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ORIGINAL PAPER

Movements and wintering areas of breeding age Thick-billed Murre *Uria lomvia* from two colonies in Nunavut, Canada

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Abstract The non-breeding movements of marine birds were poorly known until recently, but this information is essential to understanding the risk to different geographical populations from events on the wintering grounds. We tracked the migration routes and wintering areas of Thick-billed Murre *Uria lomvia* from two breeding colonies in eastern Canada: Coats Island in northern Hudson Bay and The Minarets, Baffin Island, during the period August 2007–May 2008 using geolocation loggers. Birds from The Minarets moved south rapidly post-breeding and wintered principally off Newfoundland and southern Labrador, or between Newfoundland and southern Greenland, remaining south of 55°N until at least the spring equinox. Those from Coats Island remained in Hudson Bay until at least mid-November, after which they moved rapidly through Hudson Strait to winter in southern Davis Strait and the northern Labrador Sea, mostly north of 55°N. Many individuals stayed throughout the winter in areas of heavy ice cover. Adults from the two colonies appear to be completely segregated in winter and those from Coats Island probably did not enter the area of the winter hunt in Newfoundland. Unexpectedly, some birds from The Minarets wintered in waters beyond the continental slope and outside the distribution of pack ice, demonstrating that particular individuals can be wholly pelagic throughout the winter. Coats Island birds returned through Hudson Strait as soon as open water areas became available in spring. Their sojourn in Hudson Bay coincided very closely with the occurrence of areas with <90% ice cover. In spite of the relatively large error in positions obtained from geolocation loggers, our results demonstrated the value of these devices by uncovering a number of previously unknown aspects of Thick-billed Murre non-breeding ecology in the Northwest Atlantic. Comparison of the non-breeding ecology based on SST experienced in winter show that the winter niche is broader than hitherto assumed, demonstrating that separate populations may experience different selection in the face of climate change.

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Introduction

Population monitoring of marine birds is mainly carried out at breeding colonies (e.g., Harris 1987; Rothery et al. 1988).

However, many populations move away from their breeding areas outside the breeding season, often travelling great distances (Gaston 2004). Knowledge of the non-breeding movements of marine birds is essential to understanding changes in marine bird populations in response to climate change and pollution (e.g., oiling, contaminants, Wiese et al. 2004; Mallory et al. 2006). Tracking of seabird migrations and identifying wintering areas present challenges because of the relative inaccessibility of the birds once they are no longer attached to their breeding sites. Previously, information on seabird movements was mainly inferred from band returns, but these are heavily biased by the uneven distribution of human settlements and the concentration of hunters, fisheries, oiling and other sources of mortality (Donaldson et al. 1997; Wernham et al. 2002; Gaston et al. 2008).

In recent decades, extended tracking has become possible through a variety of technical innovations (Ropert-Coudert and Wilson 2005), including satellite transmitters (Ancel et al. 1992), GPS loggers (Weimerskirch et al. 2002) and geolocation loggers (Phillips et al. 2004). These devices were initially deployed on large seabirds such as albatrosses and penguins but the decreasing size of tags has made it possible to deploy them on progressively smaller birds (Guilford et al. 2009). Auks (Alcidae) had proved especially difficult to study because external devices impede underwater performance (Paredes et al. 2005; Elliott et al. 2007) and implantation has rarely been successful (Meyers et al. 1998; Hatch et al. 2000).

Evaluation of a variety of plumage- and leg-mounted devices suggested that auks are least affected by devices attached to the lower leg and that, when placed in that position, devices <1% of body mass scarcely affect breeding performance (Elliott et al. 2007). With the development of geolocators weighing less than 10 g, it became feasible to deploy them on murres (*Uria* spp.) with a reasonable presumption that the behaviour of the birds would remain within normal limits. In this study, we report results from geolocators attached to Thick-billed Murres *U. lomvia* at two breeding colonies in the Eastern Canadian Arctic: Coats Island and The Minarets (*Akpait*).

Ship-based surveys and observations from shore suggest that Thick-billed Murres have a broad winter distribution, from West Greenland south to waters off the northeastern United States and seaward to at least the edge of the continental slope off Newfoundland and Labrador (Brown 1986; Gaston and Hipfner 2000). The exact ages, origins and breeding status of birds seen at sea are unknown, but in the absence of any band encounters of Canadian Thick-billed Murres east of Greenland, the bulk of those breeding in the Canadian Arctic has been inferred to winter within this boundary (Gaston 1980; Gaston and Hipfner 2000).

Information on movements of Thick-billed Murres from Coats Island was previously inferred from band recoveries, principally from birds shot in Newfoundland and Labrador (Donaldson et al. 1997; Gaston et al. 2008). During 1981–2002, 36,538 murres were banded at Coats Island, of which just 750 (2%) were reported away from the colony (AJG unpubl data). Among these, 85% were pre-breeders (1–3-year old, Gaston et al. 1994) when recovered. Only 52 Thick-billed Murres were banded previously at The Minarets (17 breeding adults and 35 nestlings), all in 1985, and none has been reported from elsewhere (one of the adults, recaptured in 2007, was used in this study, AJG unpubl data)). Consequently, previous information on migration and winter distribution of breeding age birds from these two colonies was available only from Coats Island and derived from 109 recoveries of birds >3 year old (Gaston and Robertson 2010). Our results are the first data on movements and wintering areas of North American murres derived from bird-borne devices. We compare them with previous information from banding (Donaldson et al. 1997; Gaston et al. 2008) and with inferences and generalizations made by earlier authors to determine the value of geolocation results compared with banding studies.

Because the distribution of sea ice is thought to have a strong effect on murre movements and wintering distributions (Gaston and Robertson 2010), we compared our results with changes in ice conditions over the period of the study. As well, we analysed data on weather conditions in the region and compared these results with climate normals for the same areas to assess how likely it was that our results would be representative of typical conditions.

Study species

The Thick-billed Murre is a large member of the Alcidae with a circumpolar distribution, breeding entirely within Arctic and sub-Arctic waters. It breeds in very large aggregations of up to half a million breeding pairs, on sea-cliffs and feeds underwater on fish and large zooplankton (Gaston and Hipfner 2000). During winter, most of the marine areas around breeding sites are covered by sea ice, and the murres move to open water, although often close to or within the marginal ice zone. Some populations make substantial migrations of thousands of kilometres (Bakken and Mehlum 2005).

