Differential responses of seabirds to environmental variability over two years in the continental shelf and oceanic habitats of southeastern Bering Sea

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Abstract

Seasonal sea-ice cover has been decreasing in the southeastern Bering Sea shelf, which might affect ecosystem dynamics and availability of food resources to marine top predators breeding in the region. In this study, we investigated the foraging responses of two seabird species, surface-foraging red-legged kittiwakes *Rissa brevirostris* (hereafter, RLKI) and pursuit-diving foraging thick-billed murres *Uria lomvia* (TBMU) to different marine environmental conditions over two years. At-sea distributions of RLKI and TBMU breeding on St. George Island, the largest seabird colony in the region, were recorded using GPS loggers, and blood samples were taken to examine their physiological condition and isotopic foraging niche in a given year. Between the study years, winter ice retreated earlier and summer water temperatures were relatively warmer in 2014 compared to those in 2013. RLKI foraging occurred mostly over the oceanic basin in both years. TBMU, however, foraged mostly over the shelf, but showed a relatively higher use of the shelf break and oceanic basin in 2013. The foraging distances from the colony peaked at 250-300 km in 2013 and bimodally at 150-250 km and 300-350 km in 2014 for RLKI, and tended to be farther in 2013 compared to those in 2014 for TBMU. Plasma levels of corticosterone did not differ between the years in RLKI, but differed in TBMU, showing higher levels of physiological stress incurred by murres in 2013, the year of relatively cooler sea surface temperatures with later sea ice retreat. $\delta^{13}N$ (a proxy of trophic level of prey) did not differ between the years in either RLKI or TBMU. These results suggest that the response of ecosystem dynamics to climate

variability in the southeast Bering Sea may differ between the ocean basin and continental shelf regions, which, in turn, may generate differential responses in seabirds relying on those habitats for foraging.

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; Dorresteijn 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 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). Although some studies found broad species- and regional-specific relationships between climate variables and breeding parameters (Byrd et al., 2008b), the mechanistic response of seabirds to local climate variability has been elusive and others suggested only weak relationships (Satterthwaite et al., 2012; Renner et al., 2014). This 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). Meanwhile, changes in behaviour and prey availability relating to environmental conditions appear to affect their physiological condition (i.e. nutritional stress as reflected in secretion of corticosterone). For example, piscivorous birds breeding on the Pribilof Islands have

89 been shown to experience greater food limitation on the continental shelf during cold
90 years, attributed to higher levels of nutritional stress (Benowitz-Fredericks et al.,
91 2008; Satterthwaite et al., 2012; Harding et al., 2013). To obtain more direct
92 mechanistic insight into their responses to ecosystem dynamics in relation to climate
93 variability, at-sea foraging behaviour of breeding seabirds should be examined in
94 concert with the physiological condition. However, there is little information
95 available for the comparative at-sea behaviour of seabirds in relation to different
96 environmental conditions in this region (Kokubun et al., 2010; Paredes et al., 2014).
97 Ship-based observations can provide information on at-sea habitat
98 utilization of species (Hunt et al., 2008; Hunt et al., 2014; Kuletz et al., 2014; Wong
99 et al., 2014) together with oceanographic characteristics (Piatt and Springer, 2003;
100 Gall et al., 2013). Although these studies are valuable to detect seasonal, annual, and
101 decadal changes in species distributions (Gall et al., 2013; Hunt et al., 2014; Kuletz
102 et al., 2014), spatial and temporal coverage as well as the context of reproductive
103 processes studied at colonies are limited. The recent availability of animal-borne
104 devices enhances our ability to examine habitat utilization of free-ranging individuals
105 (review by Burger and Shaffer, 2008), and may provide more insight into population
106 processes in relation to ocean variability (Weimerskirch et al., 2001; Paredes et al.,
107 2014).
108 In this study, we examined the foraging behaviour of two seabird species
109 that exhibit different habitat use: surface-foraging red-legged kittiwakes *Rissa*
110 *brevirostris* (hereafter, RLKI) feeding in the oceanic habitat and pursuit-diving

thick-billed murres *Uria lomvia* (TBMU) feeding mainly in the continental shelf habitats, and how they responded 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, and were set to record five successive 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. Some equipped birds were resighted, but we failed to recapture them as they nest at the cliff. Previous studies suggested that attachment

133 of small and lightweight tags (usually <5% of body mass) do not appear to affect
134 foraging and/or reproductive behaviour of individuals (e.g. Phillips et al., 2003;
135 Carey, 2011), while other studies reported an adverse effect on their behaviour as
136 well as physiological condition (e.g. Barron et al., 2010; Elliott et al., 2012). In this
137 study, the total weight of the logger including the heat-shrink tubing and tape was
138 15-16 g, which corresponds to less than 5% of the mean body mass of equipped birds
139 (the mean ± SD: RLKI 375 ± 29 g, TBMU 1024 ± 43 g). The recovery rate excluding
140 some resighted individuals was relatively high (71-82%), and the attachment of tags
141 was not resulted in, at least, the breeding abandon.

