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North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations

Rachael A. Orben1,2, David B. Irons2, Rosana Paredes3, Daniel D. Roby3, Richard A. Phillips4 and Scott A. Shaffer1

ABSTRACT

Aim Species that breed sympatrically often occupy different foraging niches to mitigate competition for prey. When resource availability declines at the end of the breeding season, most animals migrate to regions with more favourable environmental conditions. When these life-history traits combine, foraging habitat preferences may continue to influence migration patterns and habitat utilization. The Bering Sea is home to the red-legged kittiwake (RLKI), Rissa brevirostris, which is endemic, and the black-legged kittiwake (BLKI), Rissa tridactyla, which has a circumpolar breeding distribution. Since the 1970s, numbers of RLKIs at the largest colony have declined and then recovered, whilst the BLKI population has remained stable. Knowledge of the migration ecology of kittiwakes is key to understanding differences in population trajectories, and predicting possible future responses of these species to climate change.

Location Pribilof Islands, Bering Sea, subarctic North Pacific.

Methods Using geolocation loggers, we tracked adult RLKIs and BLKIs during their non-breeding migrations. We used iterative methods to assess suitable sample sizes for determining space use. Kittiwakes are surface foragers; therefore we used wet–dry data to distinguish active foraging behaviour and to test the species’ responses to environmental conditions. Stable isotope ratios of feathers grown during the non-breeding period were used to assess dietary niche.

Results RLKIs remained largely in the Bering Sea, where they experienced colder conditions and shorter days; individual birds used multiple habitats, including the continental shelves, the sea-ice edge and pelagic waters. In contrast, BLKIs migrated to the subarctic North Pacific, where they dispersed laterally across the basin; the majority of birds travelled to the western subarctic. RLKIs spent less time actively foraging than BLKIs, and consumed higher trophic-level prey.

Main conclusions The disparate wintering ranges and foraging behaviour of BLKIs and RLKIs suggest distinct environmental factors drive variation in over-winter survival. A strong association with sea ice, and specialization both in diet and foraging behaviour, may make RLKIs particularly vulnerable to climatic change.

Keywords Bering Sea, ecological segregation, geolocation, non-breeding habitat, North Pacific, resource partitioning, Rissa brevirostris, Rissa tridactyla, seabird, sibling species.
INTRODUCTION

Species that breed sympatrically often occupy different foraging niches to mitigate competition for prey (Ashmole, 1968; Kaptes et al., 2010; Jeglinski et al., 2013). However, few studies have addressed whether niche specialization during breeding has an influence, in turn, on the migration ecology of marine species (e.g. Thiebot et al., 2013). During migration, individuals must adjust to changes in niche space, not only in terms of the physical environment, but also in food-web structure, including the composition of prey and predator communities and the presence of competitors. Because specialist predators need to track particular prey resources year-round, they are likely to be especially vulnerable to changes in prey distributions and community composition (Hückstädt et al., 2012). In the marine environment, anthropogenic climate change continues to affect temperature and wind regimes, the strength and routes of ocean currents, and to increase the pH of the oceans, altering prey fields and therefore influencing the distribution of upper trophic-level organisms (Hazen et al., 2012; Weimerskirch et al., 2012; Pinsky et al., 2013). Understanding the importance of migration strategies for life histories is essential for assessing how highly mobile species may cope with environmental change.

The physical environment of the Bering Sea is annually variable, as sea ice influences the timing of the spring bloom, water column temperature and stratification. This results in a dichotomy between warm and cold years, in which different primary producers and secondary consumers are favoured (Hunt et al., 2011). Open-water spring blooms are higher in net primary productivity, occur in warmer water than ice-associated blooms, and over the long term will probably increase the carrying capacity of this ecosystem (Brown & Arrigo, 2013); however, warmer regimes disfavour Neocalanus copepods and their predators (Müeter et al., 2011; Dörrrestein et al., 2012). As the global climate changes, conditions in the Bering Sea are predicated to transition to current subarctic conditions, with greater stratification during the summer months likely to affect primary producers and have knock-on effects at upper trophic levels (Brown et al., 2011; Hunt et al., 2011).