Study area

Coats Island (62°53′N, 82°00′W), a colony of ~30,000 breeding pairs of Thick-billed Murres, is situated in the centre of northern Hudson Bay, Canada (Fig. 1). In winter,

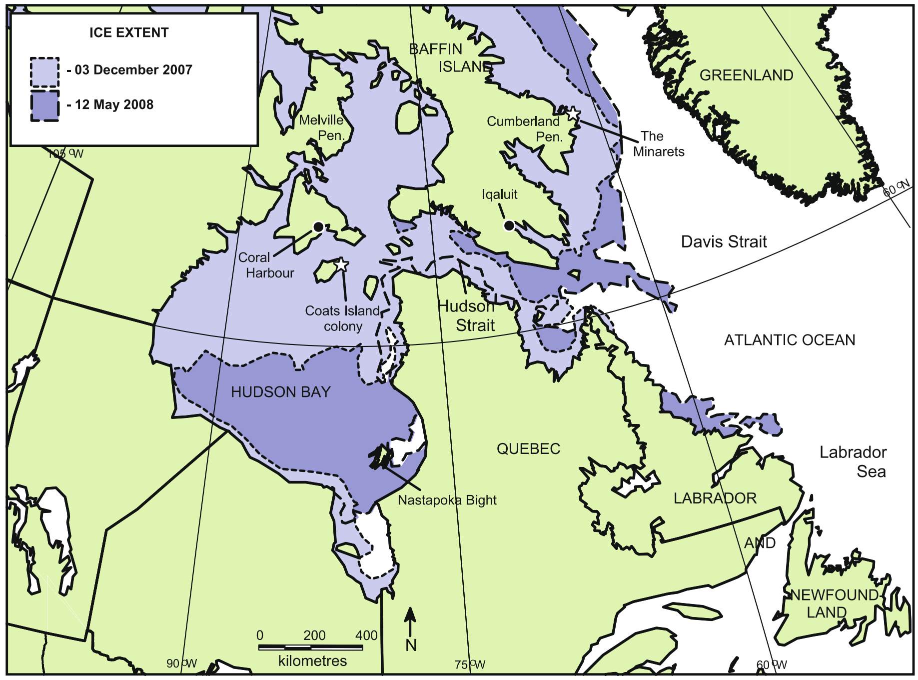

Fig. 1 Map of the study area, (from 40° N to 68° N), showing the extent of sea-ice cover on 3 December 2007 and 12 May 2008 and the position of named localities

sea ice cover in Hudson Bay is close to 100%, although the offshore pack ice remains mobile throughout (Prinsenberg 1986). Freeze-up takes place from early November onward, starting in the northwest part of the Bay and proceeding southeastward so that the whole bay is typically 100% covered by early December. Hudson Strait, the only sea corridor by which the murres can leave the bay, is also 100% ice covered by then in most years. Open water begins to appear in Hudson Strait and in the vicinity of Coats Island in late April or early May, and there is generally <50% ice cover by early July (Prinsenberg 1986).

The Thick-billed Murre colony at The Minarets (66°57′N, 61°50′W, also known as *Akpait* or "Reid Bay" [Nettleship and Smith 1975]), is situated between capes Dyer and Searle on the east coast of the Cumberland Peninsula of Baffin Island, Canada (Fig. 1). It had been visited only once previously by biologists, in 1985, when it was estimated to support ~130,000 breeding pairs (Gaston and Smith 1987), the most recent estimate. Freeze-up in the adjacent waters of Davis Strait began in late October and was complete by mid-November during 1971–2000 (Canadian Ice Service http://glaces.ec.gc.ca/App/WsvPageDsp.cfm, accessed 11 August 2009). Open water appears within 10 km of the colony by mid-July (Canadian Ice Service *ibid*.), although a floe-edge abutting mobile pack is close to the colony by late May in most years, according to local informants (personal communication to AJG, 2007).

Potential wintering areas for Thick-billed Murres from the two colonies may be expected to include all waters of the northwestern Atlantic and adjacent seas (e.g., Gulf of St. Lawrence, Bay of Fundy) south of the boundary of 100% pack-ice cover and north of the boundary between the warm northeast-flowing North Atlantic Drift and the cold, southward-flowing Labrador Current, at approximately 42°N at longitude 55°W (Taylor and Stephens 1998) and 45°N at 45°W (Taylor 1995). This region includes extensive continental shelf waters over the Grand and Labrador banks and associated features, as well as extensive deep water regions (>2,500 m) in the southern and central Labrador Sea.

Methods

Three types of geolocator (British Antarctic Survey, Cambridge) were deployed: the Mk 5 and 7, weighing, in air, 3.6 g, and the Mk 13, weighing 1.8 g (c.0.2–0.4% of adult mass). All geolocators were ground-truthed initially at Gull Island, Newfoundland (47°16′N, 52°46′W), and then again at the colonies after retrieval. The geolocation devices recorded light levels to elucidate spatial positioning; immersion in water to assess colony attendance and departures (from the duration of time spent on dry land); and sea surface temperatures year-round (following methods in Phillips et al. 2004; Guilford et al. 2009).

Birds were caught by means of neck nooses. Devices were attached in 2007–20 birds at Coats Island on 6 August and to 20 birds at The Minarets on 4 August. All birds at Coats Island were seen to be rearing chicks. All those at The Minarets were considered, on the basis of their behaviour, to have chicks, though this could not be confirmed for all sites. Each logger was attached to a Darvic band fastened around the tarsus. Seventeen out of 20 birds from Coats Island were recaptured as breeders (observed with chicks or eggs) at the same sites the following summer, and one other bird was recaptured in 2009. Fourteen (all of those seen) were recaptured at The Minarets on 3–4 August 2008. Birds were weighed on recapture, and 12 unmarked birds were trapped and weighed at the same time to provide a control sample. A blood sample was taken from each bird for sexing using W-chromosome analysis based on PCR of introns (Fridolfsson and Ellegren 1999). Capture and deployment of tags were carried out under a Government of Nunavut Wildlife Research Permit, Canadian Wildlife Service Migratory Bird permit NUN-SCI-08-55 and Environment Canada Animal Care Committee Permit 0800AG01.