142 Of the loggers retrieved, some failed to record locations. Hence, location
143 data were available for 5 and 7 RLKI (20 July–5 August) and 5 and 10 TBMU (2–12
144 August) in 2013 and 2014, respectively. Data for RLKI in 2013 were reanalyzed
145 from Kokubun et al. (2015). At the time of recapture, blood samples were taken from
146 the brachial vein of each individual, and kept on ice until centrifugation to separate
147 the plasma from the red blood cells, and both were kept frozen until assayed. Plasma
148 was used for measurement of physiological stress exposure (corticosterone: CORT)
149 and red blood cells for determining trophic level (stable isotopes: SI). CORT was
150 measured only for samples that were taken within 3 min of capture, as it takes 3 min
151 for levels of CORT to begin to rise in the blood in response to the acute stress of
152 capture and restraint (Romero and Reed, 2005).

153 During the study period, we opportunistically obtained adult diets of RLKI
154 by regurgitation at the time of logger deployment and/or retrieval. Prey species of

155 RLKI samples were identified visually or using otoliths (N = 22 in 2013 and N =15
156 in 2014) (also see Kokubun et al., 2015). TBMU chick diet was recorded from direct
157 observation of adult birds (both with and without data loggers) carrying prey items
158 back to their nests in their bill. Prey items were visually identified during observation
159 or later from photographs (N = 13 in 2013 and N = 39 in 2014).
160

161 **2.2 Data analysis**

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

176 To examine the differences in marine environment between the two study

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

189 In addition to the GPS tracking, we also analyzed behavioural data of birds
190 obtained by geolocators (2.5 g, Mk19; Biotrack Ltd., UK) and accelerometers (12
191 mm diameter × 45 mm length, 10 g, ORI-380 D3GT; Little Leonardo, Japan). As the
192 location records did not cover a complete foraging trip in several GPS tracks (see
193 Results, Fig. 1 in Appendix A), we used these data to confirm the foraging trip
194 durations in each year supplementarily. For the geolocator-carrying birds, the
195 foraging trip duration was defined as the time between the first and last landing on
196 water (i.e. immersion) before and after a long dry event, which is likely an
197 underestimation, though comparable between the years (see Fig.1 in Appendix B).
198 For the accelerometer-carrying birds, the start and end of a foraging trip was

199 identified from changes in bird posture as well as outward/inward flight activity
200 recorded as cyclic fluctuations of acceleration (see details for Takahashi et al., 2008).
201 Data were analyzed for 22 trips from 4 birds in 2013 and 14 trips from 5 birds in
202 2014 for RLKI (26 July-2 August) and 9 trips from 9 birds in 2013 and 21 trips from
203 12 birds in 2014 for TBMU (31 July-12 August).

204 CORT concentrations were measured for 8 RLKI and 20 TBMU in 2013
205 and 7 RLKI and 21 TBMU in 2014. CORT concentrations (ng ml^{-1}) were measured
206 using a radioimmunoassay (for details see Kitaysky et al., 1999). Briefly, each
207 sample was equilibrated with 2000 cpm of tritiated CORT prior to extraction with 4
208 ml re-distilled dichloromethane. After extraction, percent tritiated hormone
209 recovered from each individual sample (average hormone recovery was, mean ± SD,
210 94.68% ± 2.86) was used to correct final CORT concentrations. Samples were
211 reconstituted in phosphate-buffered saline gelatin buffer and combined with antibody
212 and radiolabel in a radioimmunoassay. Dextran-coated charcoal was used to separate
213 antibody-bound hormone from unbound hormone. All samples were analyzed in 2
214 different assays; CV = 7% for inter-assay and <2% for intra-assay).

215 Stable isotopes ($\delta^{15}N$) were measured for 8 RLKI and 20 TBMU in 2013
216 and 7 RLKI and 15 TBMU in 2014 following Hobson (1993) and Barger and
217 Kitaysky (2012). A small portion of freeze-dried samples (0.100-0.400 mg) were
218 placed in a tin capsule, sealed, and deposited in an EA autosampler. The stable
219 isotope data was obtained using continuous-flow isotope ratio mass spectrometry
220 (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 $\delta^{15}N_{air}$ according to: $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000‰$, where $R_{sample/standard}$ is the corresponding ratio $^{14}N/^{15}N$. Replicate measurement of an internal laboratory standard (Peptone) indicated measurement errors to be ± 0.16‰. 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) using Poisson (for the bathymetry and trip duration) or Gaussian (for the distance) distributions, including bird identity as a random factor. We tested the inter-annual differences in CORT (log-transformed) and SI by conducting one-way ANOVA. Statistical significance was assumed at $P < 0.05$. Values reported are means ± standard errors (SE) or standard deviations (SD).

