarope (*Phalaropus fulicaria*)	6	0.2	7	0.8
Sanderling (*Calidris alba*)	1	<0.1	1	0.1
Ring-billed Gull (*Larus delawarensis*)	1	<0.1	—	—
Mew Gull (*L. canus*)	2	<0.1	—	—
California Gull (*L. californicus*)	1	<0.1	—	—
Western Gull (*L. occidentalis*)	1	<0.1	2	0.2
Glaucous-winged Gull (*L. glaucescens*)	2	<0.1	—	—
Unidentified gull	1	<0.1	—	—
Common Murre (*Uria aalge*)	2924	86.9	554	66.4
Marbled Murrelet (*Brachyramphus marmoratus*)	1	<0.1	2	0.2
Ancient Murrelet (*Synthliboramphus antiquus*)	3	<0.1	4	0.5
Cassin's Auklet (*Ptychoramphus aleuticus*)	—	—	17	2.0
Rhinoceros Auklet (*Cerorhinca monocerata*)	30	0.9	131	15.7
Tufted Puffin (*Fratercula cirrhata*)	—	—	1	0.1
Unidentified murrelet	1	<0.1	—	—
Unidentified auklet	4	0.1	—	—
Unidentified birds	1	<0.1	2	0.2
Total	3364	100.0	834	100.0

P_i = proportion of the total number of carcasses coming ashore during the spill period that are expected to be deposited on day i.

i = index variable for day in the summation.

For the *Apex Houston* spill, we calculated N_t values for 46 beaches covered at least once between 3 and 8 February (Page and Carter 1986). For O_d, we used the first census for beaches with more than one count between 3–8 February. S was assigned the value .591, as determined at the time of the spill. Since we lacked actual estimates of the proportion of birds arriving on a given day, we substituted P_i values from data available by region for live birds. We assumed that the proportions of birds that beached daily were similar for live and dead birds during the spill period, but there is little published information on which to evaluate this assumption. However, large numbers of oiled carcasses had reached many beaches by 3 February (see Page and Carter 1986 for details), when live bird numbers began to peak. Thus, the timing of peak deposition for live and dead birds appeared similar. P_i values for live and dead oiled birds also were similar during the *Puerto Rican* spill (Fig. 3; also see Stenzel et al. 1988), but most live birds were reported to beach a few days before most dead ones during the *Hamilton Trader* spill (Hope Jones et al. 1970).

We divided N_t values by the length of the beach in kilometers for the 46 beaches covered and then

TABLE 2. SPECIES COMPOSITION OF LIVE (L) AND DEAD (D) OILED BIRDS FROM SIX COASTAL REGIONS ALONG THE CENTRAL CALIFORNIA COAST DURING THE *APEX HOUSTON* OIL SPILL

	Coastal region[1]													
	1		2		3		4		5		6		UNK	
Species[2]	L	D	L	D	L	D	L	D	L	D	L	D	L	D
Loons	—	—	5	3	6	24	14	23	12	32	50	66	8	—
Small grebes	1	—	—	3	—	12	3	11	—	16	—	64	2	—
Aechmophorus grebes	—	—	10	15	9	79	25	105	45	48	37	66	6	—
Unidentified grebes	—	—	—	—	6	—	9	—	—	—	1	—	3	—
Scoters	—	—	1	—	16	24	11	86	3	48	14	64	10	—
Common Murre	6	41	75	223	327	261	924	1478	181	462	644	1130	87	—
Auklets/murrelets	—	—	—	3	1	—	1	71	—	16	5	78	2	—
Rhinoceros Auklet	—	10	—	3	1	6	7	274	1	64	20	844	1	—
Other species	—	—	2	9	1	24	3	42	5	—	11	52	1	—
Unidentified birds	—	—	—	—	324	—	399	—	1	—	—	—	27	—
Total	7	51	93	259	691	430	1396	2090	248	686	782	2364	147	—

[1] Locations of regions are indicated in Figure 1.

[2] Live bird totals for species groups differ from those in Tables 1 and 3 due to large numbers of unidentified birds by region.

calculated mean values of N for each beach type within each region. Missing values for 6 of the 25 region-beach type combinations were assumed to be similar to those for the same beach type from a neighboring region. We calculated the total length of the different beach types in each of the six regions (from Habel and Armstrong 1978) and multiplied each length by the appropriate mean value of N for each beach type in each region and then summed carcass totals for each region.

ESTIMATED NUMBER OF OILED CARCASSES REACHING SHORE

Using this model, we estimated 5880 beached oiled carcasses, which were broken down into taxa (Tables 2, 3) in direct proportion to numbers of each taxon in each region on carcass counts (Page and Carter 1986). An unknown but presumably small proportion of these birds was likely oiled after death either at sea or on the beach. From 2 to 11 February, 61 carcasses were found without oiled plumage, compared to the 834 with oiled plumage. The 834 moderately- to heavily-oiled carcasses were not so decomposed that we could eliminate oiling as the probable cause of death. Common Murres accounted for 61.1% and Rhinoceros Auklets for 20.4% of the oiled carcasses. *Aechmophorus* grebes and scoters (*Melanitta* spp.) were the next most abundant taxa constituting 5.3% and 3.8%, respectively.

Dead-to-live bird ratios were much greater for Rhinoceros Auklets, auklets/murrelets, and small grebes than for other taxa (Table 3). Rhinoceros Auklets and auklet/murrelets, a category in which Cassin's Auklets (*Ptychoramphus aleuticus*) predominated, were distributed farther from shore and therefore were more likely to die before reaching shore than Common Murres. Loons (*Gavia* spp.) and Common Murres, which had the lowest dead-to-live bird ratios, may have been more likely to swim or fly toward shore after being coated with oil, and because of their larger body size may have required a higher dose of oil before being killed. The high among-species variability in dead-to-live ratios invalidated the use of simply derived multiples of the number of rescued, live oiled birds to estimate the total mortality of birds.