Details of data conversion and selection

Light data from the loggers were processed using MultiTrace (Jensen Software Systems, Germany), according to Phillips et al. (2004). Sunset and sunrise times were estimated from thresholds in light curves, latitude derived from day length, and longitude from the time of local midday with respect to Greenwich Mean Time and Julian day, providing two locations per day. Locations were validated on a case-by-case basis following Phillips et al. (2004) and mapped using ArcMap 9.1 (ESRI Inc.). The proportion of locations excluded because of light interference were 7% for Coats Island and 6% for The Minarets (see Supplementary Information, Table 1). A small proportion of locations (1–2%) were also excluded because they were far inland (>150 km) or outside the likely wintering range based on at-sea observations. A further 20% were excluded around the vernal and autumnal equinoxes, when day length is independent of latitude, selected by plotting the mean 7-day variance in latitude among daily positions and excluding those for periods where variance exceeded three times the average for the last week of August and February, respectively.

Even with these periods excluded, substantial latitudinal bias was evident in some locations. This asymmetric bias is present throughout the year, but magnified near the equinoxes, and arises because shading serves to shorten but never lengthen the measured day length. Consequently, we make little use of latitude data from September, October, March and the first half of April. Estimates of longitude during these periods are unaffected. Geolocation results were further validated by comparison with logger temperature data, comparing these with sea surface temperature measurements derived from satellite data (National Snow and Ice Data Center [NSIDC], based on Nimbus-7 passive microwave satellite data; ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/and SEAWIFS satellite sensors http://gdata2.sci.gsfc.nasa.gov/daac-bin/G3/results.cgi, accessed 12 Oct 2010). To reduce the effect of daily temperature fluctuations on our logger data, we analysed only temperatures between midnight and 05:00 h.

With these exclusions, we present results for the period from final colony departure to return from migration (25 August 2007–10 May 2008). Because of the inherent inaccuracy involved in geolocation (c. 185 km error on average in foraging albatrosses; Phillips et al. 2004), we have not attempted to plot individual locations or trajectories. Instead, we present mean locations for 14-day periods, starting from 5 November (hereafter termed “activity centres”). All statistical analyses were conducted using Statistica 6.1 (Statsoft Inc.), and means are presented ± SE unless otherwise noted.

Weather and ice conditions

Information on weather and ice conditions during the period August 2007–May 2008 was obtained from the appropriate Environment Canada online databases: for ice http://glaces.ec.gc.ca/App/and for weather http://climate.weatheroffice.ec.gc.ca/climateData/dailydata_e.html (daily data) and http://climate.weatheroffice.ec.gc.ca/climate_normals_e.html (30-year normals, 1971–2000). We examined data for the stations closest to our colonies: Coral Harbour, Nunavut, for Coats Island (64°12′N, 83°22′W) and for The Minarets, Iqaluit, Nunavut (63°45′N, 68°33′W), as well as data for Goose Bay, Labrador (53°19′N, 60°25′W) and St. John’s, Newfoundland (47°37′N, 52°55′W), representing stations close to the wintering area.

Temperatures at the four weather stations considered were close to 30-year monthly norms throughout the study period. Freeze-up in Hudson Bay in autumn 2007 occurred approximately 1 week later than the 30-year norm: the >90% ice cover margin in the northwestern portion of the Bay on 26 November 2007 coincided almost exactly with the norm for 19 November. By 3 December, when all but the Nastapoka Bight is normally ice covered, most of the southern part of the Bay remained ice free in 2007, as well as a corridor along the north side of Hudson Strait as far as 74° W (Fig. 1). Hudson Bay was completely ice-covered by 17 December, but an area of open water persisted in the eastern entrance to Hudson Strait until 24 December. Ice formation off The Minarets began in early November, but by that time, all tagged birds were far to the south.

During spring, open water appeared in eastern Hudson Strait by 14 April, extending, in patches, to 75°W by 5 May, by which time areas of open water were also present on the east coast of Hudson Bay, and adjacent to islands in the northeastern part of the Bay. By 12 May patches of open water were present throughout the northeastern quadrant of the Bay (Fig. 1). By 2 June, open water was available across

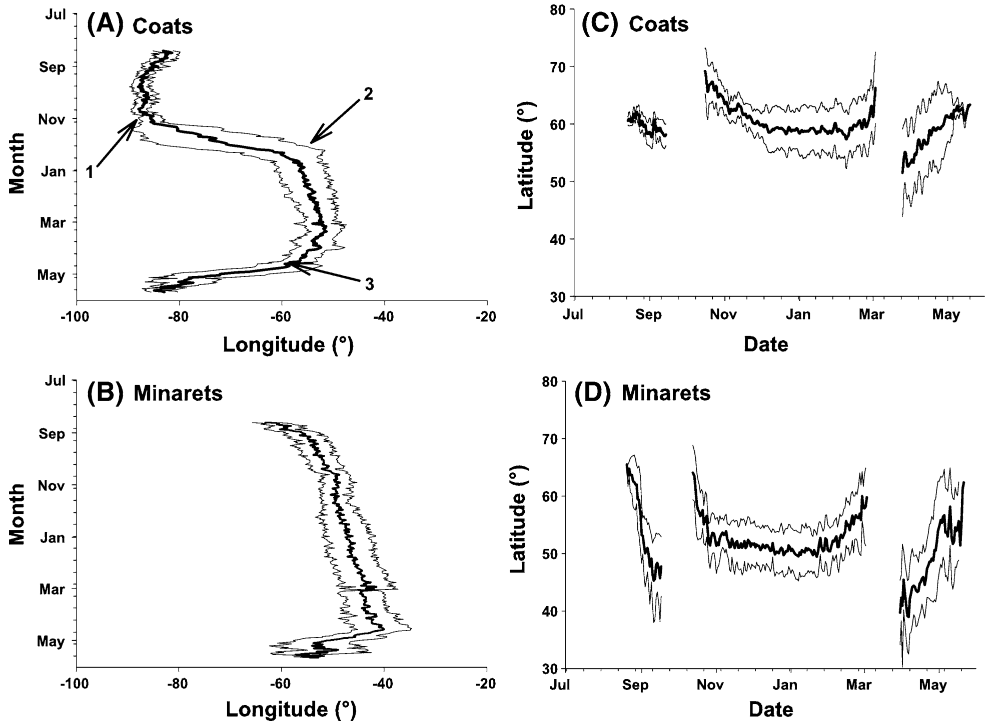

Fig. 2 Mean (±95% CI) daily longitude (**a**, **b**) and latitude (**c**, **d**) records from geolocators deployed at Coats Island (17 birds; **a**, **c**) and The Minarets (14 birds; **b**, **d**) in relation to date—records from the equinox gaps are omitted for latitude. Numbers indicate important inflection points (see "Results")

the entire northern portion of the Bay and east coast, a situation similar to the norm for 18 June. Likewise, open water was present close to the Minarets by 2 June, whereas in previous years, it would typically still have been 100 km east of the colony on 18 June.