3 Results

3.1. Foraging behaviour

For RLKI, 12 trips in 2013 and eight trips in 2014 were recorded with GPS loggers. Two trips were recorded partially, and the other trips included complete tracks (*N* =

5) and tracks recorded until close to the beginning of or during the homing commute phase (N = 13, see Fig 1a. in Appendix A), having 59 ± 26% of available location fixes during the trips. In both years, RLKI travelled predominantly towards the south from the colony and to a lesser extent towards the north and west (Fig. 1a, b). On-water locations (a proxy for foraging) occurred mostly over the oceanic basin in both years (>87% of the locations: Fig. 2) (GLMM, Z = -0.28, P = 0.78). Foraging distances from the colony peaked at 250-300 km in 2013 and bimodally at 150-250 km and 300-350 km in 2014 (Fig. 3), though mean distance did not differ significantly between the years (GLMM, t = 0.92, P = 0.36).

For TBMU, 11 trips in 2013 and 22 trips in 2014 were recorded with GPS loggers, including two partial tracks, 29 complete tracks, and 2 incomplete tracks (recorded until close to the beginning of or during the homing commute phase) (Fig. 1b in Appendix A), having 68 ± 24% of available location fixes during the trips. TBMU traveled to the southeast and west of the colony in 2013 (Fig. 1c), while birds traveled mostly towards the north and east in 2014 (Fig. 1d). In both years, TBMU foraged mostly over the shelf (GLMM, Z = 0.23, P = 0.82), but showed a relatively higher use of the shelf break and oceanic basin in 2013 (Fig. 2). The foraging distances from the colony tended to be farther in 2013 compared to these in 2014, though not significantly so (GLMM, t = -1.30, P = 0.19) (Fig. 3).

As some of the GPS data were incomplete (i.e. ended before reaching to the colony, Fig. 1 in Appendix A), the analysis of behavioral data obtained using geolocators and accelerometers was also conducted. These results showed similar

265 foraging trip durations (minimum estimate as an index: see Fig 1. in Appendix B)
266 between both years for RLKIs (12.7 ± 3.0 h in 2013 and 12.3 ± 5.1 h in 2014;
267 GLMM, t = -0.32, P = 0.75) and relatively longer foraging trip durations in 2013
268 (mean ± SD: 15.9 ± 6.9 h) compared to 2014 (10.4 ± 7.1 h) for TBMUs (GLMM, t =
269 -1.94, P = 0.06).
270

271 **3.2. Stress hormone**

272 Log-transformed baseline CORT concentrations in RLKI were 0.72 ± 0.09 ng ml^{-1}
273 and 0.72 ± 0.05 ng ml^{-1} in 2013 and 2014, respectively (Fig. 4). CORT levels did not
274 differ between years in RLKIs (ANOVA, $F_{1,13}$ = 0.01, P = 0.94). On the other hand,
275 CORT concentrations in TBMUs were significantly ($F_{1,39}$ = 24.97, P < 0.001) higher
276 in 2013 (0.78 ± 0.05 ng ml^{-1}) than in 2014 (0.38 ± 0.06 ng ml^{-1}, Fig. 4).
277

278 **3.3. Diet**

279 δ^{13} N did not differ between the years in either RLKI (13.52 ± 0.27‰ in 2013 and
280 13.65 ± 0.17‰ in 2014: $F_{1,13}$ = 1.30, P = 0.28) or TBMU (13.15 ± 0.42‰ in 2013
281 and 13.11 ± 0.42‰ in 2014: $F_{1,33}$ = 0.09, P = 0.77). Based on the diet sampling and
282 observations, regurgitated prey for RLKI mostly consisted of myctophids (the
283 percent of occurrence; 100% in 2013 and 93.3% in 2014) but also included
284 amphipods (27.3% in 2013 and 6.7% in 2014), shrimp (9.1% in 2013 and 13.3% in
285 2014), euphausiids (4.6% in 2013 and 6.7% in 2014), and squid (13.6% in 2013). For
286 TBMU, observed prey was mostly fish including age-0 and age-1walleye pollock

(53.9% in 2013 and 56.4% in 2014) and to a lesser extent included squid and meso-zooplankton (46.2% in 2013 and 33.3% in 2014) as well as unidentified prey (10.3% in 2014).

