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Arctic sea ice a major determinant in Mandt's black guillemot movement and distribution during non-breeding season

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Mandt's black guillemot (*Cepphus grylle mandtii*) is one of the few seabirds associated in all seasons with Arctic sea ice, a habitat that is changing rapidly. Recent decreases in summer ice have reduced breeding success and colony size of this species in Arctic Alaska. Little is known about the species' movements and distribution during the nine month non-breeding period (September–May), when changes in sea ice extent and composition are also occurring and predicted to continue. To examine bird movements and the seasonal role of sea ice to non-breeding Mandt's black guillemots, we deployed and recovered ($n = 45$) geolocators on individuals at a breeding colony in Arctic Alaska during 2011–2015. Black guillemots moved north to the marginal ice zone (MIZ) in the Beaufort and Chukchi seas immediately after breeding, moved south to the Bering Sea during freeze-up in December, and wintered in the Bering Sea January–April. Most birds occupied the MIZ in regions averaging 30–60% sea ice concentration, with little seasonal variation. Birds regularly roosted on ice in all seasons averaging 5 h d^{-1}, primarily at night. By using the MIZ, with its roosting opportunities and associated prey, black guillemots can remain in the Arctic during winter when littoral waters are completely covered by ice.

1. Introduction

While the Arctic supports a large and diverse marine avifauna in summer, most seabirds migrate south in autumn as several million square kilometres of sea ice growth reduces the amount of ocean available for foraging in winter. Only two seabird species have their migrations and winter distributions determined by the formation and presence of Arctic sea ice, the high Arctic populations of black guillemot (*Cepphus grylle*) and the ivory gull (*Pagophila eburnea*) [1]. Black guillemots in the western Arctic are in the subspecies *mandtii* [2], thought to have occupied a high Arctic refugium in the last glacial maximum [3] with geographical variation in the mitochondrial DNA of our study population on Cooper Island reinforcing that view [4]. Black guillemots are pursuit diving piscivores that in the Beaufort and Chukchi seas prey heavily on Arctic cod (*Boreogadus saida*) [5–7], the primary fish species associated with Arctic sea ice [8]. Black guillemots have been observed in the Alaskan Arctic at the ice edge during autumn [6], and as far north as Pt. Barrow [9] and as far south as the ice edge in the Bering Sea [10] during winter, but nothing has been documented about non-breeding habitat use, movements and regional distributions.

Arctic sea ice has been decreasing significantly in recent decades with complete loss in summer possible for mid-century [11], so it is important to document use of sea ice by one of the few Arctic avian 'sea ice obligates'. To this end, we deployed light-sensitive geolocators and data loggers on breeding

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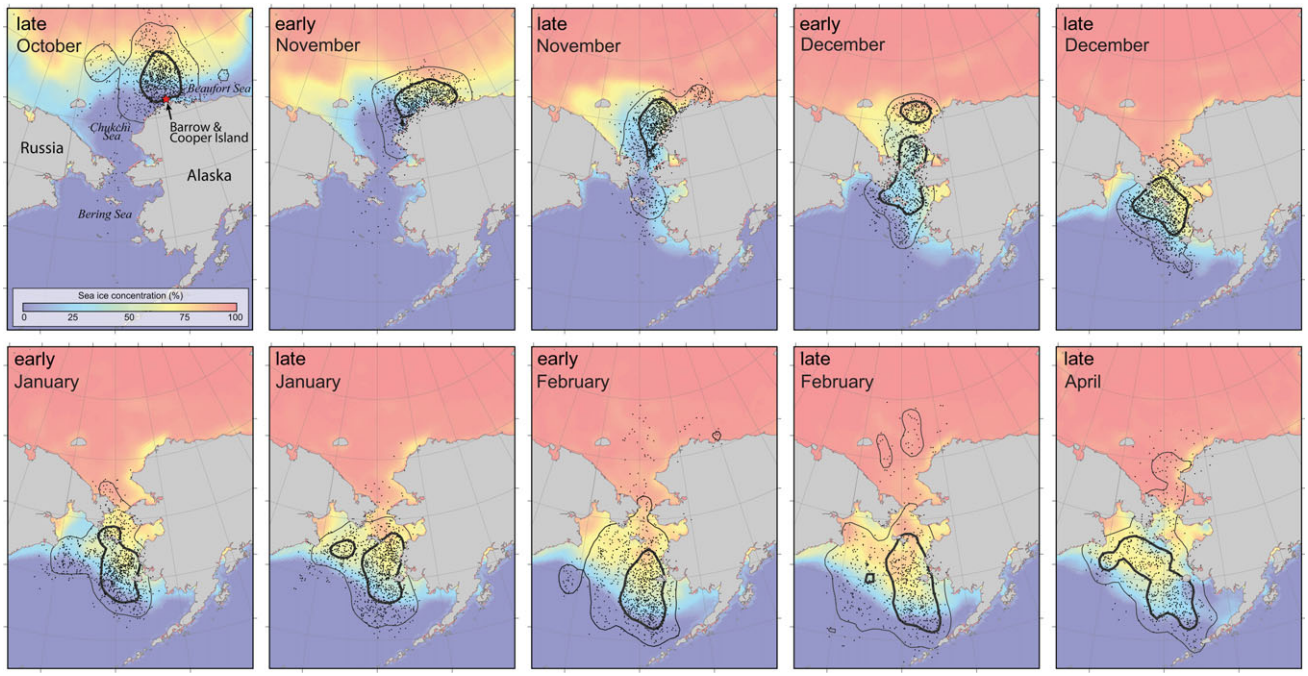