Results

Geolocator results: coats Island

We obtained data from ten males and seven females. Mass at recapture did not differ between geolocator birds and controls (mean 1,031 ± 72 [SD] g, N = 17 vs. 1,043 ± 53 g, N = 20, respectively). Logger immersion data indicated a median date of departure from the colony of 23 August for tracked birds (AJG and PAS unpubl data). Median departure of chicks from the Coats Island colony occurred by 13 August in 2007, and most adults would have ceased to visit the colony by late August, based on observations from earlier years (AJG unpubl data). Based on longitudes, all birds tagged at the Coats Island colony remained within Hudson Bay around the autumnal equinox, mostly to the west of Coats Island (Fig. 2a), at uncertain latitudes. Longitude records suggested that the centre of the distribution continued to shift west until 20 September, situated thereafter at c. 85–88° W, presumably in the western half of Hudson Bay, until 25 October (inflexion point 1, Fig. 2a), after which eastward movement occurred. In mid-November, most birds were distributed to the west of Coats Island (4 of 7 females, 6 of 10 males, Fig. 3a, b), with four birds to the east of the colony in Hudson Bay and Foxe Basin, and three birds in Hudson Strait.

The main eastward movement through Hudson Strait took place from mid-November to mid-December. The estimated dates of entry into the strait (i.e., passage east of 77°W) ranged from November to 14 December (mean 26 Nov ± 3 day, N = 17, details in "Appendix") and of exit were 11 November–21 December (mean 2 Dec ± 3 day, N = 17). The mean transit time between these two longitudes, a distance of c. 600 km, was 6 ± 1 day, giving an average rate of movement of about 100 km day^{-1}. Nine of 17 birds took 5 days or less to cover this transit. The complete eastward migration, as defined by the period between inflexion points 1–2 in Fig. 2a, lasted from 7 November to 26 December.

Inflexion point 3 on Fig. 2a suggests that the initiation of westward movement into Hudson Strait occurred about 16 April. During the spring return movement, birds passed the eastern entrance to Hudson Strait between 17 April–9 May (mean = 27 April ± 1 day, N = 17) and 77°W between 21 April–12 May (mean 1 May ± 1 day, N = 17), taking an average of 4 ± 1 day, a mean rate of movement of about 160 km day^{-1}. Hence, Coats Island breeders were present in Hudson Bay (west of 77°W) for an average of 210 days during 2007–2008. None of these dates or rates of movement differed significantly between males and females ($t_{15} < 1$, $P > 0.1$, "Appendix"). There was no relationship between dates of fall departure and spring arrival in Hudson Bay ($R^2 = 0.14$, $F_{1,15} = 0.52$, $P = 0.48$).

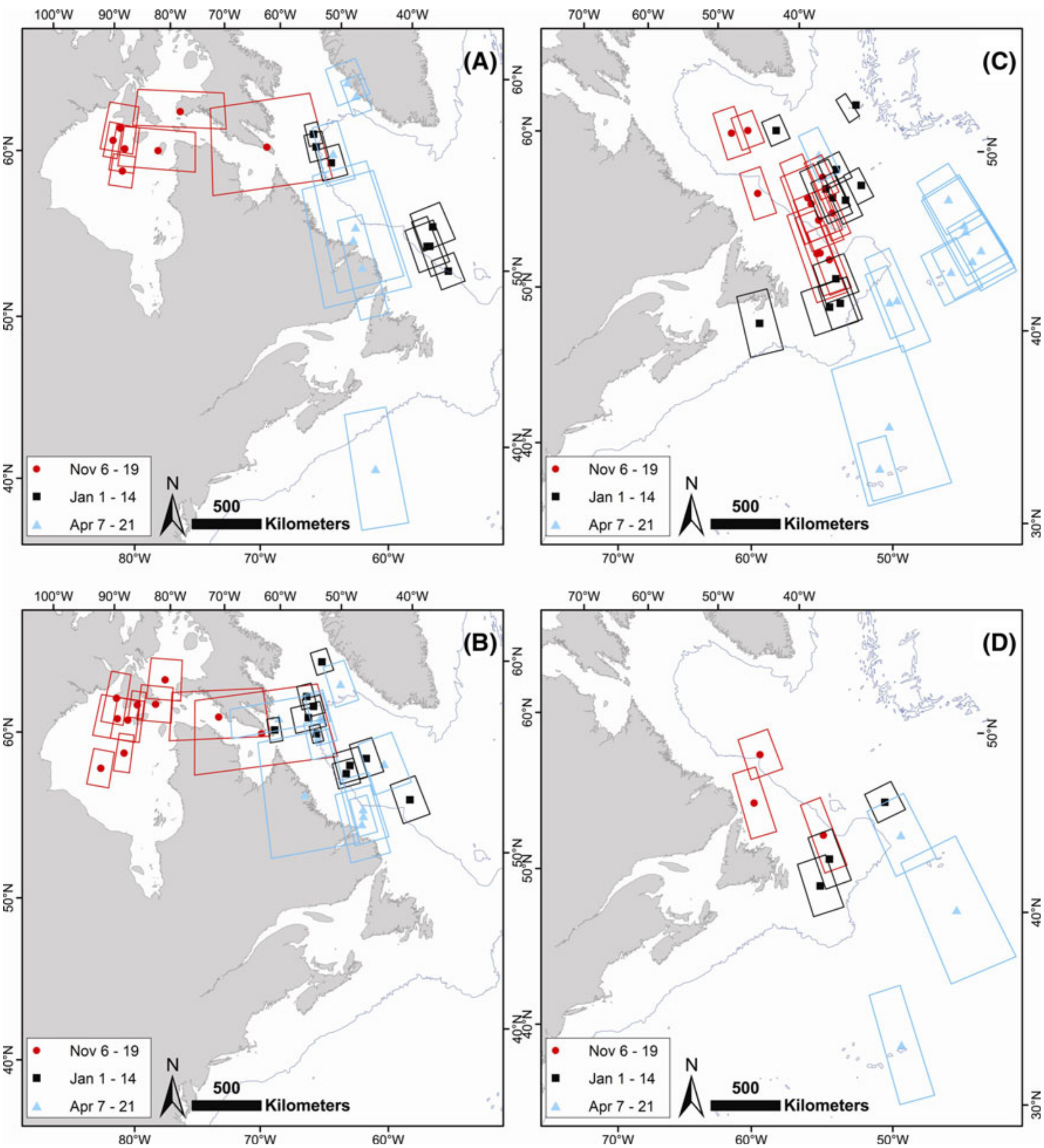

Fig. 3 Mean daily positions and standard deviation boxes for Coats Island females (**a**) and males (**b**) and Minarets females (**c**) and males (**d**) for three 14-day periods: 6–19 November 2007 (*circles*), 1–14 January (*squares*) and 8–21 April (*triangles*)