AT-SEA CARCASS LOSS MODEL

Even when numbers of beached live and dead oiled birds are known, a large fraction of the total mortality may remain unmeasured. Winds and currents may carry floating carcasses away from shore where they are never observed (Bibby and Lloyd 1977, Bibby 1981). Many carcasses that are propelled towards shore may not beach because they sink or are scavenged along the way

TABLE 3. ESTIMATED NUMBERS OF BIRDS DEBILITATED OR KILLED DURING THE *APEX HOUSTON* OIL SPILL BETWEEN 1–8 FEBRUARY 1986 FROM SALMON CREEK, SONOMA COUNTY, TO POINT LOBOS, MONTEREY COUNTY. DASHES INDICATE THAT DATA WERE NOT AVAILABLE.

Species	Alive and sent to rehabilitation centers	Dead on beaches	Ratio of dead-to-live on beaches	Lost at Sea (S_j)	Total
Loons	128	148	1.16	–	276
Small grebes	9	106	11.78	–	115
Aechmophorus grebes	155	313	2.02	–	468
Unidentified grebes	19	0	–	–	19
Scoters	61	222	3.64	–	283
Common Murre	2924	3595	1.23	969	7488
Auklets/murrelets	9	168	18.67	29	206
(Cassin's Auklet)	0	(140)	–	(29)	(169)
Rhinoceros Auklet	30	1201	40.03	335	1566
Other species/unid. birds	29	127	4.38	–	156
Total	3364	5880	1.75	1333	10,577

(Page et al. 1982). Our model for estimating numbers of dead oiled birds not reaching shore required: descriptions of the trajectories of the oil and bird carcasses, the rate of carcass loss at sea, the distribution of the birds at sea at the time of the spill, and the numbers of dead oiled birds on beaches. Ecological Consulting prepared a computer model that simulated trajectories of hypothetical oil slicks along the route of the *Apex Houston,* and trajectories of carcasses arising from the hypothetical slicks. Simulated oil slicks were treated as points driven by wind and ocean surface currents. Wind vectors were computed as the wind direction plus a variable deflection angle, D, used to simulate the Ekman effect:

$$D = 25^\circ \exp(-10^{-8}W^3/vg)$$

where: W = wind speed, v = kinematic viscosity of sea water, and g = gravitational acceleration (Samuels et al. 1982, Neumann 1939, Witting 1909). The wind drift factor, or the proportion of the wind velocity imparted to the transported material, was assumed to be 0.035 for oil (Smith et al. 1982) and 0.022 for dead birds (Hope Jones et al. 1970). Real time wind data were obtained from five different central California coastal weather stations: 1) Vandenberg Air Force Base (34.7°N, 120.5°W); 2) Meteorological Buoy 46011 (34.9°N, 120.9°W, Point Sal); 3) Point Pinos (36.6°N, 122.0°W); 4) Meteorological Buoy 46012 (37.4°N, 122.7°W, Half Moon Bay); 5) Meteorological Buoy 46026 (37.8°N, 122.7°W, Gulf of the Farallones). Wind fields were extrapolated linearly between adjacent stations for a smooth transition from one station to the next. Wind vectors at any point were weighted averages of winds from the nearest station to the north and south. Surface current data were based on the characteristic tracing model of Dianalysis of Princeton (Kantha et al. 1982). Vector fields were discretized into 30-min blocks extending from 21.5° to 49.8°N and from 137.5° to 118.5°W.

Points, representing hypothetical slicks travelling at 3.5% of wind speed, were launched at three-hr intervals along the track of the *Apex Houston* when it passed by. They were moved at three-hr intervals until contacting shore or until 8 February. Likewise, groups of simulated bird carcasses were launched at each three-hr time step along each slick trajectory and moved at 2.2% of wind speed until they contacted shore or until 8 February (Fig. 4).

An index of the relative number of carcasses that beached in different coastal regions was computed as the number of birds in a one-km² area at the beginning point of a carcass trajectory, decreased by 2.0% at each three-hr time step to account for at-sea loss (derived from Hope Jones et al. 1970). When a group of carcasses beached, it was added to the total beached from all trajectories contacting that region. R_j, the proportion of total beachings predicted in region j, was computed by dividing the number of beached model carcasses in a given region by the total number beaching in all regions:

$$R_j = \frac{L_j}{\sum_{i=1}^{b} L_i}$$

where: L_j = the number of carcasses beaching in region j after accounting for at-sea loss, the denominator is the sum for all regions involved, and b is the total number of regions. R_j values were calculated separately for each species.

P_j, the proportion of carcasses lost before making landfall in region j, was calculated carrying out the same simulation, but without at-sea loss:

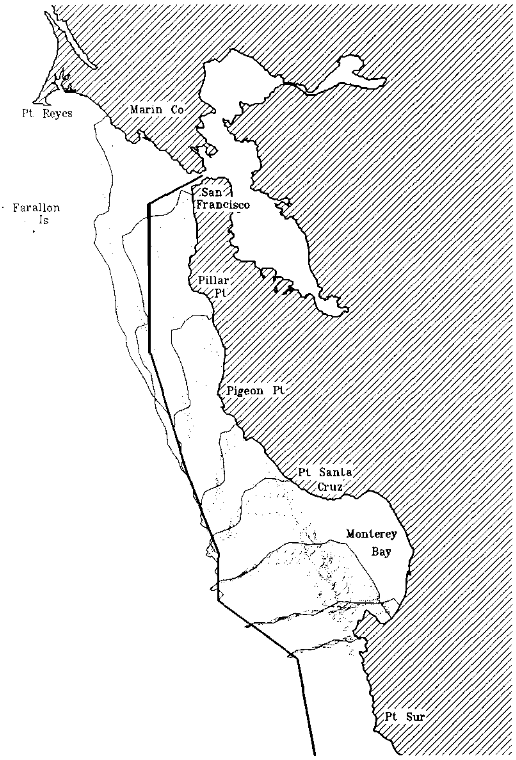

FIGURE 4. Model simulation of the *Apex Houston* oil spill. The heavy line shows the track of the *Apex Houston* and thin lines show oil slick trajectories launched at three-hr intervals from along the vessel's route between Pigeon Point and Point Lobos. Groups of simulated bird carcasses are indicated by dots for each three-hr interval.

$$P_j = 1 - \frac{L_j}{N_j}$$

where: N_j = the number that would have beached in region j without at-sea loss. P_j values were calculated separately for each species.

Distribution of Birds at Sea

A total of 1517 birds of at least 24 species was recorded on the aerial survey. Slope waters were dominated by Red Phalaropes (*Phalaropus fulicaria*), Western Gulls (*Larus occidentalis*), Cassin's Auklets, and Rhinoceros Auklets. Outer shelf waters were dominated by Brandt's Cormorants (*Phalacrocorax penicillatus*), Red Phalaropes, Western Gulls, Herring Gulls (*L. argentatus*), California Gulls (*L. californicus*), Common Murres, Cassin's Auklets and Rhinoceros Auklets. Inner shelf waters were dominated by *Aechmophorus* grebes, Surf Scoters (*Melanitta perspicillata*), Red Phalaropes, and Common Murres. Densities were not unusual for this time of year in these zones (Page and Carter 1986, Briggs et al. 1987). We chose to determine the numbers of dead oiled birds not reaching shore for Common Murres, Cassin's Auklets, and Rhinoceros Auklets, which were relatively abundant on the survey. We also applied the at-sea loss rate to these species, because it was derived from other data on alcids.

Common Murres. Hypothetical slicks launched between 01:00 and 06:00 hrs (PST) on 29 January off the northern end of Monterey Bay, when the *Apex Houston* encountered heavy seas (Fig. 4), had the greatest potential for contacting large numbers of Common Murres. Slicks passed through a small, very dense aggregation on the inner shelf west of Pigeon Point and moderately dense aggregations in the Gulf of the Farallones (Fig. 5A). The model predicted that 46.2% of carcass beachings between regions 2 and 5 would occur in regions 2 and 3, where only 20.0% were determined to have beached (Table 4). The highest proportion of carcass beachings was predicted accurately in region 4 and proportions were predicted closely in region 5. At-sea loss ranged from 8.6% for carcasses destined for region 5 to 34.1% for region 4.

Rhinoceros Auklets. Rhinoceros Auklets were aggregated in two regions on the outer shelf, northwest of the Farallon Islands and due west of Pigeon Point (Fig. 5B). Slicks bypassed the aggregation in the Gulf of the Farallones but passed through the one west of Pigeon Point. Birds affected there should have beached in region 4, where most carcasses were predicted and many found during beached bird censuses (Table 4). At-sea loss of carcasses ranged from 20.9% to 59.2% among regions 3–5.

Cassin's Auklets. Cassin's Auklets were aggregated northwest of the Farallon Islands and on the slope west of Half Moon Bay (Fig. 5C). Slicks did not pass through these high density aggregations but did pass through low densities on the inner shelf due west of Pigeon Point and off Monterey Bay. Cassin's Auklets oiled in these areas should have beached in regions 4 and 5. Model predictions were fairly accurate for three of four regions examined (Table 4). However, 30.9% of the carcasses were predicted in region 3 where none was found. At-sea loss ranged from 14.5% to 55.4% among regions 2–5.

Estimated Numbers of Oiled Carcasses Not Reaching Shore

The number of birds lost at sea was only calculated for regions 2 to 5, because there were insufficient data on the densities of birds at sea for the model to predict at-sea loss for region 6, and the model failed to show birds beaching in region 1. The number of dead birds lost at sea was estimated separately for the three alcid species as follows:

$$N_j = \frac{M_j}{1 - P_j}$$

where:

N_j = the number of carcasses expected to wash onto region j given no carcass loss at sea.

M_j = the number of carcasses that reached region j (estimated for regions 2 to 5 in Table 2).

P_j = the proportion of carcasses that did not reach region j (derived for regions 2 to 5 in Table 4).

The number of carcasses lost at sea (S_j) was estimated as: $S_j = N_j - M_j$. S_j values were summed over the four regions for each alcid species to give minimal estimates of at-sea carcass loss of 969 Common Murres, 29 Cassin's Auklets, and 335 Rhinoceros Auklets (Table 3). These estimates would have been substantially higher if it had been possible to obtain an estimate for region 6 (Monterey Bay).