3.4. Annual differences in marine environment

SSTs within the foraging range (<350 km from the colony; Fig. 3) were relatively warmer in 2014 (mean ± SD: on-shelf 12.3 ± 0.8 ºC, shelf break 11.6 ± 0.9 ºC, oceanic basin 11.7 ± 0.8 ºC) compared to 2013 (on-shelf 9.8 ± 1.0 ºC, shelf break 10.3 ± 1.2 ºC, oceanic basin 10.2 ± 1.0 ºC). 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 over two years differed between the species. Between the two study years, SST around the colony was relatively 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

309 2014. In comparison, TBMU used the oceanic basin to the south of the colony more
310 frequently in 2013, exhibiting relatively farther travel distances and higher levels of
311 CORT. Based on the δ^{15}N values (an indicator for trophic level: Hobson et al., 2002)
312 and diet sampling/observation, both RLKI and TBMU probably had similar prey
313 composition between the years.

314 During the study period, the fledgling success (the mean ± SD) of RLKI
315 and TBMU on St. George Island differed between the years; dramatically for RLKI,
316 0.57 ± 0.07 in 2013 and 0.92 ± 0.02 in 2014 and less so for TBMU, 0.95 ± 0.02 in
317 2013 and 0.89 ± 0.02 in 2014 (Mudge et al., 2015). Fledgling success may be related
318 to behaviour prior to breeding (i.e. the timing of breeding: Renner et al., 2014), but
319 the hatching date (the mean ± SD) appeared not to differ between the years for either
320 RLKI (6 July ± 7.0 days in 2013 and 4 July ± 4.8 days in 2014) or TBMU (27 July ±
321 6.6 days in 2013 and 28 July ± 7.4 days in 2014) (Mudge et al., 2015). Therefore, the
322 fledgling success during the study period may be related to food resource conditions
323 during the breeding season in the given years, suggesting better conditions in 2014
324 (relatively warmer SSTs with earlier sea ice retreat) than 2013 (relatively cooler
325 SSTs with later sea ice retreat).

326 RLKI mainly feed on myctophids over deep oceanic regions (Sinclair et al.,
327 2008; Kokubun et al., 2015). As RLKIs are a surface-feeding seabird, they are
328 considered to feed on vertically migrating myctophids (Hunt et al., 1981). The water
329 column in the deep ocean may show less inter-annual variation in water temperature
330 compared to that of the shallower shelf region (see Results in this study) where the

deep cold pool (temperature remains below <2 ºC) 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 kittiwakes (*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 Appendix C). However, it has been 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). Compared to TBMU, RLKI exhibited consistently high levels of CORT in both years with different fledgling success. This may reflect potential competition with black-legged

353 kittiwakes that also feed on myctophids in the ocean basin (Sinclair et al., 2008;
354 Renner et al., 2012). In the Pribilof islands, black-legged kittiwakes had switched
355 their reliance upon Pollock during the 1970s and 1980s to myctophids by the 1990s
356 (Sinclair et al., 2008). Accordingly, red-legged kittiwakes are the species most
357 threatened by population declines since the 1980s. Hence, there is a possibility that
358 the foraging effort of RLKI is at the limit, as the indication of elevated CORT
359 includes the increase in foraging effort (Kitaysky et al., 2010). Such the inter-specific
360 competition appears to be relatively higher during cold years (Satterthwaite et al.,
361 2012; Paredes et al., 2014), possibly resulted in the lower fledgling success in 2013,
362 the year of relatively cooler SSTs with later sea ice retreat. In fact, the mean (± SD)
363 growth rate (g/day) of RLKI was better in 2014 (14.9 ± 3.7 g) than 2013 (11.7 ± 3.6
364 g) (Mudge et al., 2015).

365 Compared to RLKI, TBMU exhibited fluctuating physiological condition
366 and flexible behavioral changes in parallel to the ocean variability between the years,
367 yet without a difference in fledgling success. Late sea ice retreat is associated with an
368 early, cold-water phytoplankton bloom, relatively low biomass of small shelf
369 copepods, and poor survival of larval and juvenile forage fish, including their main
370 prey (juvenile walleye pollock: Hunt et al., 1996; Sinclair et al., 2008; Renner et al.
371 2012). On the other hand, early sea ice retreat is associated with a later, warm-water
372 plankton bloom, a large biomass of small shelf copepods later in the season, and high
373 abundance of larval and juvenile forage fish (Hunt et al., 2002). Moreover, forage
374 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 them with a larger area of suitable habitat (Ciannelli and Bailey, 2005; Kotwicki et al., 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 year of warmer SSTs and earlier sea ice retreat) compared to 2013 (the year of cooler SSTs and later sea ice retreat). 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; Pinaud et al., 2005; Harding et al., 2007;

397 Bertrand et al. 2012), but longer and farther foraging trips likely cause higher levels
398 of nutritional stress (2013 in this study), especially for TBMU whose flight cost is
399 presumed to be high (Houston et al., 1996).