During winter, most birds remained between 54°–67°N. In January and early February, activity centres of females formed two groups, one in southern Davis Strait (three birds) and the other in the southern Labrador Sea (four birds), while most male distributions were centred in southern Davis Strait and the northern Labrador Sea, corresponding with the northern group of females. Trends in mean longitude during the equinox period in March showed a continued eastward movement, possibly indicating movement southeastward, as the coasts of Labrador and Newfoundland tend in that direction (Fig. 2a). Post-equinox, in mid-April, both males and females were distributed widely from southern Labrador to southern Davis Strait. One was centred well south of Nova Scotia, in waters influenced by the Gulf Stream, six were off central Labrador, and three were off west Greenland. The rest were scattered offshore in the northern Labrador Sea.

Geolocator results: the minarets

Results were obtained from eleven females and three males. All moved south rapidly after breeding, with all but one crossing south of 62°N by 1 September (mean date of passing 62°N = 28 Aug ± 0.8 day, N = 14). Rapid movement

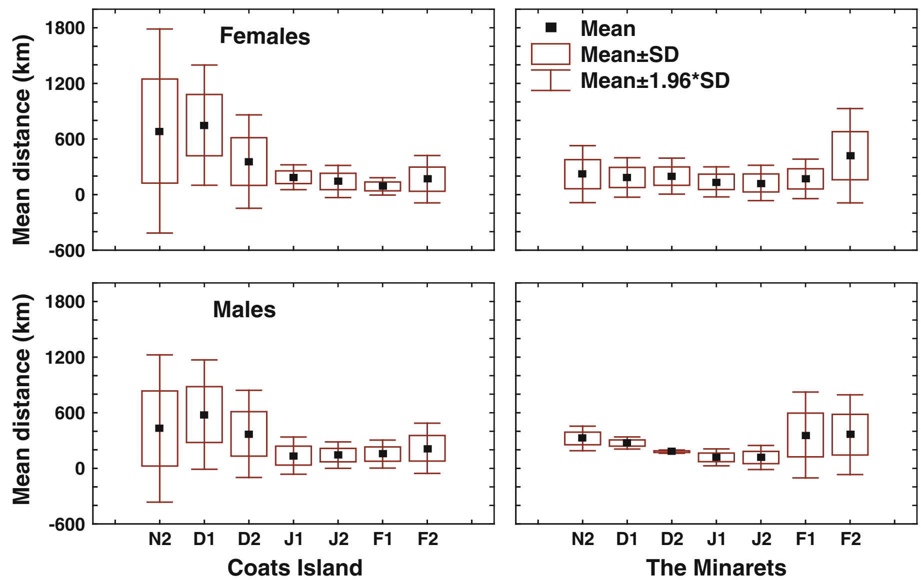

Fig. 4 Mean distances between 14-day activity centres, beginning with the difference between the period 6–19 November and 20 November—3 December (N2); *D* December, *J* January, *F* February

southward continued so that by 6 September all but two birds were south of 52°N (mean 1 Sep ± 1.0 day, N = 12), indicating an average rate of movement of about 300 km day^{-1}. In mid-November, all but two birds were centred south of 55°N, mostly on the edges of the Newfoundland and southern Labrador banks (Fig. 3c, d).

One female wintered off the south coast of Newfoundland and four other birds on the Grand Bank and surrounding waters, while another female spent the winter southeast of the southern tip of Greenland. The remaining birds were widely dispersed mid-way between Newfoundland and southern Greenland, mostly over deep water beyond the continental slope (Fig. 3c, d) and south of 52°N. With only three males in our sample, differences between the sexes could not be distinguished, but there was no sign of the tendency, seen for Coats Island birds, for males to remain farther north.

Like the Coats Island birds, those from the Minarets showed a continuing eastward movement during February and March (Fig. 2b, possibly indicating a southeasterly shift). By mid-April, most birds were spread in a broad arc to the east of the Newfoundland banks and far off the continental slope, except for three birds (one female, two males), which were centred farther south, in Gulf Stream waters (Fig. 3c, d). All birds were north of 52°N by 19 May (mean = 29 Apr ± 2.9 day). The mean date of passing 62°N in spring was 5 May ± 2.0 day, suggesting an average rate of northward movement between 52–62°N of about 170 km day^{-1}. As for the Coats Island birds, there was no evidence that these dates or rates of movement differed significantly between males and females, although the sample of males was very small ($t_{13} < 1$, $P > 0.1$, "Appendix"). Nor was there any relationship between dates of fall departure and spring arrival in the vicinity of the colony ($R^2 = 0.21$, $F_{1,12} = 3.16$, $P = 0.10$).

Geolocator results: both colonies

Birds from both colonies showed a tendency to remain in the same area throughout January and early February. Distances from one 14-day mean to the next generally averaged <200 km during December and January (Minarets) and January and February (Coats) (Fig. 4), suggesting relatively localized marine distributions mid-winter. Those birds wintering in outlying areas (birds with error boxes for 1–14 January that do not overlap with others in Fig. 3a, b, c) remained in those regions until latitudes became uncertain around the vernal equinox.