Red-legged kittiwakes (RLKIs), Rissa brevirostris (Bruch, 1853), and black-legged kittiwakes (BLKIs) Rissa tridactyla (Linnaeus, 1758), breed sympatrically on a few islands in the Bering Sea. St George Island, of the Pribilof Island group, on the south-eastern Bering Sea shelf, is home to approximately 70% of all RLKIs and a large population of BLKIs (in 1977, 220,000 pairs of RLKIs and 72,000 pairs of BLKIs Byrd et al., 2008a). RLKIs are currently listed as ‘Vulnerable’ by the World Conservation Union (BirdLife International, 2013). On St George, the population trends of these two species have diverged. RLKIs decreased by roughly 44% between 1976 and 1986, but subsequently increased such that recent counts suggest populations have recovered to levels recorded in the mid-1970s (Klostermann et al., 2011). In contrast, the BLKI population has remained relatively stable (Byrd et al., 2008a; Klostermann et al., 2011). The differing population trends of the two species, despite strongly correlated breeding productivity (Byrd et al., 2008b), suggest that some degree of non-breeding niche separation may play a role in population regulation; however, basic life-history differences, such as longevity, may also contribute. At the smaller colony on St Paul Island, populations of both kittiwake species are declining, although here the causes are likely to be a combination of low local food availability (Paredes et al., 2012) and targeting of RLKIs for subsistence hunting (Byrd et al., 2008a).

During the breeding period the two kittiwake species appear to occupy different foraging niches. On St George, diet and trip duration indicate that RLKIs forage predominantly over the basin and tend to specialize on lipid-rich myctophid fishes (Lance & Roby, 1998), while BLKIs feed on a broader suite of prey from both the basin and shelf (Paredes et al., 2012; Renner et al., 2012). There is evidence that RLKIs have the capacity to forage on neritic prey (Hunt et al., 1981); however, since the 1990s, myctophids have increased in occurrence in the diet of both species, probably increasing interspecific competition (Sinclair et al., 2008; Renner et al., 2012). It is unknown how the release of the central-place breeding constraint affects RLKI foraging, particularly whether they continue to act as specialized foragers. Compared with BLKIs, RLKIs have physiological adaptations for their particular foraging style, including shorter bills and larger eyes, that suggest specialization for foraging at low light levels is an important life-history strategy (Storer, 1987). Outside the breeding period, the habitat use and diet of RLKIs is largely unknown, but they are thought to be highly pelagic; limited at-sea survey data indicate that they could range from the pack-ice edge to south-east Alaska, California and the Kuril Islands (Byrd & Williams, 1993). In contrast, BLKIs from coastal Alaska migrate south along the coast of North America (McKnight et al., 2011).

In the present study, we characterized and compared the non-breeding foraging ecology of these two sympatric kittiwake species to determine whether niche partitioning occurs in space, time or dietary trophic level. For both species on the Pribilof Islands, we determined the distribution, habitat utilization, activity patterns and trophic partitioning based on stable isotope analysis. We used remotely sensed environmental data to examine how these species respond to habitat conditions. In light of these results, we speculate on the potential mechanisms that could drive population regulation in these congeners.

