

1 Introduction

The Bering Sea is a productive marine ecosystem (Springer et al., 1996; Grebmeier, 2012) that supports immense populations of diverse marine fauna (Highsmith and Coyle, 1990; Piatt and Springer, 2003; Aydin and Mueter, 2007; Grebmeier, 2012). Sea-ice cover has been decreasing in duration and concentration over the southeastern Bering Sea shelf (Post et al., 2013), which influences the temperature of the water column in the region, including the extent of the “cold pool” (Stabeno and Overland, 2001; Overland and Stabeno, 2004; Sarmiento et al., 2004; Stabeno et al., 2007; Steele et al., 2008). Such shifts in the physical environment have been shown to affect the ecosystem, including the seasonality and biomass of primary production, metabolic rates, distribution, and abundance of consumers, and changes in pelagic–benthic coupling (Grebmeier et al., 2006; Mueter and Litzow, 2008; Hunt et al., 2011; Wassmann, 2011; Wassmann et al., 2011; Dorresteyn et al., 2012). The Bering Sea is a transition region between Arctic and sub-Arctic seas, and, hence, physical and biological changes in this region may also influence the extent of sea-ice cover and species abundance and composition in the adjacent Arctic Sea (i.e. the Chukchi Sea, Shimada et al., 2006; Matsuno et al., 2012; Yamamoto et al., 2015).

Predicting the effects of climate change on marine top predators is a major challenge in ecology. Long-term monitoring of seabird demography has been conducted on the Pribilof Islands (Byrd et al., 2008a; Renner et al., 2012; Mudge et al., 2015), which host one of the largest concentrations of piscivorous seabirds in the North Pacific. Previous studies have demonstrated that historical fluctuations in productivity (i.e. reproductive success) and the diet of seabirds (Byrd et al., 2008a; Sinclair et al., 2008; Renner et al., 2012) might reflect broad-scale changes in climate (e.g. regime shift: Benson and Trites, 2002), but the mechanistic response of seabirds to local climate variability has been elusive. Although some studies found relationships between climate variables and seabird productivity (e.g. Sydeman et al., 2012), others suggested only weak relationships (Byrd et al., 2008b; Satterthwaite et al., 2012; Renner et al.,

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2014). This weak relationship is probably due, in part, to reproductive failure that may occur at several stages of the breeding process (e.g. nest building, egg-laying, incubation, and chick-rearing). It may also be influenced by reproductive effort associated not only with foraging conditions in the current season, but also those during the previous breeding season (Harrison et al., 2011; Catry et al., 2013). Furthermore, seabirds can adapt their behaviour by increasing foraging range and effort in response to changes in the environment, potentially masking effects on some breeding parameters (Kitaysky et al., 2000; Pinaud et al., 2005; Harding et al., 2007). To obtain more direct insight into their responses to ecosystem dynamics in relation to climate variability, at-sea foraging behaviour of breeding seabirds should be examined in concert with their physiological condition (i.e. nutritional stress as reflected in secretion of corticosterone), as elevated corticosterone levels indicate high reproductive effort and increased post-reproductive mortality (Kitaysky et al., 2010; Satterthwaite et al., 2010). However, there is little information available for the comparative at-sea behaviour of seabirds in relation to inter-annual climate variability in this region (Kokubun et al., 2010; Paredes et al., 2014).

Ship-based observations can provide information on at-sea habitat utilization of species (Hunt et al., 2008, 2014; Kuletz et al., 2014; Wong et al., 2014) together with oceanographic characteristics (Piatt and Springer, 2003; Gall et al., 2013). Although these studies are valuable to detect seasonal, annual, and decadal changes in species distributions (Hunt et al., 2014; Kuletz et al., 2014; Gall et al., 2013), spatial and temporal coverage as well as the context of reproductive processes studied at colonies are limited. The recent availability of animal-borne devices enhances our ability to examine habitat utilization of free-ranging individuals (review by Burger and Shaffer, 2008), and may provide more insight into population processes in relation to ocean variability (Weimerskirch et al., 2001; Paredes et al., 2014).

In this study, we examined the foraging behaviour of two seabird species that exhibit different habitat use: surface-foraging red-legged kittiwakes *Rissa brevirostris* (hereafter, RLKI) feeding in the oceanic habitat and pursuit-diving thick-billed murre *Uria lomvia* (TBMU) feeding mainly in the continental shelf habitats, and how they re-

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sponded to changes in environmental conditions over two years. The effects of ocean variability on an ecosystem may differ between water masses, and, hence, seabird responses may show different patterns (Benowitz-Fredericks et al., 2008; Byrd et al., 2008b), which, in turn, could provide information on how ecosystem dynamics respond to fluctuations in marine environmental conditions (Frederiksen et al., 2007; Piatt et al., 2007).

