SEASONAL MOVEMENTS AND PELAGIC HABITAT USE OF MURRES AND PUFFINS DETERMINED BY SATELLITE TELEMETRY

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Abstract. We tracked the movements of Common Murres (Uria aalge), Thick-billed Murres (U. lomvia), and Tufted Puffins (Fratercula cirrhata) using surgically implanted satellite transmitters. From 1994–1996, we tagged 53 birds from two colonies in the Gulf of Alaska (Middleton Island and Barren Islands) and two colonies in the Chukchi Sea (Cape Thompson and Cape Lisburne). Murres and puffins ranged 100 km or farther from all colonies in summer, but most instrumented birds had abandoned breeding attempts and their movements likely differed from those of actively breeding birds. However, murres whose movements in the breeding period suggested they still had chicks to feed foraged repeatedly at distances of 50–80 km from the Chukchi colonies in 1995. We detected no differences in the foraging patterns of males and females during the breeding season, nor between Thick-billed and Common Murres from mixed colonies. Upon chick departure from the northern colonies, male murres—some believed to be tending their flightless young—drifted with prevailing currents toward Siberia, whereas most females flew directly south toward the Bering Sea. Murres from Cape Thompson and Cape Lisburne shared a common wintering area in the southeastern Bering Sea in 1995, and birds from Cape Lisburne returned to the same area in the winter of 1996. We conclude that differences in foraging conditions during summer rather than differential mortality rates in winter account for contrasting population trends previously documented in those two colonies.

Key words: Common Murre, Fratercula cirrhata, satellite telemetry, Thick-billed Murre, Tufted Puffin, Uria aalge, Uria lomvia.

INTRODUCTION
Information on the feeding areas, foraging ranges, and migration patterns of seabirds is difficult to obtain because of the large distances traveled and the difficulty of tracking individuals over the open ocean. Traditional methods entail costly shipboard or aerial surveys (Nettleship and Gaston 1978, Bradstreet 1979, Schneider and Hunt 1984) or indirect calculations based on estimated flight speeds and time-activity budgets (Cairns et al. 1987). In the breeding season, foraging ranges are of interest, because flight distances have a large influence on energy expenditure (Gaston 1985). Movements in winter must be determined to identify critical marine habitats, yet few data are available on wintering populations of seabirds from known breeding places—none pertaining to any Alaskan colony.

Small (30–50 g) satellite transmitters have recently become available for use in wildlife telemetry (Ely et al. 1993, 1997, Falk and Möller 1995, Petersen et al. 1995). Implantable devices used by Petersen et al. (1995) have proven effective when deployed on birds as small as 1,000 g, and telemetry is now a possible alternative to conventional survey methods for many kinds of oceanic birds.

We implanted satellite transmitters in three species of diving seabirds (Common Murres Uria aalge, Thick-billed Murres U. lomvia, and Tufted Puffins Fratercula cirrhata) at four locations in Alaska. In general, we were interested in the utility of this approach for determining where birds forage in summer in relation to particular colonies and where birds from particular colonies go in winter. Flightless murre chicks are led to sea by their male parents, who continue to provide parental care for several weeks as the young gradually learn to feed themselves (Harris and Birkhead 1985). However, the existence and location of possible “nursery” areas is unknown for murres in Alaska, as elsewhere. Thus, we also endeavored to locate key foraging areas of fledgling murres by deploying transmitters on breeding males late in the season.

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Based on earlier success with Spectacled Eiders (Somateria fischeri) (Petersen et al. 1995) and pilot efforts in the present study, we used implanted transmitters for murre telemetry. We instrumented Tufted Puffins at one colony to gauge the feasibility of this approach in a smaller species (about 800 g). In practice, we encountered problems of altered behavior, bird mortality, and equipment failure in each of our study species (Meyers et al. 1998, Hatch et al., in press). We were able nonetheless to gather considerable data pertinent to our objectives, and those results are the focus of this paper.