MATERIALS AND METHODS

Global location sensor (GLS) loggers (2.5 g, Mk9/Mk19; British Antarctic Survey, Cambridge, UK) were attached to leg bands on kittiwakes in July 2010, on St Paul Island (57°11′ N, 170°15′ W; BLKI = 31, RLKI = 5) and St George Island (56°34′ N 169°37′ W; BLKI = 28, RLKI = 22) of the Pribilof Islands, Alaska, USA. The birds were captured when attending nests, which typically contained one chick, using a
telescoping noose pole or foot snare. Birds were recaptured using a foot snare or hand-held CO2-powered net gun (Super Talon Animal Catcher; Advanced Weapons Technology, La Quinta, CA, USA). Body measurements were taken from all birds. Wing loading was calculated as body mass divided by the wing area. The latter was the area of the right wing (plus the rootbox, the area of the body between the wings), which was traced in the field then a cut-out weighed (accuracy 0.001 g) and a standard curve used to calculate area (Pennycuick, 2008). Sex was determined from DNA extracted from blood samples (Fridolfsson & Ellegren, 1999).

All data processing and spatial analyses were conducted using Matlab 2009a (The Mathworks, Natick, MA, USA). Statistical tests were run in R 3.0.0 (R Core Team, 2013). The results are shown as means ± SD. Significance was set to \( P < 0.05 \).

**Movement and area utilization**

Loggers were used to record light levels, and TRANSEDIT and LOCATOR (British Antarctic Survey) were used to identify dawn and dusk transitions using a threshold of 10, and to calculate locations based on a Sun angle of \(-3.5\) for the Mk9 loggers and \(-3.0\) for the Mk19 loggers (values selected on the basis of stationary calibration data). Locations were calculated following Phillips et al. (2004), by smoothing locations twice and then applying an iterative forward/backward averaging speed filter based on a maximum travel speed of 48 km h\(^{-1}\) sustained over 12 h (Coulson, 2011). Geolocation has an error of approximately 180–200 km that increases around the equinoxes (Phillips et al., 2004; Shaffer et al., 2005), therefore analysis was restricted to the period 15 October–27 February. Smoothed tracks were used to identify the furthest location (maximum range) from the colony, as well as the date and bearing of that location. To calculate departure and return dates, sea-surface temperatures (SST) were used to estimate latitudes for those loggers that recorded temperature (BLKI = 27, RLKI = 8) and then the tracks were speed filtered (Shaffer et al., 2005).

Utilization distributions (UDs) were calculated using smoothed locations for the pooled samples by year and month to show general movement patterns, and for each bird using the IKNOS toolbox (Y. Tremblay, University of California Santa Cruz, Santa Cruz, CA, USA, unpublished data). The grid cell size was set at 80 km. To enable comparisons between species and iterations, the smoothing parameter was selected using the entropy dataset (latitude 0.0171, longitude 0.0068; Sheather & Jones, 1991). Portions of UDs overlapping land were subtracted from area calculations. The 50% and 95% UDs were considered to represent the core area and overall range, respectively.

Bootstrapping was used to calculate standard deviations for area estimates, to determine whether enough individuals were tracked to make reasonable inferences of area use (Hindell et al., 2003; Soanes et al., 2013) and to assess overlap between groups (Breed et al., 2006). To assess whether sample sizes were sufficient, the areas of the 50% and 95% UDs were calculated with the addition of a new bird selected at random until all individuals were included. This was repeated for 1000 iterations. To determine spatial partitioning between species, colonies (BLKIs only, because of small sample size of RLKI from St Paul) and sexes, the amount of overlap between observed distributions was compared with the overlap from 1000 bootstrapped selections from the pooled dataset. The area of overlap divided by the area of the 95% UD of the overall dataset was used as the test statistic, and the P-value was determined as the proportion of iterations that resulted in a smaller overlap than observed (Breed et al., 2006).