2 Materials and methods

2.1 Study site

Fieldwork was conducted on St. George Island (56°34' N, 169°37' W) in the Pribilof Islands, Alaska, USA, over two years in July–August 2013 and 2014. Birds were captured from their nesting sites using a noose pole, and GPS loggers (GiPSy-2 with chip antenna or GiPSy-4 with patch antenna: TechnoSmart, Rome, Italy) were attached to the backs of 19 RLKI and 11 TBMU in 2013 and 14 RLKI and 14 TBMU in 2014 using Tesa® tape and cyanoacrylate glue (Loctite® 401). The loggers were housed in heat-shrink tubing for water-proofing. The total weight of the logger including the heat-shrink tubing and tape was 15.1–16.3 g, which corresponds to less than 5% of the mean body mass of equipped birds (the mean ± SD: RLKI 375.3 ± 29.0 g, TBMU 1024.0 ± 43.0 g). The loggers were set to record five fixes every min for GiPSy-2 and one fix every min for GiPSy-4.

The equipped birds were recaptured after 2–6 days since the deployment, and the loggers were recovered. We retrieved the loggers from 15 RLKI and 9 TBMU in 2013 and 10 RLKI and 11 TBMU in 2014, representing 71–82% recovery rate. Of the loggers retrieved, some failed to record locations. Hence, location data were available for 5 and 7 RLKI and 5 and 10 TBMU in 2013 and 2014, respectively. Data for RLKI in 2013 were reanalyzed from Kokubun et al. (2015). At the time of recapture, blood samples were taken from the brachial vein of each individual, and kept on ice until centrifugation to

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separate the plasma from the red blood cells, and both were kept frozen until assayed. Plasma was used for measurement of physiological stress exposure (corticosterone: CORT) and red blood cells for determining trophic level (stable isotopes: SI). CORT was measured only for samples that were taken within 3 min of capture, as it takes 3 min for levels of CORT to begin to rise in the blood in response to the acute stress of capture and restraint (Romero and Reed, 2005).

During the study period, we opportunistically obtained adult diets of RLKI by regurgitation at the time of logger deployment and/or retrieval. Prey species of RLKI samples were identified visually or using otoliths ($N = 22$ in 2013 and $N = 15$ in 2014) (also see Kokubun et al., 2015). TBMU chick diet was recorded from direct observation of adult birds (both with and without data loggers) carrying prey items back to their nests in their bill. Prey items were visually identified during observation or later from photographs ($N = 13$ in 2013 and $N = 39$ in 2014).

2.2 Data analysis

GPS locations were re-sampled every 1 min by averaging fixes recorded within each min for GiPSy-2. We used a forward-backward speed filter (McConnell et al., 1992), and positions that exceeded 20 m s^{-1} were considered erroneous and removed (Paredes et al., 2012; Evans et al., 2013). We defined foraging trips as any time period when the birds beyond a 500 m buffer around the colony for more than 30 min. We determined locations of resting on water (as a proxy for foraging) during foraging trips based on flight speed (Zavalaga et al., 2011; Kokubun et al., 2015). Flight speed less than 3 m s^{-1} for RLKI (Paredes et al., 2012) and 5 m s^{-1} for TBMU (Evans et al., 2013) were considered “resting on water.” The straight-line distances between the colony and on-water locations were measured, as were the bottom depths where the birds were resting on the water. The marine habitats were categorized into three regions based on bathymetry as follows; on-shelf (0–200 m bottom depth), shelf break (200–1000 m bottom depth), and oceanic basin (> 1000 m bottom depth, Paredes et al., 2012).

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To examine the differences in marine environment between the two study years (2013 vs. 2014), satellite remote-sensed monthly mean sea surface temperatures in August (SST: NOAA POES AVHRR, GAC, 0.1° degree) within 350 km around the colony (within the foraging ranges of RLKI and TBMU; see Results) and the timing of sea ice retreat in the southeastern Bering Sea (a Bering Sea Ice Retreat Index: IRI) were obtained from the National Oceanic and Atmospheric Administration (NOAA): available at <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp> for SST and <http://access.afsc.noaa.gov/reem/ecoweb/dataWindow.php?Data=IRI> for IRI. IRI represents the number of days after March 15 in which areal sea ice concentration was greater than 10% in a 2° × 1° box (bounded by 56.5–57.5° N and 163–165° W). Locations and environmental data were analyzed and mapped using the ESRI® ArcGIS.