Sea water temperatures

Mean daily water temperatures recorded prior to presumed colony departure dates in mid-August ranged from 1.7 to 4.0°C at The Minarets and from 7.2 to 9.6°C at Coats Island. During the period from August to November, temperatures recorded by Coats Island birds, then all presumably in northern Hudson Bay, fell from approximately 9°C in late August to approximately 2°C by the end of November (Fig. 5a). This trend represented a drop in temperature from ~9 to ~0°C in nighttime SST over the same period (based on SEAWIFS satellite sensors http://gdata2.sci.gsfc.nasa.gov/daac-bin/G3/results.cgi, accessed 12 Oct 2010). From mid-December to mid-January, most temperatures remained in the 2–3°C range (means for January range 0.7–4.6°C), but thereafter some birds apparently shifted to warmer water with most temperatures in the 4–5°C range from mid-February to late March. All temperatures had returned to below 2°C by 17 April after which they remained in the same range into early June. The sharp change in temperature between about 25

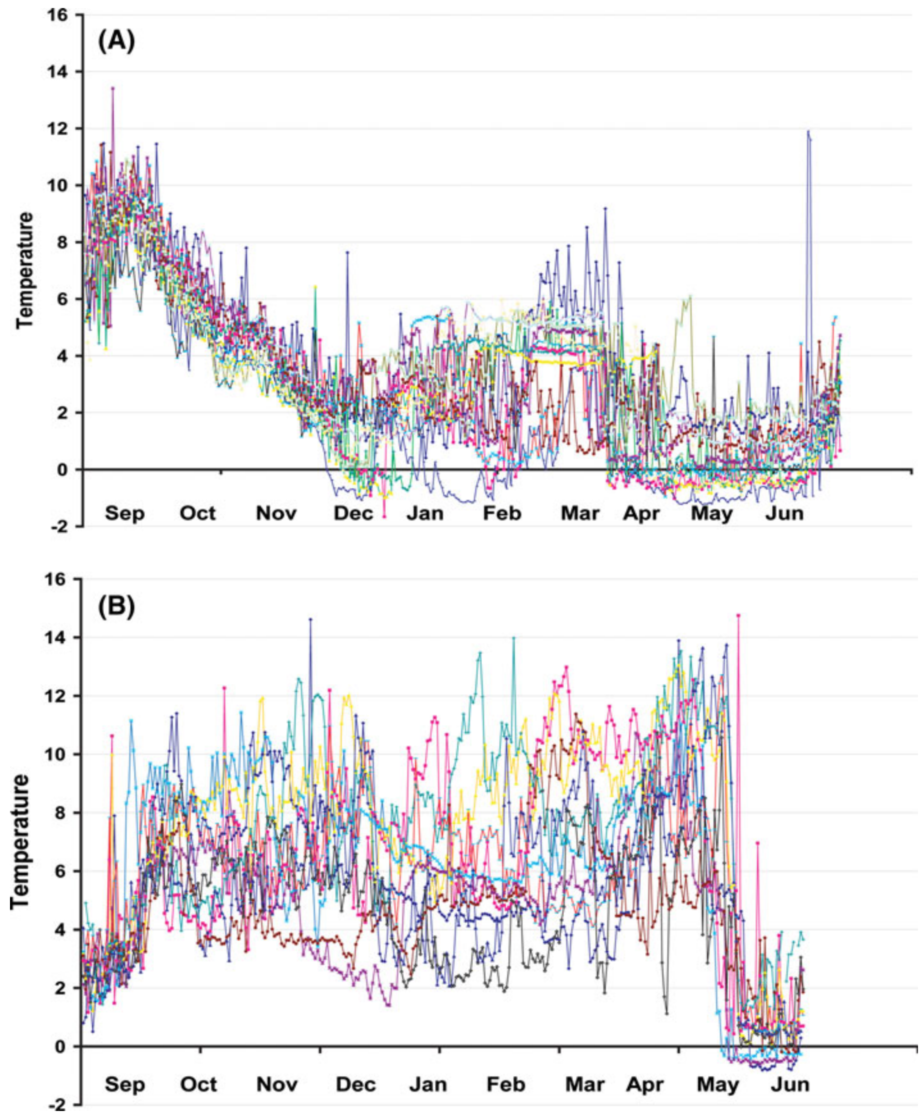

Fig. 5 Mean daily night temperatures (midnight-05:00 h) for individuals from (**a**) Coats Island; (**b**) The Minarets. Each *line* represents one bird

March–17 April indicates a rapid movement into colder water during that period, presumably corresponding with arrival in or close to Hudson Strait, a phenomenon obscured by equinox-related inaccuracy in the geolocator data.

Night temperatures from loggers on Minarets birds showed a sharp increase to ~6–9°C between 21 August and 5 September (Fig. 5b). Temperatures remained similar or increased slightly up to the end of November, although one bird, later two, showed temperatures below 4°C. Thereafter, temperatures varied among individuals, with mean temperatures in January ranging from 2.7 to 10.4°C. After 21 April, all temperatures fell to below 2°C by 6 May, varying thereafter but remaining below 4°C through to June. The steep temperature changes in late April corresponded with the period of northward migration.

Discussion

Logger effects and methodological limitations

The proportion of birds recaptured at Coats Island (85%) was similar to the proportion of banded birds resighted annually at this colony (annually survival range 84–100%, AJG and PAS unpubl data). One more bird was captured the following year; hence, the overall survival rate from August 2007–July 2008 was >90%, which is comparable with the long-term average for unequipped adults (Wiese et al. 2004). All birds recaptured at Coats Island had eggs, suggesting that any handicap imposed by the loggers was insufficient to prevent breeding. This information was not obtained at the Minarets, but it is generally difficult to catch birds without eggs or chicks so probably most birds recaptured had been successful in breeding to that point.

The apparent bias in latitude estimates for longer periods around equinoxes than the 3–4 weeks noted in other studies (e.g., Phillips et al. 2007) could have resulted from shading of the logger sensors or light attenuation underwater around dawn and dusk. The effect of errors in recorded day length on latitude estimation attenuates away from the equinoxes, as the influence of latitude on day length increases (Hill 1994). Although consistently shortened day-lengths would in theory result in all winter records being displaced to the north of their true position, movements of Coats Island birds during migration fell within or close to the expected migration corridor through the Hudson Strait, which is only 2°–3° of latitude in width. This observation suggests that bias in November and December was small. Likewise, the close correspondence between the fall in SST in northern Hudson Bay during August–December and the trend in Coats Island logger temperatures over the same period suggests that nighttime logger temperatures were a good indicator of SST.

To date, most studies using geolocation loggers have involved birds that travel over much longer distances than those in this study (e.g., Phillips et al. 2006; Gonzalez-Solis et al. 2007; Guilford et al. 2009; Stutchbury et al. 2009). An exception is the study of Atlantic Puffins by Harris et al. (2010). The smaller scale of movements involved in our study meant that the inherent error in geolocation had greater impact on our results, especially on latitude estimation outside the main equinox periods. However, given that Coats Island birds accurately traced the course of Hudson Strait on passage in both directions, that activity centres were stable for most of the winter and that estimated dates of return to the vicinity of colonies based on location data were as expected for the population as a whole, we can be confident that the broad patterns described are representative of the birds' wintering movements and distributions.