DISCUSSION

TOTAL NUMBER OF BIRDS DEBILITATED OR KILLED

By adding live and dead oiled birds on beaches to those lost at sea, we estimated a minimum of 10,577 birds debilitated or killed in the *Apex Houston* oil spill (Table 3). In fact, a few thousand additional birds met a similar fate because: 1) numbers of live oiled birds were underestimated because of incomplete rehabilitation center records (Page and Carter 1986, Carter et al. 1987); 2) numbers of dead birds lost at sea were underestimated because there was no estimate for region 6 (Table 4) and at-sea loss was estimated for only 3 of the 26 species affected; and 3) numbers of beached birds and birds lost at sea were estimated only for the area and time of peak beachings. In fact, an additional 494 live oiled

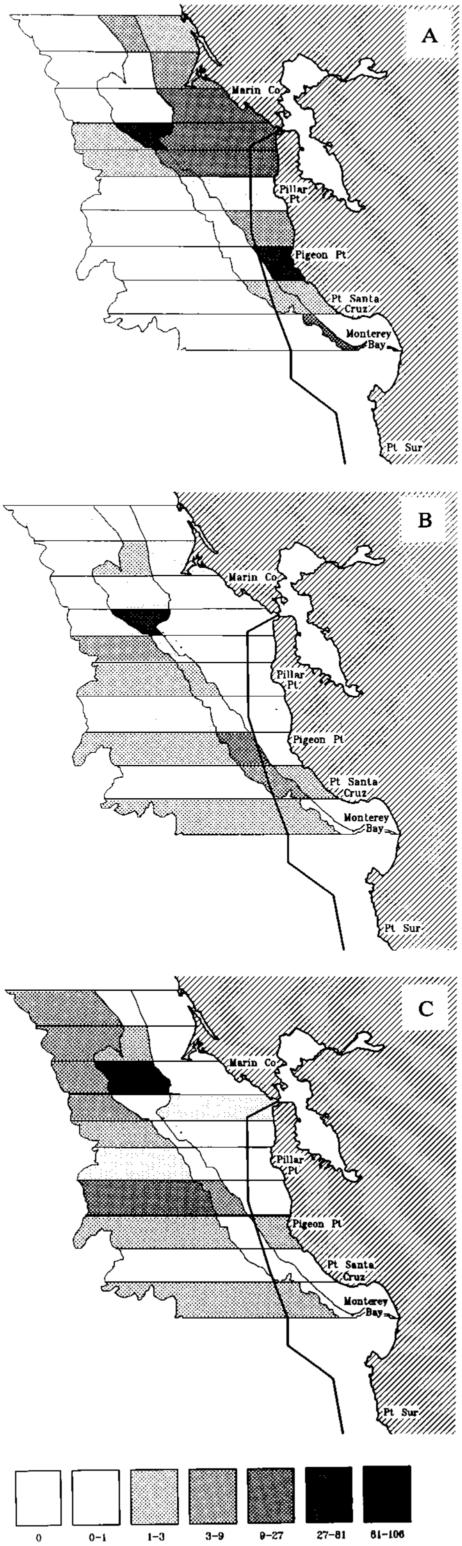

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FIGURE 5. At-sea densities of (A) Common Murres, (B) Rhinoceros Auklets, and (C) Cassin's Auklets based on transects flown on 5 February 1986. Density blocks are defined in an east-west direction by bathymetry: 0–100 m, inner shelf; 100–200 m, outer shelf; and 200–3000 m, slope. North-south divisions were constructed so that each block contained one transect line. Intensity of stipling indicates bird densities per km^2, as shown in the key. The dark line starting at the entrance of San Francisco Bay is the track of the *Apex Houston.*

TABLE 4. PERCENT OF COMMON MURRE, RHINOCEROS AUKLET, AND CASSIN'S AUKLET CARCASSES LOST AT SEA. MODEL BEACHED CARCASS INDICES ARE PROPORTIONS OF HYPOTHETICAL CARCASS BEACHINGS IN REGIONS 2–5 AND ESTIMATED BEACH CARCASS INDICES ARE PROPORTIONS OF 2424 COMMON MURRES, 347 RHINOCEROS AUKLETS, AND 62 CASSIN'S AUKLETS THAT BEACHED IN REGIONS 2–5, RESPECTIVELY

Coastal region	Predicted time of carcass arrival	Model beached carcass index (R_j)	Percent carcasses lost at sea (P_j)	Estimated beached carcasses (see Table 2)	Estimated beached carcass index
Common Murre					
2	2–3 Feb	0.234	26.1	223	0.092
3	3–4 Feb	0.228	23.9	261	0.108
4	3–4 Feb	0.393	34.1	1478	0.610
5	2–3 Feb	0.145	8.6	462	0.191
Rhinoceros Auklet					
2	—	0.000	0.0	3	0.009
3	3–4 Feb	0.208	59.2	6	0.017
4	3–4 Feb	0.663	53.0	274	0.790
5	2–3 Feb	0.129	20.9	64	0.184
Cassin's Auklet					
2	2–3 Feb	0.078	21.5	3	0.048
3	3–4 Feb	0.309	55.4	0	0.000
4	3 Feb	0.450	37.0	43	0.694
5	2–3 Feb	0.162	14.5	16	0.258

birds were sent to rehabilitation centers between 9 February and mid-March, 510 dead oiled birds were found on 23 carcass counts on 19 beaches between 20–27 February, and a few hundred oiled birds were reported from south of Point Lobos (Page and Carter 1986).

Had PRBO not developed the beached bird model and Ecological Consulting the at-sea carcass loss model, only the approximately 3000 oiled birds sent to rehabilitation centers would have been documented as casualties from the spill. Our study results show that beached carcass counts and aerial surveys of birds at sea must be incorporated into oilspill contingency plans if the total extent of mortality is to be fully appreciated (see Carter and Page 1989).

Although the *Apex Houston* spill involved only about 26,000 gallons of oil, the extent of seabird mortality rivaled some of the worst known incidents (Evans and Nettleship 1985) and far exceeded that of the highly publicized *Puerto Rican* oil spill (PRBO 1985, Dobbin et al. 1986). Casual observers were surprised that such a small spill killed so many birds. However, the *Apex Houston* spill coincided with the period of peak abundance of wintering birds in central California (Briggs et al. 1987) and oil slicks passed through dense aggregations of seabirds.