Figure 1. Pooled locations (dots) of adult Mandt's black guillemots ($n = 45$) in twice-monthly periods during four non-breeding seasons (2011–2015) with average sea ice concentration during the same periods. Polygons depict 90% (thin) and 50% (thick) utilization distributions. Birds were tagged with geolocators at their Cooper Island breeding colony near Barrow, Alaska.

black guillemots at the Cooper Island colony to extend our knowledge of the subspecies during the non-breeding period.

2. Material and methods

Geolocators were deployed and retrieved at Cooper Island, Alaska (71°20′ N, 155°41′ W, figure 1). Breeding black guillemots were fitted with 1 g geolocators near the end of four breeding seasons, 2011–2014, and retrieved the following year. We used British Antarctic Survey (Cambridge, UK) units (Mk13 or Mk14) in 2011–2012 and Migrate Technology (Cambridge, UK) units (C-65) in 2013–2014. We attached the geolocator to a plastic leg band on the bird's tarsus with a cable tie. The number of geolocators deployed annually were 6, 9, 26 and 18; with 5, 7, 23 and 10 retrievals, respectively.

We derived noon and midnight positions based on sunset and sunrise times estimated from light intensity levels that were sampled every 60 s with maximums stored every 5 min. We used Intiproc software (Migrate Technology) to estimate latitude, based on day length and longitude, based on time of midday with respect to GMT. Black guillemots sometimes roosted on sea ice near the time of sunrise and sunset, obscuring the light sensor and preventing reasonable position estimates. We excluded estimates before 16 October and between 1 March and 15 April, because latitudes are unreliable around the vernal and autumnal equinoxes, and after 1 May, because birds were moving northward into areas with near 24 h of daylight. After exclusions, we used 1334, 1855, 4993 and 2564 position estimates for analysis of the four non-breeding periods, respectively.

We used the kernelkcbase function in the R library adehabitatHR [12] with a 150 km smoothing parameter to generate twice-monthly utilization distributions (UDs) on a fixed 50 km resolution grid. Twice-monthly UDs were computed with all years pooled, and for individual years. We used the pooled UDs to map generalized movements, and the year-specific UDs to calculate average sea ice concentration [13] within 50% UD contours during the period of occupancy and ± one month.

We used wet/dry logs from Migrate Technology geolocators to investigate time spent out of water, diurnally and seasonally. Black guillemots in the western Arctic are regularly seen roosting on sea ice (G. Divoky 2016, personal observation), and we believe dry state to be primarily indicative of roosting although an unknown portion of the dry hours may be of a bird tucking its tarsus and geolocator into its plumage while in the water, as has been observed for other alcids [14]. Loggers interrogated wet/dry state every 30 s and stored cumulative wet-counts every 4 h. We assumed wet/dry state reflected a 30 s period and computed time dry for each 4 h logging period. To examine diurnal variation in time dry, we used mid-time of each 4 h logging period to bin data into four 6 h diurnal periods, starting at 03.00, 09.00, 15.00, 21.00 local time (GMT-10 h). We also partitioned data at monthly scales to examine seasonal variations: post-breeding in the Beaufort and Chukchi seas during September–November, movements to the Bering Sea during December, winter in the Bering Sea during January–March, and initial spring migration during April.