Migration

Our results demonstrated very different migration strategies for the two populations. Murres from The Minarets moved south rapidly after the completion of breeding (probably by about 20 August; Gaston and Smith 1987, AJG unpubl. data), whereas birds from Coats Island initially moved west into northwestern Hudson Bay and then shifted eastward as ice cover began to develop in the northwest part of the Bay. Following a fairly rapid movement through Hudson Strait between mid-November and early December, the distribution of most birds remained centred in the northern Labrador Sea or southern Davis Strait throughout the winter.

The coincidence of dates of departure and arrival in Hudson Bay with dates of freeze-up and breakup of sea ice in Hudson Bay and Hudson Strait was striking. The mean date of movement through Hudson Strait (26 November–2 December) was the period during which >90% ice cover formed across the western mouth of Hudson Strait and open water on the east coast of the Bay became disconnected from open water in Hudson Strait. Likewise, in spring, the period of mean westward passage through Hudson Strait (27 April–1 May) coincided with, or slightly preceded, the opening up of open water in Hudson Strait and limited areas in northeastern Hudson Bay (Fig. 1). These results suggest strongly that Coats Island murres devote as much time as possible to feeding within Hudson Bay, entering and departing in response to prevailing ice conditions. Observations in earlier years suggested that murres arrived at the Coats Island colony in mid-May (AJG unpubl data). The geolocator results point to similar timing in 2008. The immersion data suggested first arrival on land about 16 May (AJG and PAS unpubl data). The timing of breeding at Coats Island has been shown to be related to spring ice breakup in Hudson Bay (Gaston and Hipfner 1998). Our results suggest that this may, in part, be determined by the availability of open water on the migration route through Hudson Strait.

Conversely, murres from The Minarets moved rapidly away from the area of the colony immediately after breeding, approximately 2 months before the start of ice formation in Davis Strait, moving south to waters off southern Labrador and Newfoundland by September, and remaining thereafter at latitudes where they would probably not encounter sea ice until December at the earliest. Night temperature records in winter suggested that most birds were in water with SST in the range 5–10°C throughout. Comparison with satellite SST mapping suggests that it is unlikely that any birds in water >5°C SST would have been on the Newfoundland shelf, confirming the geolocator results. In contrast, in spring, as birds from The Minarets approached the colony, they moved well inside the limit of 90% ice cover in May, presumably making use of small areas of open water available in mobile pack ice. At this time, temperature records were 0°C or colder (Fig. 5b). Autumn migration for this population must be initiated by some cue other than ice conditions. An intermediate movement appears to have occurred during the vernal equinox period, because activity centres in mid-April were much more dispersed than during winter, with individual females spread in a broad arc from south of Newfoundland to south of Greenland. This early spring dispersal has not been described previously. The data indicate a similar spreading out of Coats Island females in April although, with one exception, all were considerably farther north.

Comparison with banding data

Prior to this study, information on movements of murres from Coats Island was available from the banding of nestlings and adults carried out during 1981 and 1984–2002. This effort provided 109 encounters of birds banded as breeders or banded as nestlings and encountered at breeding age (4th winter or older; Gaston and Robertson 2010). Results were summarized by Gaston (1980), Donaldson et al. (1997) and Gaston et al. (2008). Most encounters (85%) came from Newfoundland and Labrador, where widespread hunting occurs during the winter (Elliot 1991; Chardine et al. 2008; Montevecchi et al. 2007). Recoveries of birds of breeding age mainly occurred in Newfoundland in late winter (February–March; Donaldson et al. 1997). Previous studies assumed that older birds either remained north of Newfoundland or kept well offshore, as hunting occurs mainly within a few kilometres of shore (Elliot 1991). Based on the geolocator results, it seems that most adult birds from Coats Island did not reach Newfoundland waters in the winter of 2007–2008 and this may be typical of adults, as it is consistent with the low recovery rates of adults banded at Coats Island (<0.1% in most years between 1997–2006; Gaston and Robertson 2010).

Observations of Thick-billed Murres at sea in Hudson Strait suggested that birds originating from the large colony at Digges Sound, at the northwest tip of the Ungava Peninsula, moved through Hudson Strait soon after departing from the colony in mid-August (Gaston 1982; Brown 1986). For that reason and because the earliest reports of banded first-year birds off Newfoundland are in October (Donaldson et al. 1997), it had been assumed previously that birds from Coats Island left Hudson Bay in September (Gaston 1980). Consequently, our finding that the exodus of Coats Island breeders from Hudson Bay occurred only after mid-November was unexpected.

A small number of murres of breeding age from Coats Island have been recovered in Greenland ($N = 16$), where there is extensive hunting for Thick-billed Murres along the entire west coast (Falk and Durinck 1992). The ratio of Greenland-to-Newfoundland encounters has increased over the past 25 years: during 1982–1995, only one encounter was reported from December–April, whereas an additional five encounters have been reported subsequently, suggesting that more birds may be spending late winter close to Greenland in recent years (AJG unpubl data). The geolocator results confirmed that Coats Island birds occur regularly off southwest Greenland in winter and spring.

Wintering habitat

Another novel finding for the Coats Island birds was the proportion wintering relatively far north, in southern Davis Strait and between the mouth of Hudson Strait and southern Greenland. Several of the mean January and February locations were within areas judged to be >90% ice covered based on ice maps. According to ice-anomaly charts (NSIDC), ice concentrations in this region were greater in February 2008 than the 1979–2000 norm. Consequently, it is unlikely that birds were using that area because of unusually light ice conditions, and there is no reason to regard this wintering behaviour as atypical.

Depth loggers placed on birds during the breeding season suggest that foraging is restricted to shallow depths after the end of civil twilight in the evening and ceases altogether at approximately the end of nautical twilight, resumes only after the onset of nautical twilight in the morning, and is depth restricted until the end of civil twilight (Croll et al. 1992; Elliott and AJG unpubl. data). At the latitude of the northernmost December locations (64°N) at the winter solstice, the period of civil twilight plus daylight is 6.7 h and nautical twilight an additional 2.3 h. As murres are visual hunters (Gaston and Hipfner 2000), birds wintering at the highest latitudes observed in our study would have had only 9 h of light in which to forage, including a 2.3-h period when diving depth would be restricted. This observation adds to previous evidence that light conditions place significant constraints on seabirds wintering at mid to high latitudes (Daunt et al. 2006; Fort et al. 2009).