400 In this study, chick-rearing RLKI did not change their foraging locations
401 largely in relation to marine environmental changes probably due to their reliance on
402 myctophids, which live in the deep waters of the pelagic zone (Sinclair and Stabeno,
403 2002), for feeding young (Kokubun et al., 2015). However, their foraging effort
404 might also be affected by the position and strength of local eddies, which are
405 reflected by atmospheric control (the North Pacific Index and Multivariate ENSO
406 Index: Ladd et al., 2012; Ladd, 2014). TBMU showed fluctuations in physiological
407 condition and flexible foraging behavior, which probably corresponded to ocean
408 variability (exhibited longer and farther trips in the relatively cooler year of 2013).
409 Hence, although we compared foraging behaviour of seabirds in different
410 environmental conditions only over two years with limited sample sizes, our study
411 has suggested that there is possible interspecific differences in species' response to
412 warming, which may reflect differences in ecosystem dynamics between habitats
413 they use for foraging, as the decrease in sea-ice extent showed negative effects on
414 foraging behaviour for other species in a different Arctic region (e.g. black
415 guillemots *Cepphus grylle mandtii*: Divokey et al., 2015). Elevated stress levels may
416 have a cascading effect on subsequent life stages, such as migration, post-breeding
417 survival, breeding propensity, and timing of breeding (Verhulst and Nilsson, 2008;
418 Schoech et al., 2009; Goutte et al., 2010; Kitaysky 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 (Kitaysky et al., 2010; Satterthwaite et al., 2010; Schultner et al., 2014).

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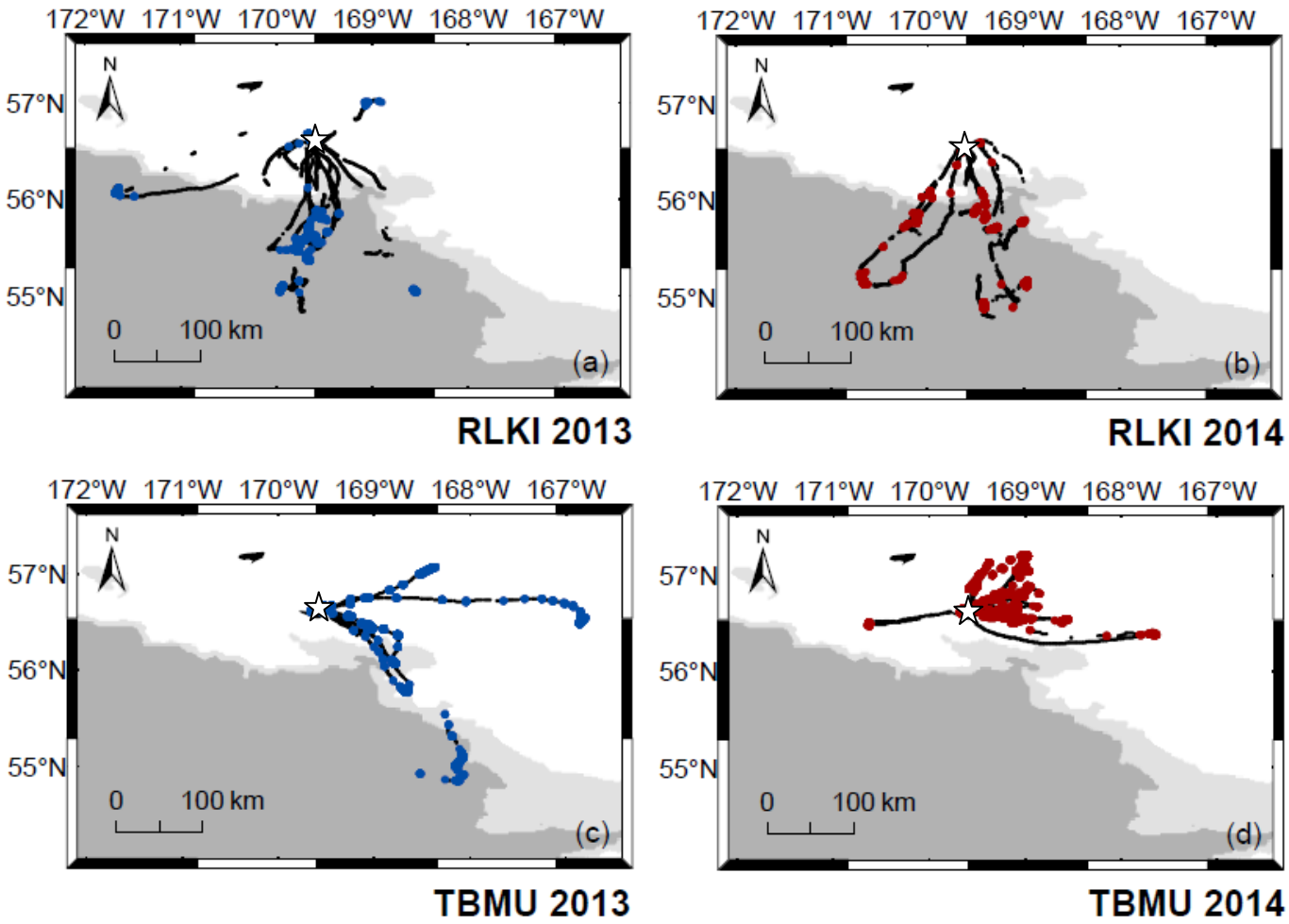
Figure legends