In addition to the GPS tracking, we also analyzed behavioral data of birds obtained by geolocators (2.5 g, Mk19; Biotrack Ltd., UK) and accelerometers (12 mm diameter × 45 mm length, 10 g, ORI-380 D3GT; Little Leonardo, Japan). As the location records did not cover a complete foraging trip in several GPS tracks (see Results), we used these data to confirm the foraging trip durations in each year supplementarily. For the geocator-carrying birds, the foraging trip duration was defined as the time between the first and last landing on water (i.e. immersion) before and after a long dry event, which is likely an underestimation, though comparable between the years (see Fig. 1 in Supplement A). For the accelerometer-carrying birds, the start and end of a foraging trip was identified from changes in bird posture as well as outward/inward flight activity recorded as cyclic fluctuations of acceleration (see details for Takahashi et al., 2008). Data were analyzed for 22 trips in 2013 and 14 trips in 2014 for RLKI (26 July–2 August) and 9 trips in 2013 and 21 trips in 2014 for TBMU (31 July–12 August).

CORT concentrations were measured for 8 RLKI and 20 TBMU in 2013 and 7 RLKI and 21 TBMU in 2014. CORT concentrations (ng mL⁻¹) were measured using a radioimmunoassay (for details see Kitaysky et al., 1999). Briefly, each sample was equilibrated with 2000 cpm of tritiated CORT prior to extraction with 4 mL re-distilled

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dichloromethane. After extraction, percent tritiated hormone recovered from each individual sample (average hormone recovery was, mean ± SD, 94.68% ± 2.86) was used to correct final CORT concentrations. Samples were reconstituted in phosphate-buffered saline gelatin buffer and combined with antibody and radiolabel in a radioimmunoassay. Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. All samples were analyzed in 2 different assays; CV = 7% for inter-assay and < 2% for intra-assay).

Stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were measured for 8 RLKI and 20 TBMU in 2013 and 7 RLKI and 15 TBMU in 2014 following Hobson (1993) and Barger and Kitaysky (2012). A small portion of freeze-dried samples (0.100–0.400 mg) were placed in a tin capsule, sealed, and deposited in an EA autosampler. The stable isotope data was obtained using continuous-flow isotope ratio mass spectrometry (CFIRMS). The instrumentation used was a Delta + XP interfaced with a Costech ESC 4010 elemental analyzer. Stable isotope ratios are reported in δ (Delta) notation as parts per thousand (‰) deviation from the international standards $\delta^{13}\text{C}_{\text{PDB}}$ and $\delta^{15}\text{N}_{\text{air}}$ according to: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000\text{‰}$, where $R_{\text{sample/standard}}$ is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{14}\text{N}/^{15}\text{N}$. Replicate measurement of an internal laboratory standard (Peptone) indicated measurement errors to be ± 0.16‰ for N and ± 0.13‰ for C. Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility.

2.3 Statistical analysis

Statistical analyses were carried out in R software (version 2.15.3, R Development Core Team, 2008). Differences in foraging parameters (bathymetry and distance from the colony in on-water locations and trip duration) between the years were examined with generalized linear mixed models (GLMM) including bird identity as a random factor. We tested the inter-annual differences in CORT (log-transformed) and SI by conducting

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oceanic basin 10.2 ± 1.0 °C). IRI was 36.7 in 2013 and 0.02 in 2014, representing later sea ice retreat in 2013.

4 Discussion

Surface-feeding RLKI and pursuit-diving TBMU showed differences in habitat use. RLKI foraged extensively over the deep oceanic basin, while TBMU foraged mostly on the shelf. The behavioral and physiological responses to the ocean variability differed between the species. Between the two study years, SST around the colony was cooler in 2013 than in 2014, probably reflecting the later sea ice retreat in 2013 as winter sea ice conditions strongly influence water temperatures during the following summer (Khen, 1999; Overland et al., 1999; Kokubun et al., 2010; Stabeno et al., 2012).