The long-term impact of the mortality on Common Murres remains unknown. In central California, the murre population declined by over 50% between 1982 and 1986, mostly due to gillnet mortality (see Atkins and Heneman 1987; Takekawa et al. 1990). The *Apex Houston* and *Puerto Rican* oil spills, which together killed over 9500 murres, contributed to this crash, but it is not known what portion of murres killed belonged to the resident breeding population. Probably most of the Rhinoceros Auklets affected were from breeding populations farther north (Briggs et al. 1987), because only small numbers breed in central California (Sowls et al. 1980), and because breeding at the Farallon Islands continued to increase in 1986 and 1987 (PRBO, unpubl. data). The Marbled Murrelets (*Brachyramphus marmoratus*) that were killed represented 1% to 5% of the central California breeding population (see Carter and Erickson 1988).

FUTURE RESEARCH

It is not necessary to use our beached bird model when beached birds can be counted accurately through daily counts (PRBO 1985). However, such situations seldom occur, and large numbers of birds usually have beached over several days before any attempt is made to count them, as in the *Apex Houston* spill. It would be valuable to improve the beached bird model by considering the following points:

1. Single censuses should be conducted on as many beaches as possible, because they provide the independent values for carcass numbers on which means for each region-beach type combination are based, and because the species composition of the carcasses is derived directly from these censuses (Carter and Page 1989).
2. We used mean carcass persistence (S) over

two days on two beaches (N = 4) at the time of the spill in the model. Carcass persistence could vary with carcass type, location, and tidal condition. Page et al. (1982) provide evidence that beach type affects carcass persistence. Further research should determine which variables affect carcass persistence the most, so that these could be considered when sampling for S. Predetermined values of S could be used if these would not bias the outcome in the model.

3. The proportion of the carcasses beaching each day (P_i) was assumed to be similar to live birds in the *Apex Houston* spill, but this assumption would not apply to all situations (e.g., Hope Jones et al. 1970). A lag in the beachings of dead oiled birds could be incorporated into the model, although it would be preferable to obtain actual values of P_i for carcasses at the time of the spill. P_i values will vary substantially between spills, between coastal regions and possibly also with beach type. P_i values must be determined from data collected during the spill and at minimum for several regions for large spills.

4. Our method should be applied separately for each abundantly occurring species within each region. This was not possible during the *Apex Houston* spill because large numbers of live oiled birds attributed to some regions were not categorized by species at rehabilitation centers (see Tables 1, 2).

5. Error estimates for each of the variables in the beached bird model and for the total estimate of beached carcasses should be developed. Sensitivity analyses should be used to identify which variables most affect the overall accuracy of the estimates.

In contrast to the beached bird model, an at-sea loss model should always be used because there is no other way to determine the number of dead oiled birds that do not reach shore. Depending on how far from shore a spill occurs, the extent of onshore transport of oil and carcasses, and the abundance and distribution of birds at sea, carcasses lost at sea may or may not account for a large proportion of the overall seabird mortality. Our model was derived from a more detailed model, which also accounted for turnover of birds within slick areas at sea (Dobbin et al. 1986, Ford et al. 1987). Our model required less information about slicks at sea and fewer assumptions about seabird behavior at sea. At-sea loss models should be refined by considering the following points:

1. We modeled oil and carcass trajectories based mainly on wind speed and direction. While this seemed reasonable for floating carcasses, trajectories did not take into account movements by oiled birds before death or the effects of strong nearshore surface currents. Such modelling omissions may have caused inconsistencies such as the appearance of small numbers of live and dead oiled birds at the Farallon Islands and in region 1 (north of Point Reyes), where our model predicted neither slicks nor carcasses. Detailed on-scene descriptions of slicks at sea would alleviate some problems, as in the *Puerto Rican* spill when at times slicks moved opposite to the direction predicted by winds alone.

2. We used a constant at-sea carcass loss rate of 15% per day based on one prior study in which oiled alcid carcasses were launched at sea (Hope Jones et al. 1970). As Ford et al. (1987) point out, the actual rate may not be a constant and may not be the same for all species and all spills.

3. We assumed only three fates for birds: they die at first contact with oil, survive until rescued on shore, or survive at sea until after the spill. The daily at-sea loss rate was applied only to the first group. If birds survived beyond the moment of impact and moved toward shore, estimates of the time required for carcasses to reach shore would be longer than actual values, resulting in an overestimate of the number of carcasses lost at sea.

4. Ford et al. (1987) discuss the merits and drawbacks of aerial surveys used during the *Apex Houston* and *Puerto Rican* spills. Spatial and temporal persistence of seabird aggregations at sea must be studied to evaluate the appropriateness of a single survey some time after the spill for use in models. Better techniques are required for surveying coastal areas within a few kilometers of shore where large numbers of birds often aggregate.

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DIFFERENTIAL RESPONSES OF COMMON AND THICK-BILLED MURRES TO A CRASH IN THE CAPELIN STOCK IN THE SOUTHERN BARENTS SEA

W. VADER, R. T. BARRETT, K. E. ERIKSTAD, AND
K.-B. STRANN

Abstract. Common Murres (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) are common breeding birds in the Barents Sea, with complementary but overlapping distributions. Along the coast of North Norway, west of the North Cape, murre populations have been decreasing at least since 1965, probably as a result of breeding birds drowning in fishing nets. East of the North Cape and probably on Bear Island the populations have at least been stable until 1985. After 1985, numbers of breeding Common Murres decreased steeply in the entire area, by 70–85% in North Norway and ca. 90% on Bear Island, while populations of Thick-billed Murres decreased only slightly on the mainland and not at all on Bear Island. The numbers of murres wintering in the Barents Sea also decreased after 1986. It is thought that the differential decrease in numbers of breeding birds was a direct result of the sudden collapse of the Barents Sea capelin (*Mallotus villosus*) stock in 1985 and 1986, on which the Common Murres, but not the Thick-billed Murres, totally depended.