METHODS
STUDY AREAS AND SPECIES
The Barren Islands (59°55'N, 152°10'W) lie at the mouth of Cook Inlet (Fig. 1), an oceanographically dynamic area influenced by strong tidal currents from the inlet and a low-salinity, rapidly flowing Alaska Coastal Current (Muench et al. 1978). Circulation patterns and bottom topography result in a highly productive local system that supports some 600–800,000 pelagic birds of 15 species (Sowls et al. 1978). About 90,000 Common Murres nest on two islands (Nord and East Amatuli), whereas Tufted Puffins occur on all seven islands in numbers estimated at 200,000. Thick-billed Murres are scarce at the Barren Islands. We took Tufted Puffins from burrows on West Amatuli Island and Common Murres from ledges on the northeast side of East Amatuli.

Cape Lisburne (68°53'N, 166°13'W) and Cape Thompson (68°09'N, 166°00'W) lie north and south, respectively, of Point Hope on Alaska’s northwest coast (Fig. 1). Some 100,000 murres, mostly (70%) Common Murres, nest at Cape Lisburne, whereas Cape Thompson supports an estimated 390,000 murres of both species (75% Thick-billed Murres, Fadely et al. 1989). We took murres at the eastern end of the Cape Lisburne complex, from ledges easily accessible on foot from the U.S. Air Force radar station nearby. At Cape Thompson, we caught Thick-billed Murres in colony 3 (as designated by Swartz 1966) near the mouth of Ikijaktusak Creek, and Common Murres in colony 4, comprising cliffs surrounding Cape Thompson itself.

Oceanographically, the eastern Chukchi Sea is characterized by the convergence and accelerated northward flow of three major currents through Bering Strait, representing Anadyr, Bering Shelf, and Alaska Coastal water masses, respectively (Fleming and Heggarty 1966, Coachman et al. 1975). Sea ice usually does not move out of the Point Hope region before early to mid July, and because of advancing ice in winter, the nearest potential off-season areas for murres from Chukchi colonies are in the southeastern Bering Sea, or possibly in polynyas off the coast of St. Lawrence Island.

Middleton Island (59°26'N, 146°20'W) is well isolated in the north-central Gulf of Alaska near the edge of the continental shelf (Fig. 1). The island has a declining population of some 5,000 Common Murres (1998 estimate) and fewer than 500 Thick-billed Murres. We implanted two Common Murres on Middleton in 1994 as a pilot effort to our main study in 1995–1996. Both birds were males that appeared to be nonbreeders at the time they were captured.

Mean (± SD) body mass of Tufted Puffins instrumented in this study was 806 ± 47 g (n = 5) before the implants. Common Murres averaged 1,017 ± 70 g (n = 28) and Thick-billed Murres weighed 940 ± 90 g (n = 20).

EQUIPMENT AND FIELD PROCEDURES
Our telemetry device was a 35-g platform transmitter terminal (PTT) manufactured by Micro-
wave Telemetry, Inc. (Columbia, Maryland). The body of the transmitter measured 55 × 35 × 10 mm; the antenna was 200 mm long. PTTs were constructed to meet specifications issued by Service Argos, Inc., the company that operates receiving equipment aboard NOAA (National Oceanic and Atmospheric Administration) polar-orbiting weather satellites and distributes data to users of its Data Collection and Location System (Argos 1988). A PTT in its active mode transmitted a 32-bit message over 360 msec, with a repetition interval of 70 sec. Besides location information (computed from Doppler shifts in detected frequency; Argos 1988, Harris et al. 1990), each message contained calibrated indices to the internal body temperature of the bird and remaining battery potential.

PTTs were programmed to transmit initially in one of two classes of duty cycle, designated “short cycle” and “long cycle” in reference to the frequency of transmission and expected battery life. In 1994, one PTT transmitted on a cycle of 8 hr on/8 hr off for 50 cycles (about 33 days), then switched to a pattern of 6 hr on every 4.67 days. A second unit was programmed to be alternately on for 6 hr and off 12 hr for 5 cycles (90 hr total), before switching to the long cycle (6 hr on every 4.67 days). In 1995, we used a short cycle of 6 hr on/12 hr off (14 transmitters) and a long cycle of 6 hr on/66 hr off (21 transmitters). Our short cycle in 1996 was 8 hr on/8 hr off (8 transmitters), and we extended the long cycle that year to 6 hr on/120 hr off (8 transmitters). Short-cycle PTTs switched to the long cycle after 32 days (expected battery life) in 1995 and after 40 days (expected time at the colony after deployment) in 1996. We chose to emphasize winter location data over local movements in summer, hence the 3:2 ratio of long- to short-cycle PTTs in 1995.