Our study provides the first information on the movements and winter distribution of birds from The Minarets. We found a rapid southward movement post-breeding, with some birds of both sexes apparently wintering in continental shelf waters off Newfoundland, while another group was centred well outside continental shelf waters, mid-way between Newfoundland and southern Greenland. Many of the mean locations were outside the area previously covered by published shipboard surveys. Likewise, according to ice maps (NSIDC), they were well beyond the limit of sea ice at that date. The locations, as well as the temperature records, suggest (contra Gaston and Hipfner 2000) that Thick-billed Murres are not tied either to continental shelf and slope waters or to partial sea-ice cover, during the non-breeding season, but may be totally pelagic in their distribution at that time.

Our results provide information on colony-specific habitat requirements throughout the year, essential for understanding the potential effects of increased shipping and industrial development in Arctic waters. Based on a relatively small sample of individuals, we show that wintering areas of Thick-billed Murres from eastern Canadian colonies may be strongly segregated, confirming the tentative conclusions of Donaldson et al. (1997). Moreover, habitat preferences differed, with all Coats Island birds wintering close to pack-ice, whereas most birds from The Minarets wintered outside the normal limits of pack-ice. The timing of southward migration differed between the two colonies by almost 3 months so that birds from The Minarets spent nearly 8 months in Subarctic or Boreal waters, mostly far offshore in the northwestern Atlantic, whereas those from Coats

Island spent 7 months within the relatively enclosed and seasonally ice-covered waters of Hudson Bay and Hudson Strait. This difference has the implications for many aspects of their biology and conservation: temperature differences in the winter range are likely to affect physiological demands and energy budgets (Fort et al. 2011), while the effects of climate change will differ between regions (Parry et al. 2007). In terms of management of the Thick-billed Murre population in the Northwest Atlantic, our results suggest strongly that different colonies may be exposed to different levels of anthropogenic risk, as most threats from human activities (hunting, bycatch, oiling and other forms of contamination) are currently greatest in the southern parts of the wintering range. Differences between colonies will need to be considered in future management actions.

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Appendix

See Table 1.

Table 1 Key dates for the movements of geolocator-equipped birds from Coats Island (a) and The minarets (b)

Logger #	Sex	Location	Passed 77°W	Passed tip of labrador	Passed 52°N	Passed 52°N	Passed 77°W	Days through strait fall	Days through strait Spring	Time in hunt area
a										
4236	F	Coats Island	11-Nov	19-Nov	22-Dec	5-May	12-May	8	3	135
4239	M	Coats Island	14-Dec	21-Dec	*25-Mar*	*30-Mar*	7-May	7	9	*5*
4247	F	Coats Island	3-Dec	6-Dec	*29-Mar*	*30-Mar*	30-Apr	3	2	*1*
4252	M	Coats Island	10-Dec	20-Dec	*29-Mar*	*30-Mar*	5-May	10	5	*1*
4256	M	Coats Island	19-Nov	22-Nov	*25-Mar*	10-Apr	26-Apr	3	7	*16*
5219	M	Coats Island	9-Dec	18-Dec	28-Mar	3-Apr	1-May	9	2	6
5222	M	Coats Island	9-Dec	15-Dec	Never	Never	21-Apr	6	4	0
5223	F	Coats Island	10-Dec	19-Dec	*27-Mar*	15-Apr	25-Apr	9	6	*19*
5224	M	Coats Island	10-Nov	17-Nov	*28-Feb*	*28-Feb*	8-May	7	7	*0*
5226	F	Coats Island	6-Nov	11-Nov	22-Dec	25-Mar	5-May	5	2	94
5228	F	Coats Island	17-Nov	20-Nov	7-Dec	10-Apr	26-Apr	3	2	125
5234	F	Coats Island	6-Dec	9-Dec	9-Apr	22-Apr	4-May	3	3	13
5235	M	Coats Island	3-Dec	8-Dec	*27-Mar*	*30-Mar*	30-Apr	5	2	*3*
5237	M	Coats Island	9-Nov	11-Nov	*26-Feb*	11-Apr	29-Apr	2	3	*45*
5238	M	Coats Island	3-Dec	6-Dec	14-Apr	14-Apr	30-Apr	3	2	0
5241	M	Coats Island	10-Nov	7-Dec	Never	Never	8-May	27	5	0
5245	F	Coats Island	27-Nov	28-Nov	*26-Mar*	*27-Mar*	3-May	1	1	*1*
MEAN	–	Coats Island	26-Nov	2-Dec	5-Mar	4-Apr	1-May	6.5	3.8	27.3
STERR	–	Coats Island	3.3	3.5	11.4	4.0	1.4	1.5	0.6	11.3
RANGE	–	Coats Island	38	40	129	67	21	26	8	135

Logger #	Sex	Location	Passed 62°N	Passed 52°N	Passed 52°N	Passed 62°W	Time in hunt area	Colony dept until <62°N
b								
5250	F	Minarets	31-Aug	3-Sep	2-May	4-May	242	2
5255	F	Minarets	27-Aug	31-Aug	30-Apr	5-May	243	2
4254	M	Minarets	31-Aug	5-Sep	19-May	21-May	257	–
5251	M	Minarets	25-Aug	*23-Oct*	2-May	4-May	*192*	8

Table 1 continued

Logger #	Sex	Location	Passed 62°N	Passed 52°N	Passed 52°N	Passed 62°W	Time in hunt area	Colony dept until <62°N
5243	F	Minarets	22-Aug	25-Aug	21-Apr	26-Apr	240	2
5240	F	Minarets	31-Aug	6-Sep	22-Apr	29-Apr	229	2
5247	F	Minarets	1-Sep	*20-Oct*	5-Apr	5-May	*168*	8
5259	F	Minarets	29-Aug	31-Aug	2-May	9-May	245	3
4241	F	Minarets	31-Aug	5-Sep	14-May	19-May	252	–
5236	F	Minarets	27-Aug	29-Aug	4-May	10-May	249	2
4253	M	Minarets	30-Aug	4-Sep	27-Apr	8-May	236	–
4243	F	Minarets	27-Aug	1-Sep	21-Apr	27-Apr	233	–
5242	F	Minarets	31-Aug	1-Sep	1-May	5-May	243	2
5244	F	Minarets	29-Aug	2-Sep	28-Apr	30-Apr	239	0
MEAN	–	Minarets	28-Aug	8-Sep	29-Apr	5-May	233.4	3.1
STERR	–	Minarets	0.8	5.1	2.9	2.0	6.7	0.9
RANGE	–	Minarets	10	59	44	25	89	8

Dates in italic were affected by the equinox uncertainty

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