Key Words: Common Murre; Thick-billed Murre; *Uria aalge*; *Uria lomvia.*; capelin; population decline.

Common Murres (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) are large alcids with partly overlapping holarctic distributions in the boreal, low- and high-arctic regions (cf. Nettleship and Evans 1985). Birkhead and Nettleship (1987a, b, c) have recently shown that the two species have a similar nesting biology, although with significant differences in timing of breeding and chick diet.

The Barents Sea is shallow and very productive (Zenkievitch 1963, Wassman and Sakshaug 1987) with a diverse, mainly subarctic seabird fauna (Norderhaug et al. 1977, Golovkin 1984). Both murre species breed in the area, with *U. aalge* more numerous along the coast of Europe and *U. lomvia* on the arctic islands (Fig. 1). Both species also winter in the area, although some Spitsbergen Thick-billed Murres move to Greenland in winter (Brown 1985).

This paper documents recent changes in the breeding populations of both species in what is considered to be a direct response to a collapse in the Barents Sea capelin stock.

METHODS

In the 1960s and 1970s the sizes of the breeding populations of Common Murres and Thick-billed Murres in North Norway were estimated by Brun (1965, 1969, 1979). Brun repeated some of his counts at intervals of several years and documented large changes (Brun 1979). Since 1980 the breeding populations of Common Murres and Thick-billed Murres have been monitored on Hornøy (Fig. 1) through almost annual counts of individuals on selected plots, plus total counts of all individuals in the colony (see Folkestad 1984). In 1985, a similar monitoring scheme was initiated on Hjelmsøy and Syltefjord (Fig. 1), the then two biggest Common Murre colonies in Norway. Data on the breeding success of murres and other seabird species breeding in the region were otherwise collected annually either through direct observations in the field or through reports sent to the authors.

A survey of the distribution of seabirds at sea in the Barents Sea north to 74°30′N was initiated in 1985. This survey was conducted through a series of at-sea transects and counts from ships and the air both during and, mostly, outside the breeding season (Strann and Vader 1987, Erikstad et al. 1990, Erikstad unpubl.).

Data on the diets of murres were gathered either through direct analyses of the contents of the stomachs of birds shot at sea, direct observations of fish either brought in to chicks or dropped on the breeding ledges, or through a literature review.

RESULTS

Between 1965 and 1985 the numbers of Common Murres nesting in northern Norway, west of the North Cape, decreased, whereas they were stable (Syltefjord) or increased (Hornøy) at sites east of the North Cape (Table 1).

After 1985 there was a dramatic drop in the numbers of Common Murres breeding at all colonies, including the two eastern colonies, Hornøy and Syltefjord (Table 1). Numbers of birds in the monitoring plots on Hjelmsøy, Syltefjord and Hornøy dropped by as much as 90% between 1986 and 1987 (unpubl.), as did single counts of the total numbers at each colony (Table 1). Although the absolute numbers of Thick-billed Murres also decreased at some of these colonies, they did so to a lesser extent than for Common Murres (Table 1). On Bear Island, where the numbers of breeding murres had been counted for the first time in 1986, Common Murres de-

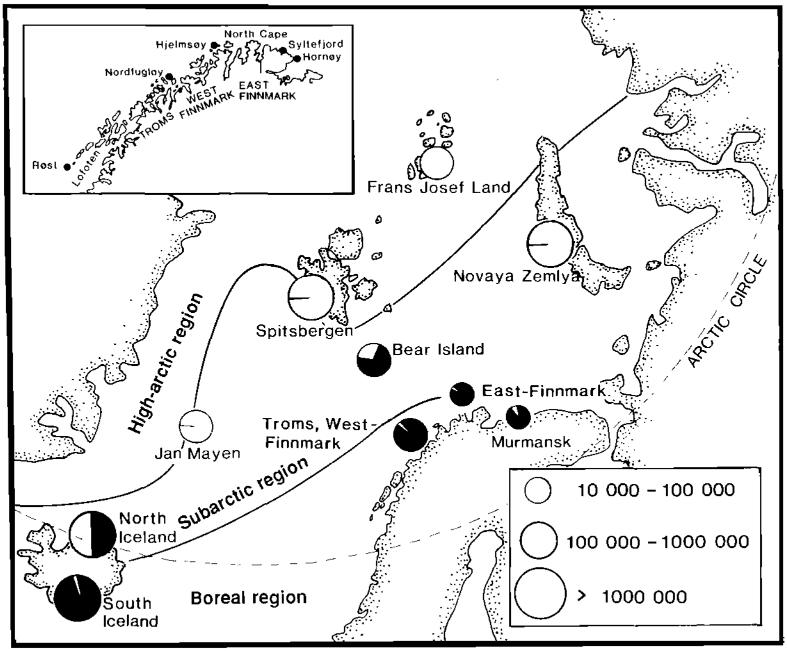

FIGURE 1. Approximate numbers and relative frequency of Common Murres (shaded circles) and Thick-billed Murres (open circles) breeding in the Barents Sea and adjacent N.E. Atlantic (Data from Einarsson 1979, Barrett and Vader 1984, Golovkin 1984, Mehlum and Fjeld 1987, and V. Bakken, pers. comm.). The boundaries of the boreal, low- and high-arctic regions are from Nettleship and Evans (1985).

creased by about 90% from 1986 to 1987, while numbers of Thick-billed Murres remained at least stable (Bakken and Mehlum 1988).