RLKI showed a consistent use of the oceanic habitat with similar levels of CORT in both years, though they reached to relatively farther areas in 2013 than 2014. In comparison, TBMU used the oceanic basin to the south of the colony more frequently in the relatively colder year of 2013, exhibiting relatively farther travel distances and higher levels of CORT. Based on the $\delta^{15}\text{N}$ values (an indicator for trophic level: Hobson et al., 2002) and diet sampling/observation, both RLKI and TBMU probably had similar prey composition between the years. $\delta^{13}\text{C}$ signatures normally decline along the continental shelf-ocean basin gradient (Hobson et al., 1994; Young et al., 2015), however $\delta^{13}\text{C}$ values (also an indicator for origin of prey) were lower when birds were foraging extensively on the shelf, particularly in TBMU. This is possibly due to differences in the influx of oceanic water into the shelf region (Dorresteijn et al., 2012) that might be affected by the strength of oceanic circulation along the Bering Sea basin, for example the Aleutian North Slope Current (ANSC) that flows east along the northern edge of the Aleutian Islands (Ladd, 2014; also see Fig. 1 in Supplement B).

During the study period, the fledgling success of RLKI and TBMU on St. George Island differed between the cold (2013) and warm (2014) years: dramatically, 0.57 in 2013 and 0.92 in 2014 for RLKI, and, less so for TBMU, 0.95 in 2013 and 0.89 in 2014

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(Mudge et al., 2015). Fledgling success may be related to behaviour prior to breeding (i.e. the timing of breeding: Renner et al., 2014), but the hatching date (the mean \pm SD) appeared not to differ between the years for either RLKI (6 July \pm 7.0 days in 2013 and 4 July \pm 4.8 days in 2014) or TBMU (27 July \pm 6.6 days in 2013 and 28 July \pm 7.4 days in 2014) (Mudge et al., 2015). Therefore, the fledgling success during the study period may be related to food resource conditions during the breeding season in the given years, suggesting better conditions in the warm year, 2014, than during the cold year, 2013.

RLKI mainly feed on myctophids over deep oceanic regions (Sinclair et al., 2008; Kokubun et al., 2015). As RLKIs are a surface-feeding seabird, they are considered to feed on vertically migrating myctophids (Hunt et al., 1981). The water column in the deep ocean may show less inter-annual variation in water temperature compared to that of the shallower shelf region (see Results in this study) where the deep cold pool (temperature remains below < 2 °C) forms in relation to the timing of sea ice retreat (Stabeno et al., 2012). Previous studies suggested that the availability of prey for seabirds in shelf habitats may be less stable (Einoder et al., 2011) and less predictable over long-time scales compared to basin habitats (Weimerskirch, 2007). Furthermore, myctophids are supposed to be still available when prey availability over the shelf is low (Sinclair et al., 2008; Paredes et al., 2014). Nonetheless, RLKI showed a slight difference in foraging locations over the oceanic basin between the years, which may be affected by other factors besides SST and IRI (Sinclair et al., 2008). Recently, Paredes et al. (2014) hypothesized that the existence of meso-scale eddies, that typically develop in the Aleutian Basin (Mizobata et al., 2002), may affect the vertical distribution of myctophids for kittiwakes (Godø et al., 2012). The sympatric and closely-related black-legged kittiwake (*Rissa tridactyla*) foraged at locations near the perimeter of anticyclonic eddies (upwelling) and inside or near cyclonic eddies (downwelling), and experienced higher levels of nutritional stress when eddies were weak possibly due to low availability of prey (Paredes et al., 2014). Similarly, RLKI in this study may have altered their foraging locations in relation to the existence of these eddies (Fig. 1 in Ap-

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pendix B). However, it is not certain how distribution and abundance of myctophids are actually related to the strength of eddies, and no correlations were found between eddy kinetic energy and fledging success of black-legged kittiwakes (Paredes et al., 2014). Elevated CORT indicates that birds are consuming less food, lower-quality food, or working harder (Kitaysky et al., 2010), and lower productivity has been reported during cold years in adults of black-legged kittiwakes (Satterthwaite et al., 2012) which appears to coincide with our results (lower fledgling success during a relatively cooler year). However, RLKI exhibited consistently high levels of CORT in both years compared to TBMU. This may reflect potential competition with black-legged kittiwakes that also feed on myctophids in the ocean basin (Sinclair et al., 2008; Renner et al., 2012), especially during cold years (Paredes et al., 2014). This inter-species competition may contribute to the relatively lower fledgling success of RLKI in the cold year, 2013.