3. Results

(a) Distribution and movements

Black guillemots fitted with geolocators completed breeding between 22 August and 5 September. Although no reliable geolocator locations were obtained until 16 October, sea surface temperature (SST) and wet/dry state in early September indicated birds moved north to the sea ice after departing the breeding colony. The Cooper Island black guillemots undergo a full-body moult immediately after breeding, usually completed by late September off northern Alaska [6], with movements prevented or impaired during flight feather replacement. Post-breeding movements were primarily northward with the majority of black guillemots between 72° and 75° N in late October with some individuals possibly as far north as 77° N.

Westward movement into the Chukchi Sea did not occur until late November as ice covered the Beaufort Sea. Most birds moved into the Bering Sea from late November to late December as the Chukchi Sea became ice-covered. From

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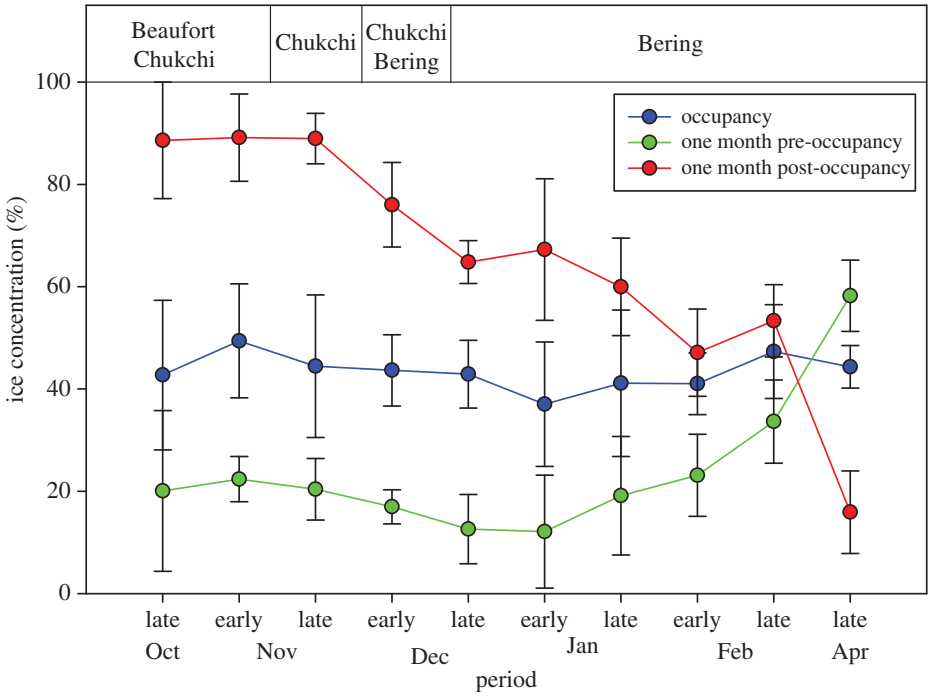

Figure 2. Average sea ice concentration (± 1 s.d.) within annual ($n = 4$ years) twice-monthly 50% utilization distributions (UDs) of Mandt's black guillemots (blue), and within the same UDs one month before (green) and one month after (red) occupancy.

Table 1. Mean hours per day Mandt's black guillemots spend out of water, diurnally and seasonally, during the non-breeding period.

		03.00–09.00		09.00–15.00		15.00–21.00		21.00–03.00		
period	location	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	hours dry
Sep–Nov	Beaufort/Chukchi	1.35	1.56	0.55	0.68	1.37	1.51	1.72	1.86	4.99
Dec	Chukchi/Bering	1.72	2.01	0.52	0.69	1.05	1.48	1.73	2.04	5.02
Jan–Mar	Bering	2.38	2.18	0.47	0.65	1.04	1.35	2.58	2.38	6.47
Apr	Bering	1.28	1.56	0.74	0.90	1.32	1.46	1.79	1.88	5.14
Sep–Apr		1.78	1.94	0.54	0.71	1.20	1.45	2.05	2.13	5.14

January through to April, black guillemots broadly occupied the partially ice-covered Bering Sea shelf, although a few individuals returned to the Arctic Basin in February in some years. Most birds remained in the Bering Sea through late April, when sea ice was rapidly melting and retreating. A directed migration northward out of the Bering Sea occurred in late April and early May when large numbers of black guillemots begin to stage in open water leads off Pt. Barrow before returning to Cooper Island in early June (C. George 2015, personal communication.).