Data collected at sea in the Barents Sea in January–February 1986 and 1987 also show that the numbers of both murre species decreased, each by ca. 70% between the two surveys, and they were nearly completely missing from the traditional capelin (*Mallotus villosus*) areas in 1987 (Erikstad unpubl.).

DISCUSSION

It is thought that the decline in Common Murre numbers in North Norway has occurred as a result of two major negative factors and in two stages: before and up to 1985, and post-1985.

PRE-1985

In the Lofoten Islands, west of the North Cape, Common Murres have suffered from food shortages at least since 1970. This, together with a complementary increase in predation pressure through netting, may partly explain the decline on Røst from ca. 11,000 pairs in 1960–1964 to fewer than 1000 pairs in 1988 (Tschanz and Barth 1978, Folkestad 1984, Bakken 1989). In this same area Atlantic Puffins (*Fratercula arctica*) were equally hard hit (Lid 1981, Anker-Nilssen 1987, Barrett et al. 1987). What little data exist on the food situation and breeding success farther north, on Nord-Fugløy and Hjelmsøy, suggests that murres there have not suffered from food shortages to the same degree shown on Røst. We attribute the steep decline in murre numbers at these colonies more to drowning in fishing nets than to reproduction failure. In early spring, cod (*Gadus morhua*) fisheries occasionally kill very large numbers (> 100,000 in 1985), whereas large summer driftnet and, until the early 1970s, longline fisheries for salmon regularly drown thousands of local breeding birds (Brun 1979, Vader and Barrett 1982, Strann et al. 1990).

East of the North Cape, where salmon driftnets are not permitted, the size of the murre colonies increased between 1975 and 1985 (Table 1).

POST-1985

Between 1985 and 1987, the numbers of breeding murres on all colonies suddenly declined very steeply, on both sides of the North Cape, thereby ruling out salmon fishing as the only cause. Circumstantial evidence points towards a sudden food shortage being the major factor.

Belopol'skii (1957), working in the eastern Barents Sea, classified the Common Murre as a

TABLE 1. CHANGES IN NUMBERS OF COMMON MURRES (*Uria aalge*) AND THICK-BILLED MURRES (*U. lomvia*) BREEDING AT FOUR COLONIES IN NORTH NORWAY, 1965–1987 (FROM BRUN 1965, 1969, 1979; BARRETT AND VADER 1984; THIS STUDY)

	No. of individuals					% change	
	1965	1975	1985	1986	1987	1965–1985	1985–1987
Common Murre							
Nord Fugløy[1]	30,000	8000	200	<100	—	−99	No data
Hjelmsøy[1]	220,000	140,000	22,000	10,000	2000	−99	−80
Syltefjord[2]	25,000	18,000	22,000	18,000	3000	−12	−83
Hornøy[2]	1450	1000	7500	—	1600	+500	−79
Thick-billed Murre							
Hjelmsøy[1]	>2000	1700	740	220	275	−ca. 60	−63
Syltefjord[2]	(present)	180	1600	2000	1000	+ca. 800	−37
Hornøy[2]	110	—	450	—	300	+310	−33

[1] West of North Cape.

[2] East of North Cape.

stenophagous fish-eater and the Thick-billed Murre as polyphagous, with a tendency toward stenophagy during the nesting period. This view has been strengthened by later diet studies in the North Atlantic (Bradstreet and Brown 1985). While both feed on pelagic fish when locally abundant (Tuck 1961, Erikstad and Vader 1989, Tables 2 and 3), the Thick-billed Murre is better adapted to bottom exploitation and invertebrate feeding than the Common Murre (Spring 1971).

Until 1985, the smelt-like capelin was one of the dominating pelagic fish species in the Barents Sea and was a key species in this sea's ecosystem (Hamre 1986). Likewise, the coastal stocks of sand lance (*Ammodytes* spp.) were important prey for predatory fish (e.g., cod) and seabirds in North Norway (Furness and Barrett 1985, Pethon 1985, Haug and Sundby 1987). Between 1985 and 1987, the Barents Sea stock of capelin collapsed completely (Fig. 2), and in 1987 fishermen noted a near complete absence of sand lance along the coast of West Finnmark (pers. obs., T. Haug pers. comm.). The latter resulted in a complete breeding failure at a large colony (>2000 pairs) of Shags (*Phalacrocorax aristotelis*) in West Finnmark, where Shags are normally totally dependent on sand lance during the breeding season (pers. obs.). Fisheries scientists do not fully understand why the capelin vanished so quickly, but causes probably include overfishing, uncommonly large year-classes of the predatory cod after 1983, and a reduction in recruitment due to changes in the physical oceanography of the Barents Sea (Hamre 1986, Ushakov and Ozhigin 1986).

In January 1987, several thousand dead Common Murres were washed ashore along the coast of North Norway. Analyses of organochlorine and heavy metal levels in their livers ruled out death by poisoning. The birds were emaciated and it is thought that they died of starvation. Dead Common Murres were also reported washed ashore in East Finnmark during the early summer of 1987, but no samples were taken for pollution analysis. No Thick-billed Murres were reported dead in the two incidents. In March 1987, Thick-billed Murres shot in the central Barents Sea were in good body condition, the majority having a fat index (measured according to Jones et al. 1982) of 2–3 (Erikstad 1990). Virtually no Common Murres were seen. It appears that during the winter 1986/1987, Common Murres either died of starvation or left the Barents Sea, while Thick-billed Murres fared better.