Compared to RLKI, TBMU exhibited fluctuating physiological condition and flexible behavioral changes in parallel to the ocean variability between the years, yet without a difference in fledgling success. Late sea-ice retreat is associated with an early, cold-water phytoplankton bloom, relatively low biomass of small shelf copepods, and poor survival of larval and juvenile forage fish, including their main prey (juvenile walleye pollock: Hunt et al., 1996; Sinclair et al., 2008; Renner et al., 2012). On the other hand, early sea-ice retreat is associated with a later, warm-water plankton bloom, a large biomass of small shelf copepods later in the season, and high abundance of larval and juvenile forage fish (Hunt et al., 2002). Moreover, forage fish species including juvenile walleye pollock are less abundant on the continental shelf during cold years because they either disperse or travel deeper to avoid cold waters (Hollowed et al., 2012), as juvenile pollock are associated with warm bottom temperatures (Brodeur et al., 1998). A northern location of the ice edge during spring may be linked to higher SST and water temperature at depth (Kokubun et al., 2010; Stabeno et al., 2012). The cold pool acts as a cross-shelf migration barrier for subarctic fish species (e.g. walleye pollock and Pacific cod), forcing these fish to remain on the outer shelf and separating them from food sources in the middle shelf and coastal domain. Thus, a warmer shelf would provide

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them with a larger area of suitable habitat (Kotwicki et al., 2005; Ciannelli and Bailey, 2005). In addition, distribution and availability of euphausiids and copepods, the prey species for juvenile walleye pollock (Schabetsberger et al., 2000; Ciannelli et al., 2002), likely change in relation to inter-annual differences in water temperatures in the shelf region (Smith, 1991; Ohashi et al., 2013; Yamamoto et al., 2015). Hence, we assume that the abundance/availability of pollock on the shelf was probably relatively higher in 2014, the warmer year. Piscivorous birds breeding on the Pribilof Islands have been shown to experience greater food limitation on the continental shelf during cold years, attributed to higher levels of nutritional stress (Benowitz-Fredericks et al., 2008; Satterthwaite et al., 2012; Harding et al., 2013). The closer proximity of St. George to the continental shelf-break may be considered to be an important buffer in years when food supply on the shelf is poor (Byrd et al., 2008b; Renner et al., 2014). Previous studies showed that TBMU breeding on St. George Island traveled longer distances to forage at the shelf break and the ocean basin in a cold year (Harding et al., 2013). Seabirds are known to increase foraging ranges in response to reductions in prey availability (Suryan et al., 2000; Bertrand et al., 2012; Pinaud et al., 2005; Harding et al., 2007), but longer and farther foraging trips likely cause higher levels of nutritional stress (2013 in this study), especially for TBMU whose flight cost is presumed to be high (Houston et al., 1996).

In this study, chick-rearing RLKI did not change their foraging locations largely in relation to marine environmental changes probably due to their reliance on myctophids, which live in the deep waters of the pelagic zone (Sinclair and Stabeno, 2002), for feeding young (Kokubun et al., 2015). However, their foraging effort might also be affected by the position and strength of local eddies, which are reflected by atmospheric control (the North Pacific Index and Multivariate ENSO Index: Ladd et al., 2012; Ladd, 2014). TBMU showed fluctuations in physiological condition and flexible foraging behavior, which corresponded to ocean variability (longer and farther trips in a cold year). Hence, there might be interspecific differences in these species' response to warming in the Bering Sea, which may reflect differences in ecosystem dynamics between oceanic

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and shelf habitats they use for foraging. Furthermore, elevated stress levels may have a cascading effect on subsequent life stages, such as migration, post-breeding survival, breeding propensity, and timing of breeding (Schoech et al., 2009; Kitaysky et al., 2010; Verhulst and Nilsson, 2008; Goutte et al., 2010; Harrison et al., 2011) and, as a result, overall productivity (Kitaysky et al., 2007, 2010; Renner et al., 2014). We suggest that year-round monitoring of foraging distribution and stress incurred by birds, including those during the post-breeding migration, should be conducted to understand further how these species are affected by changing climate (e.g. Schultner et al., 2014).