We conducted the field work on 16 July 1994 at Middleton Island, from 15–18 July at the Barren Islands in 1995, and from 1–3 August 1995 and 2–4 August 1996 at Cape Lisburne. We visited Cape Thompson from 4–6 August in 1995. We used noose poles to catch murres off their breeding ledges at all four study sites and pulled incubating Tufted Puffins from burrows on West Amatulii Island. Workers had only a limited view of ledges containing accessible murres, thus the breeding status of individuals (egg present or not) was undetermined in most cases. Birds were transported to a field camp where they were implanted and released within a few hours of capture.

Procedures for anesthesia and surgical implantation of the PTTs by a trained veterinarian followed closely the protocols developed by Korschgen et al. (1984, 1996). Briefly, the transmitter was inserted into the abdominal cavity through a mid-ventral incision, with the wire whip antenna exiting dorsally through the skin to one side of the tail. To maximize signal propagation, we attempted to position the antenna so that it pointed directly upward when the bird was on the water (Korschgen et al. 1984). Gender was determined using a fiber-optic endoscope to view the gonads. After surgery, we allowed the subjects to recover from anesthesia for 2–4 hr before releasing them to the water within 5 km of their capture sites. All birds were released in apparently healthy condition and PTTs began transmitting location data immediately. A total of 28 Common Murres, 20 Thick-billed Murres, and 5 Tufted Puffins were implanted with transmitters during the study.

DATA ACQUISITION AND ANALYSIS
We downloaded data every 2–3 days from Argos’ online data distribution system. Data were analyzed using Arc/Info® and Arcview® GIS software. We rejected 24% of the locations obtained because of suspect quality codes reported by Argos and lack of positional redundancy of locations obtained close together in time (Hatch et al., in press).

We calculated foraging ranges by averaging distances from the colony to a locus of telemetry points that comprised a foraging bout. In general, we defined a foraging bout as any collection of at-sea locations that occurred between returns to the colony. However, because trips to the colony were probably missed, we further narrowed the definition to distinguish points more than 10 km apart. When a bird moved more than 10 km, subsequent locations were considered to be a new bout. The 10-km rule is arbitrary but allows a consistent method of quantification until more detailed information on local movements is available.

Breeding status after release was undetermined for most individuals in the study. To characterize movements during and outside of the breeding season, we used 1 September as an approximation of dispersal timing in murres and puffins from the colonies studied.
RESULTS

One PTT deployed in a Common Murre from Middleton Island in 1994 provided location data from soon after release on 16 July through 6 September. From 16–24 July, this bird foraged mainly about 40 km north of Middleton Island in a shoal area known as Wessels Reef. After 24 July it migrated from the Middleton area to waters surrounding the Barren Islands and northern end of Afognak Island. All subsequent movements were confined to that area, which closely matched the foraging range of Common Murres from the Barren Islands, as described below.

Common Murres tagged at the Barren Islands stayed within a 100-km radius of the islands for the duration of the study. Movements were mainly in a north-south direction, ranging from the mouth of Kachemak Bay to waters around Marmot Island (Fig. 2). We found no indication of differences in habitat use between the sexes. We know that we caused the nest failure of most, possibly all, of the implanted birds when eggs rolled off breeding ledges or were taken by Glaucous-winged Gulls (Larus glaucescens) during capture. With few exceptions, tagged birds did not commute regularly between distant foraging areas and their nest sites on East Amatuli.

Tufted Puffins tagged at the Barren Islands ranged up to 100 km west and more than 150 km east of West Amatuli Island in the first 2 months after release. We made no attempt to determine the breeding status of the birds after release. Individual patterns of movement indicated that some, possibly all, of the puffins abandoned their nests as a result of our disturbance. The longest record obtained for any of the five puffins indicated a bird that possibly attended its nest site after release. That bird foraged in close proximity to the Barren Islands until 20 August, when it moved to a pelagic feeding area centered about 100 km east of Afognak Island. It remained in that vicinity until we lost the signal on 20 September.