(b) Ice habitat

Black guillemots occupied sea ice habitat in the marginal ice zone (MIZ) during the entire non-breeding period (figure 2). While sea ice was forming during October to late February, birds consistently occupied broad areas where the mean ice concentration was 43% (s.d. 9.8), averaging 20% more than a month earlier and 20% less than a month later. In April, with sea ice melting and retreating, this pattern reversed and birds continued to occupy regions with similar ice concentrations by moving north into areas that earlier had had more ice. SST data loggers in the 2013 and 2014 deployments showed birds moved from relatively warm waters (more than 3°C) near the colony to waters averaging less than 1°C (i.e. near sea ice) for the remainder of the non-breeding period.

(c) Behaviour

Black guillemots averaged over 5 h per day out of water throughout the non-breeding period (table 1). Most time out of water involved night-time roosting on sea ice, with an average of 3.8 h dry from 21.00 to 09.00 (GMT-10 h), and less than 1 h from 09.00 to 15.00. Seasonal variation was low with the exception of January–March in the Bering Sea when birds spent almost 1.5 h more out of the water than the other three seasonal periods.

4. Discussion

Our study provides, to our knowledge, the first detailed information on movements and habitat use of one of the Northern Hemisphere's most northerly wintering seabirds and a truly pagophilic population adapted to occupy Arctic sea ice habitats

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throughout the year. Most members of the genus *Cepphus* inhabit near shore littoral waters in breeding and non-breeding seasons [15], where they use a prey base that is more predictable, less patchy and at shallower depths, while maintaining access to coastal roosting sites. In regions where the littoral zone is ice-covered for much of the year, pelagic sea ice offers a proxy to coastal habitat by providing sympagic fauna and a roosting substrate. Mandt's black guillemot probably became adapted to sea ice habitats when restricted to an unglaciated but ice-covered refugium in the Arctic during the last glacial maximum [4], and the observations presented here demonstrate a continued association with that habitat.

The physical and biological changes associated with sea ice formation and melt are the primary factors influencing black guillemot movements in the western Arctic. Migration in the non-breeding period was primarily facultative, being correlated with the advancement of sea ice. Interannual movements responded to short-term variations (i.e. $\pm$ two weeks) in sea ice distribution that were averaged in figure 1. While unpredictable annual and seasonal variation in prey availability is the primary stimulus for most facultative movements in birds [16], the southward movements appeared not to be limited solely to prey but in response to the southward shift of the MIZ. Movement related to suitable sea ice habitat and not necessarily prey has been recorded in Antarctic seabirds [17]. It is not known if Arctic cod also move with the advancing ice. Black guillemots prey on Arctic cod at the advancing ice edge in autumn [6,18], and the size and depth of Arctic cod in the Bering are suitable for black guillemots [19]. While Arctic cod or alternative prey may be most available at the ice concentrations favoured by black guillemots in the MIZ, benefits offered by physical ice characteristics may play an important role in habitat preferences. Because black guillemots spend approximately 20% of the day roosting on sea ice, birds may be selecting areas with appropriate ice thickness and concentration for roosting. The benefits of roosting versus sitting on the water are negatively correlated with water temperature, so ice suitable for roosting would be essential when occupying the freezing winter waters of the Bering Sea, as it is for spectacled eiders (*Somateria fischeri*) wintering there [20]. Conditions south of preferred ice may be less optimal for roosting, foraging and protection from storms owing to an abundance of thin frazil ice in low concentrations or competition from seabird species less adapted to sea ice. The observed departure from areas of increasing ice concentration could be in response to decreased foraging opportunities in heavy ice, or to increased risks of occupying areas where open water could rapidly disappear from wind-driven compaction or sudden freezing, which is known to be a source of mortality for wintering black guillemots [21]. While most individuals occupied the MIZ, it is important to note that once ice formation was nearly complete in February, birds broadly occupied much of the Bering/Chukchi shelf with some positioned southerly, whereas others had returned to the Arctic Basin.

Recent losses in summer sea ice have impacted black guillemot breeding success on Cooper Island, owing to diminished accessibility to Arctic cod, but annual adult survival has shown no trend over the past four decades [7] indicating no decadal trend in prey availability in the MIZ. Future changes in Arctic sea ice can be expected to cause major alterations in the distribution and timing of Mandt's black guillemot movements and distribution as summer ice is predicted to disappear and winter ice to greatly decrease in this century [22,23].

Ethics. Animal handling protocols were approved by US Geological Survey (bird banding permit no. 21675).

Data accessibility. Location and wet/dry sensor data are available in the electronic supplementary material.

Authors' contributions. G.J.D. conceived the study assisted by I.J.S. G.J.D. conducted the fieldwork. G.J.D. and D.C.D. performed analyses. All authors wrote the manuscript, approved the final version, and agree to be held accountable for the manuscript's contents.

Competing interests. We have no competing interests.

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