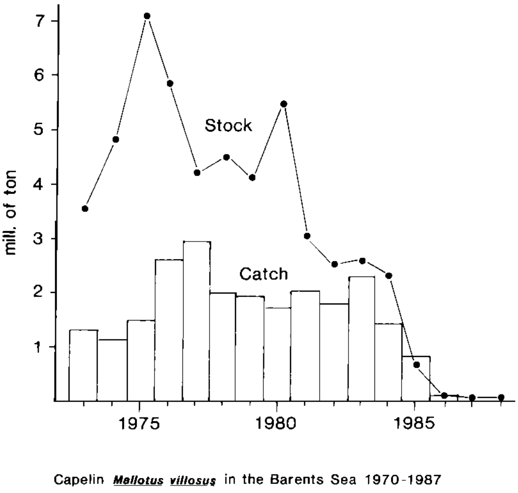

FIGURE 2. Estimated stock and total catch of the capelin (*Mallotus villosus*) in the Barents Sea, 1973–1987 (Hamre 1986 and pers. comm.).

TABLE 2. WINTER DIETS OF COMMON MURRES (*Uria aalge*) AND THICK-BILLED MURRES (*U. lomvia*) IN AREAS IN THE NORTH ATLANTIC WHERE THEY ARE NORMALLY SYMPATRIC

Area	Common Murre	Thick-billed Murre	Source
Finnmark coast April 1986	100% capelin	100% capelin	Erikstad and Vader 1989
Troms coast April 1985	Mostly capelin	Mostly capelin	Strann et al. 1990
S. Barents Sea March 1987	not present	Mainly gadids and crustacea	Erikstad 1990
Newfoundland Winter ca. 1955	90% capelin	90% capelin	Tuck 1961
Newfoundland Winter 1981–1983	not studied	Mostly young cod, squid, crustacea	Gaston et al. 1983

Those collected in March had remains of gadids and crustaceans in their stomachs (Erikstad 1990).

There are few data on adult murre diets from localities where both species occur (Table 2). Tuck (1961) found capelin to be absolutely dominant in both species wintering off Newfoundland, but later data have shown that at least within 10 km of the Newfoundland coast young cod, squid and crustaceans are also important winter prey of the Thick-billed Murre (Gaston et al. 1983). In East Finnmark, during the 1986 capelin spawning season, both species fed exclusively on capelin (Erikstad and Vader 1989), as did the very large concentrations of Common Murres drowned in fishing nets in Troms in spring 1985 (Strann et al. 1990) (Table 2). Thick-billed Murres collected near the ice-edge at 77–80°N, 18–23°E in July–August 1986 had mainly fed on amphipods (Lønne et al. MS), whereas stomachs of birds collected farther south, at ca. 75°N, 30'E, contained mostly gadid fish (cod and arctic cod *Boreogadus saida*) and krill (Erikstad 1990).

Although these North Atlantic studies (see also Bradstreet and Brown [1985] and Blake et al. [1985]) plus several from the Pacific (Springer et al. 1984, 1986; Ogi et al. 1985) support the notion that adult Common Murres specialize on small pelagic, schooling fish and that Thick-billed Murres eat both fish and crustaceans, Ogi et al. (1985), Blake et al. (1985) and Sanger (1987) show that at certain times and in certain areas Common Murres can rely heavily on invertebrates. The general picture, however, supports Spring's (1971) conclusion that both species will feed on any readily available, pelagic organism, but that, unlike the Common Murre, the Thick-billed Murre is better adapted to switch to bottom and invertebrate feeding in the absence of pelagic food sources.

The chick diets of murres breeding sympatrically in the North Atlantic consist exclusively of fish for both species (Table 3; Bradstreet and Brown 1985). Nevertheless there is a clear difference; Common Murres catch pelagic, schooling fish, whereas Thick-billed Murres also take many demersal organisms (Bradstreet and Brown 1985). On Hjelmsøya, West Finnmark in 1983, before the crash in the capelin stock, Common

TABLE 3. CHICK DIETS OF SYMPATRICALLY BREEDING COMMON MURRES (*Uria aalge*) AND THICK-BILLED MURRES (*U. lomvia*) IN CANADA AND THE BARENTS SEA

Area	Common Murre	Thick-billed Murre	Source
Labrador 1982–1983	75% capelin 10–15% gadids 10–15% *Lumpenus*	20–30% capelin 65–70% *Lumpenus*	Birkhead and Nettleship 1987c
Hornøy 1983	60% capelin 40% sand lance	25% capelin 75% sand lance	Furness and Barrett 1985
Hjelmsøy 1983	99% capelin[1]	33% capelin[2] 22% sand lance 24% squid	This study
Seven Islands 1938	86% sand lance 18% herring	80% sand lance 16% herring	Kaftanowski 1938 (*in* Tuck 1961)

[1] % of 79 food items.
[2] % of 49 food items.

Murres fed their chicks on capelin, while Thick-billed Murre chicks had a more varied diet, including small squid (*Gonatus fabricii*) (Table 3).

We contend that a food shortage, a direct result of the collapse in the stocks of capelin, a pronouncedly pelagic schooling fish, exacerbated by the reduction in sand lance, is the most plausible cause of the sudden drop of Common Murres at North Norwegian colonies in 1987. The breeding population of Common Murres either died the preceding winter, or food resources were so adverse that they were unable to build up energy reserves necessary for egg formation and therefore abandoned any breeding attempt (Wiens 1984). Thick-billed Murres, although also lower in numbers than previous years, had fared better, either due to their ability to utilize alternative food sources or because of the tendency for at least some birds to migrate north to the ice edge (where no Common Murres were seen in 1987–1988) or west, and out of the Barents Sea during the winter (Spring 1971, Brown 1985, Bakken and Mehlum 1988).

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