Murres in the northern colonies ranged more widely than those at the Barren Islands—up to 200 km during the first month after release. We detected no difference between species in the foraging areas at either colony in 1995 (Fig. 3a). There was, however, nearly complete separation of the foraging areas of Cape Thompson and Cape Lisburne murres during the breeding season (i.e., before 1 September). Birds from Cape Lisburne foraged almost exclusively northwest to northeast of the colony, whereas those from Cape Thompson foraged southwest to southeast and north to Point Hope (Fig. 3b).

The at-sea distribution of murres from Cape Lisburne during the breeding season in 1996 was similar to that in 1995 (Fig. 4). Birds in 1996 used the area just west of the colony somewhat less than in 1995, and did not drift as far north, but overall the distributions were similar. The area of intersection comprised 29,000 km² of mostly pelagic and some coastal habitat.

Five murres, including one whose chick was observed to have fledged (D. G. Roseneau, pers. comm.), may have engaged in incubation or chick-rearing after release in 1995, as indicated by their flight ranges and regularity of foraging trips. Mean (± SD) foraging distances during the breeding season were 79 ± 36 km (range 8–104 km, n = 6 foraging bouts), 53 ± 29 km (range 8–96 km, n = 28), and 63 ± 53 km (range 7–135 km, n = 4), respectively, for a Thick-billed Murre and two Common Murres commuting from Cape Thompson. The best documented of those was a male Common Murre (PTT 7916) that foraged alternately to the north-
west and southwest of the Cape Thompson colony (Fig. 5). At Cape Lisburne, the distances to foraging places averaged 66 ± 26 km (range 47–84 km, $n = 2$) in one commuting Thick-billed Murre and 79 ± 26 km (range 44–114, $n = 8$) in a single commuting Common Murre.

Breeding murres began leaving the Chukchi colonies around 1 September in 1995. After departure, birds dispersed widely over the Chukchi Sea or flew directly south through Bering Strait. Tagged birds of both species eventually settled in the vicinity of the Pribilof Islands (Fig. 6a). There was no difference between Cape Thompson and Cape Lisburne murres in that respect (Fig. 6b). Whereas males tended to drift north and west toward Siberia, most females flew directly south from the colonies (Fig. 7a). Three males (one Thick-billed Murre from Cape Lisburne; one Thick-billed and one Common Murre from Cape Thompson) made roughly counterclockwise movements, averaging 15–20 km day$^{-1}$, over large portions of the Chukchi Sea in September–October. All three murres moved abruptly south through Bering Strait in mid November.

Waters around the Pribilof Islands seemed to be the final destination of wintering murres in 1995, as most birds remained there for the duration of our study. One male Thick-billed Murre made repeated trips between the Pribilof Islands and St. Lawrence Island, presumably using open water areas that form off the coasts of St. Lawrence in winter. The latest transmissions from any bird tagged in 1995 provided locations through mid April 1996. Other individuals were tracked through the months of November (six birds), December (two birds), and January (three birds).

The final location data obtained from the 1996 deployment at Cape Lisburne came on 7 December. We were able to track only three individuals (two Common Murres, one Thick-billed Murre) past the point at which they moved south through Bering Strait, but those few data suggested the wintering areas of Cape Lisburne murres were similar in 1995 and 1996 (Fig. 7b).

DISCUSSION

Observations on implanted and control birds at Cape Lisburne in 1996 showed that instrumented murres ($n = 16$) reduced or ceased attendance at the colony after release, and none continued to nest successfully (Meyers et al. 1998). In addition, mortality in the first 30 days after release was 40% among 30 murres implanted in 1995 (Hatch et al., in press). Because the experimental treatment seriously affected the health and behavior of at least some instrumented birds, our
tracking results for those that survived must be interpreted cautiously. Failed murres spend less time at the colony than active breeders (Hatch and Hatch 1989), thus they can and presumably do range farther from their colonies than birds actively engaged in incubation or chick-rearing. We believe the identification of wintering areas should not be similarly affected, however. Birds tracked for 3–6 months after release would appear to have accommodated physically to the procedure, and it seems likely that murres visit the same wintering areas whether they breed successfully or not.