Figure 1. Foraging trip trajectories of red-legged kittiwakes: RLKI (a, b) and thick-billed murres: TBMU (c, d) in 2013 and 2014, respectively. Black dots represent location fixes and blue or red circles represent on-water (i.e. foraging) locations. The star indicates the breeding colony, St. George Island. The background shows the bathymetry: white: on-shelf (0-200 m bottom depth), light grey: shelf break (200-1000 m) and grey: oceanic basin (>1000 m).

Figure 2. The marine habitats of on-water locations during the foraging trips in red-legged kittiwakes (RLKI), and thick-billed murres (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).

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

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


172°W 171°W 170°W 169°W 168°W 167°W
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(a)
RLKI 2013
(b)
RLKI 2014
(c)
TBMU 2013
(d)
TBMU 2014

Figure 1

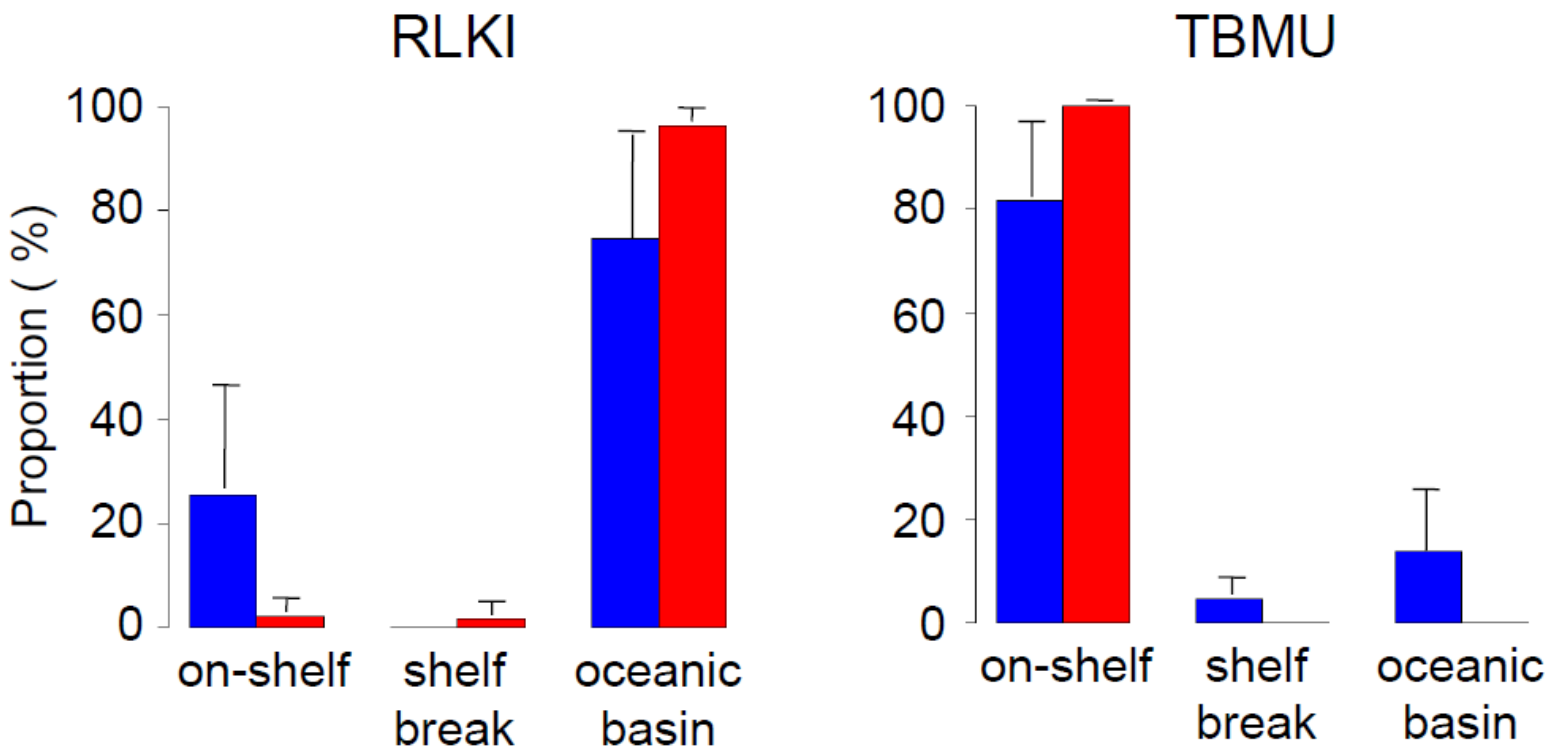
RLKI
TBMU
Proportion (%)
100
80
60
40
20
0
on-shelf
shelf break
oceanic basin