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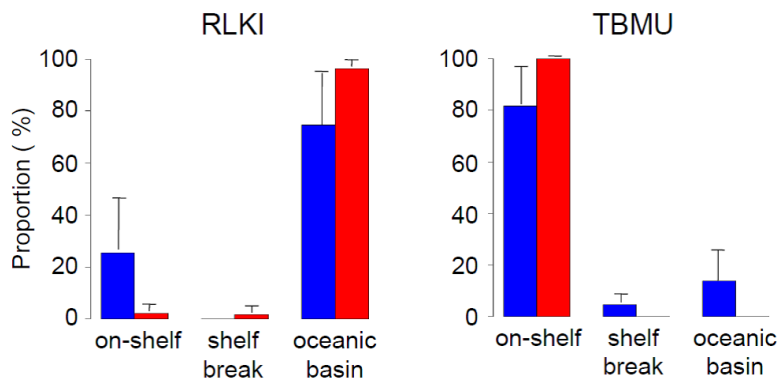


Figure 2. The marine habitats of on-water locations during the foraging trips in red-legged kittiwakes (RLKI), and thick-billed murre (TBMU); on-shelf (0–200 m bottom depth), shelf break (200–1000 m bottom depth), and oceanic basin (> 1000 m bottom depth). Red bars represent 2013 and blue bars in 2014 (the mean and standard error).

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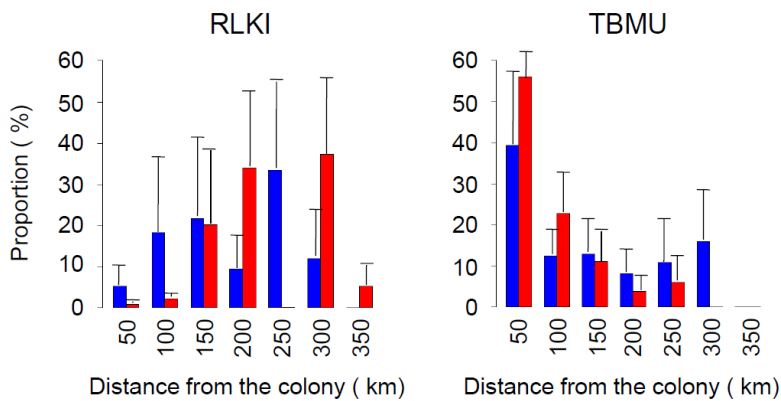


Figure 3. The straight-line distances between the colony and on-water locations of red-legged kittiwakes (RLKI), and thick-billed murre (TBMU) in 2013 (blue bars) and 2014 (red bars). The mean and standard error are presented.

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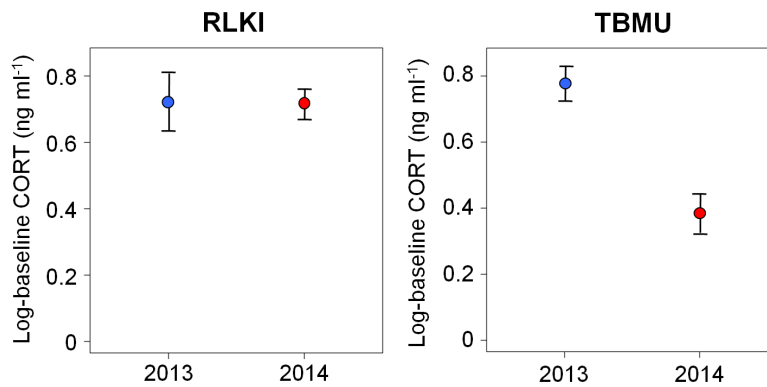


Figure 4. The mean and standard errors in plasma corticosterone concentrations of red-legged kittiwakes (RLKI), and thick-billed murre (TBMU) in 2013 (blue symbol) and 2014 (red symbol).

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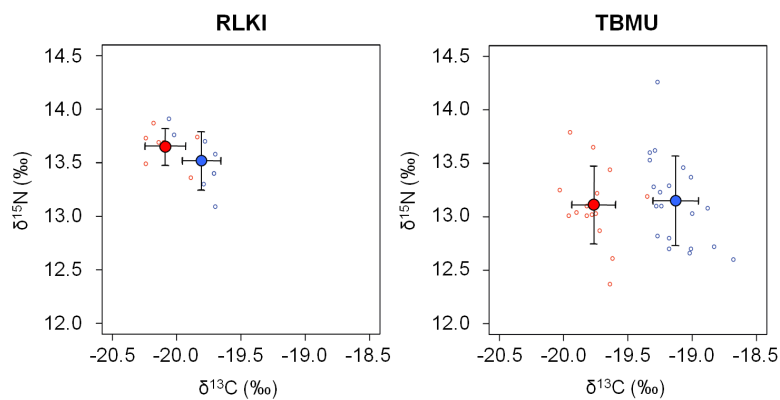


Figure 5. Stable isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of red-legged kittiwakes (RLKI), and thick-billed murre (TBMU) red-blood cells in 2013 (blue open circles) and 2014 (red open circles). The filled circles represent the mean and standard error.

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