Several birds that appeared from our telemetry data to be still engaged in incubation or chick-rearing after release at Cape Thompson and Cape Lisburne foraged regularly up to 100 km from their colonies. This is in marked contrast to Common Murres in Shetland, where breeding adults remained within 10 km of their colony (Monaghan et al. 1994). Further study of known successful breeders is needed, but our initial results suggest there is considerable flexibility in the time and energy budgets of murres at different colonies, as anticipated by Burger and Piatt (1990). In designing studies to investigate murre foraging habitats oceanographically, it is important to realize that the feeding areas available to birds from Alaskan colonies in summer may be 30,000 km² or larger.

Our main conclusion regarding the summer foraging behavior of Common Murres from the Barren Islands is that nearshore waters along the north coasts of Shuyak and Afognak Islands were...
important feeding areas in 1995. Infrared satellite imagery available for 30 June 1994 (NOAA Satellite Data Service Division, Ashville, Tennessee) shows a distinct zone of upwelling and cold surface temperatures in that area. We suspect this is a recurring habitat feature generated by strong tidal flows in and out of Cook Inlet (Meunch et al. 1978), but we are unable to say from our 1-year study whether this is a defining characteristic of feeding habitat used perennially by murres from the Barren Islands.

The instrumented bird that departed Middleton Island in late July 1994 moved to the vicinity of the Barren Islands, possibly to spend the winter. This is an area in which large numbers of murres contacted oil and died in April 1989 during the Exxon Valdez oil spill (Piatt et al. 1990). Wintering murres did not return to their breeding sites on Middleton Island until 17 April 1989 (S. A. Hatch, unpubl. data), so it is possible that birds from this and other colonies outside the spill zone were included in the mortality associated with the Exxon Valdez spill. Wider application of telemetry could be useful in assessing the likely geographic extent of impacts from this and other mass mortality events affecting murres.

Male murres that departed the Chukchi colonies, some we suspect with chicks, appeared to drift north and west toward Siberia, as would be expected given the prevailing currents and flightless condition of young. Ocean circulation in the Chukchi Sea is generally counterclockwise at speeds averaging 15–20 cm sec$^{-1}$ (13–17 km day$^{-1}$; Fleming and Heggarty 1966, Coachman et al. 1975). After several weeks,
FIGURE 6. (a) Distributions post-breeding (after 31 August) of Common Murres (eight individuals, 451 locations) and Thick-billed Murres (five individuals, 175 locations) from Cape Thompson and Cape Lisburne (colonies combined) in 1995. (b) Distributions of murres (species combined) from Cape Thompson (nine individuals, 413 locations) and Cape Lisburne (four individuals, 210 locations) after the breeding season in 1995.

when chicks presumably had become capable of flight, all of the tagged birds moved rapidly south through Bering Strait, well ahead of advancing ice. If our interpretation is correct—that this pattern reflects at-sea chick-rearing by males—then any designation of a nursery area for murres from the study colonies would have to include all of the southern Chukchi Sea.

We did not identify the wintering area of murres from the Barren Islands as none of our records for that colony extended beyond late September. We can state with some assurance,
however, that the shared wintering area of murres from Cape Thompson and Cape Lisburne is the southeastern Bering Sea in the vicinity of the Pribilof Islands. Shipboard and aerial surveys show concentrations of murres in this area during fall and winter (Gould et al. 1982), but previously there was no information on the origins of those birds. Our study indicates the wintering population includes birds from colonies in the Chukchi Sea. A remaining question is whether local breeders, especially those from large colonies on the Pribilof Islands, are also present in winter.

Monitoring at Cape Thompson has revealed a long-term decline in murre numbers (about 50% since 1960), whereas the population at Cape Lisburne more than doubled in size between 1976 and 1995 (Fadely et al. 1989, Roseneau 1996). The decline at Cape Thompson might have resulted from reduced winter food causing elevated over-winter mortality of adults, as proposed for a murre colony at Bluff in Norton Sound (Murphy et al. 1986). However, telemetry indicates that murres from Cape Thompson and Cape Lisburne share a common wintering area, and divergent population trends would therefore not have been predicted on the above hypothesis. We conclude that differential winter mortality is an unlikely explanation that can be rejected in favor of the alternative possibility of differences in foraging conditions near the breeding grounds. The separation we found between summer feeding areas at these two colonies is consistent with the idea that better food resources in the breeding season support higher productivity and recruitment at Cape Lisburne.

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