Figure 2

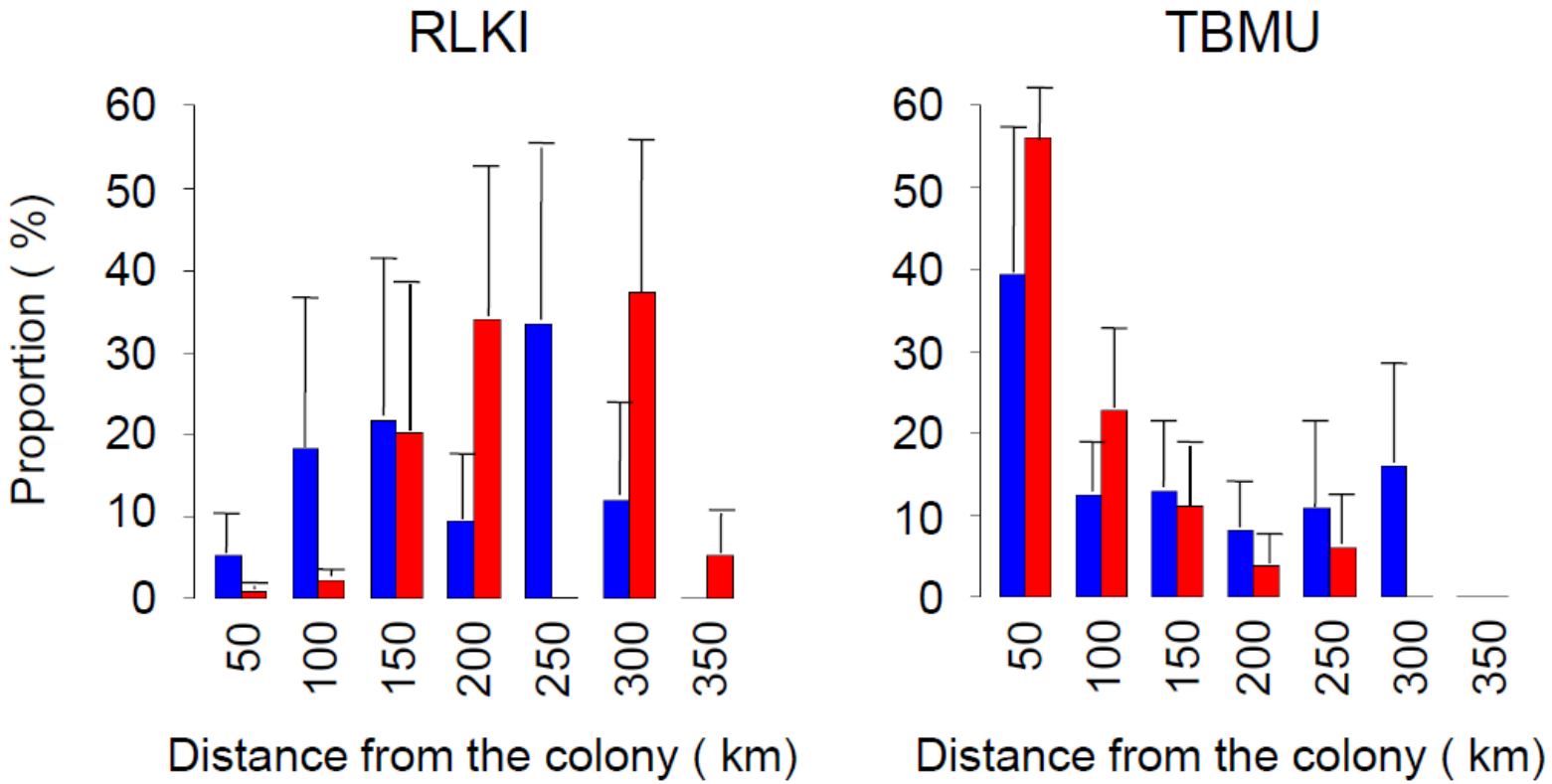
RLKI
TBMU
Proportion (%)
0
10
20
30
40
50
60
50
100
150
200
250
300
350
Distance from the colony (km)
Distance from the colony (km)

Figure 3

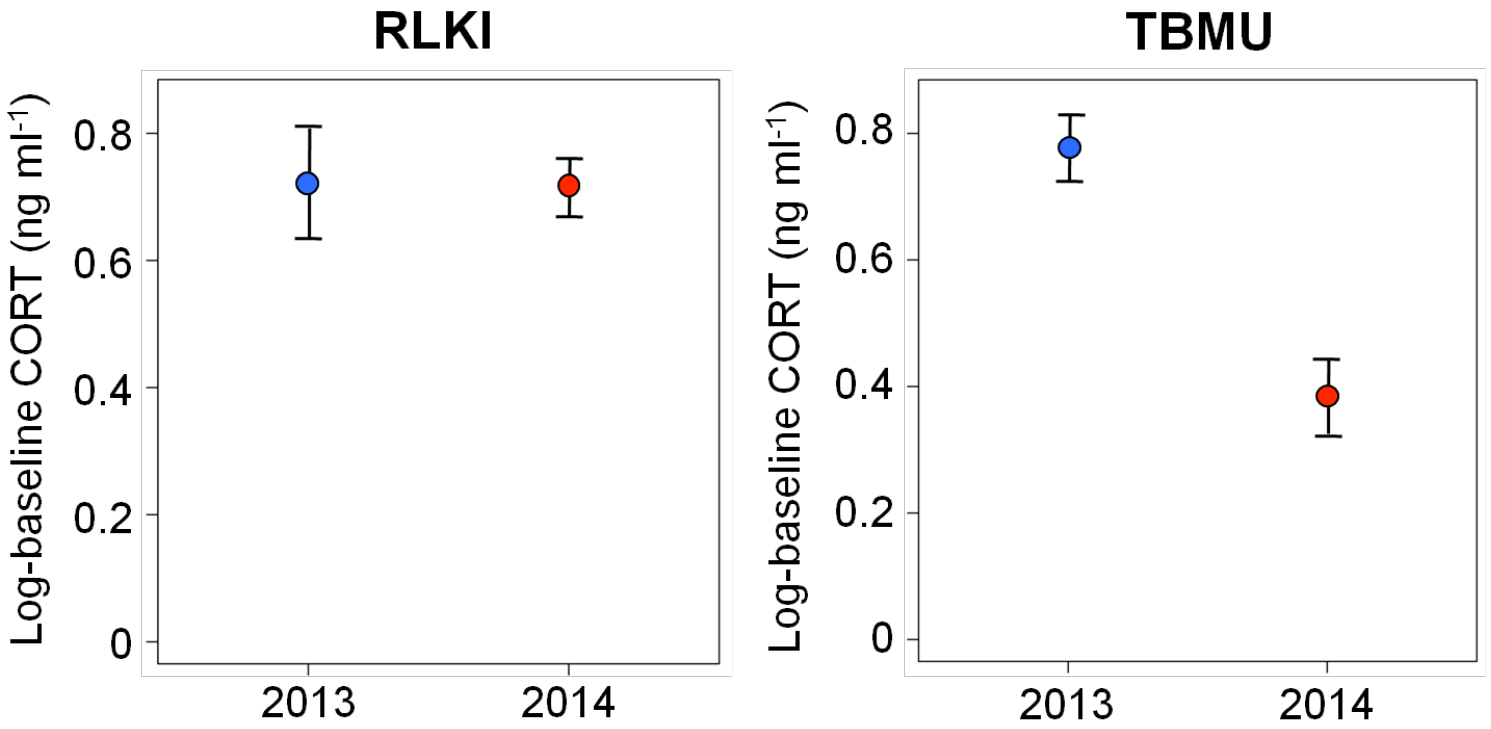

Figure 4