**Habitat**

Habitat use was characterized in terms of oceanographic, topographical, astronomical and atmospheric variables extracted at a grid scale of 2° latitude by 1° longitude. SSTs were extracted as an 8-day blended product from National Oceanic and Atmospheric Administration (NOAA)'s Environmental Research Division (Pacific Grove, CA, USA) (http://oceanwatch.pfeg.noaa.gov/thredds/catalog.html). Sea-surface height (SSH) and surface currents used to calculate eddy kinetic energy (EKE) were extracted from the Navy Layered Ocean Model (http://www7320.nrlssc.navy.mil/global_nkom/) using the nctoolbox (https://github.com/nctoolbox/). The distance to the coast was calculated using mean high water (National Geophysical Data Center, NOAA, Boulder, CO, USA). The distance to the sea-ice edge (5% contour) was calculated from daily Advanced Microwave Scanning Radiometer–EOS (AMSR-E; National Space Development Agency of Japan, Tokyo, Japan) georeferenced images captured aboard the Aqua satellite (National Aeronautics and Space Administration, Washington, DC, USA) projected using ArcGIS 9.0 (ESRI, Redlands, CA, USA). Bathymetry was extracted from 2-minute gridded global data (Smith, 1997). Day and twilight length (nautical) were calculated for each estimated location (Reda & Andreas, 2003). The fraction of the Moon illuminated was extracted from the US Naval Observatory (Washington, DC). Surface values of air temperature, wind speed, relative humidity, precipitation and barometric pressure were extracted from the NCEP/NCAR reanalysis I and NCEP/DOE reanalysis II datasets (Kanamitsu et al., 2002; NCEP/NCAR).}

**Activity patterns**

Kittiwakes are surface foragers, and immersion (wet–dry) sensors are particularly suited to monitoring their activities, as frequent switches between wet and dry indicate periods of more intensive foraging behaviour. Following Paredes et al. (2012), activity data, recorded in 10-min blocks, was classified into three categories: (1) active foraging, with periods of frequent switches between wet and dry; (2) on water,
The feathers were analyzed for δ13C and δ15N using a Carbo-Elba elemental analyzer interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, University of California Santa Cruz, Santa Cruz, CA, USA). Data were corrected for sample mass and instrument drift. Measurement precision (standard deviation), based on within-run replicate measures of the laboratory standard (pugel), was 0.08 for δ13C and 0.08 for δ15N (n = 24).

RESULTS

Overall, 86% of tagged birds were resighted in the following breeding season (St Paul, BLKI 87%, RLKI 60%; St George, BLKI 92%, RLKI 82%). These may be underestimates of survival as there was almost complete breeding failure of BLKIs during incubation and poor overall hatching success of RLKIs (Klostermann et al., 2011; Thomson & Drummond, 2012). Overall, 71% of loggers were recovered; nine loggers failed. Complete datasets were available for analysis from 34 BLKIs (St Paul, 15; St George, 19) and 17 RLKIs (St Paul, 2; St George, 15). Mean mass at recapture was not significantly different from that at deployment (paired t-test, P > 0.05).

Morphometrics

BLKIs were larger than RLKIs in all measurements; however, there was no significant difference in aspect ratio or wing loading (see Appendix S1 in Supporting Information). Male BLKIs were larger than female BLKIs in all measurements except wing area, whereas male RLKIs were larger than female RLKIs in only head plus bill length (F1,30 = 4.70, P = 0.038). There were no significant differences between the sexes in either species regarding aspect ratio and wing loading (see Appendix S1).

Movements and area utilization

During the non-breeding period, both species migrated away from their colonies. Their distributions were spatially segregated, with almost no overlap of 50% UDs (Fig. 1). The core

![Figure 1 At-sea utilization distributions (UDs) for red-legged kittiwakes (RLKIs), Rissa brevirostris (shades of red, n = 17), and black-legged kittiwakes (BLKIs), Rissa tridactyla (shades of blue, n = 34), in the subarctic North Pacific, from 15 October 2010 to 27 February 2011. The 25%, 50% and 75% UDs are represented by continuously lighter shades, and the lightest solid line represents the 95% UD.](image)
Figure 2 Monthly utilization distributions (UDs) derived from smoothed locations for red-legged kittiwakes (RLKIs), Rissa brevirostris (shades of red, n = 17), and black-legged kittiwakes (BLKIs), Rissa tridactyla (shades of blue, n = 34), in the subarctic North Pacific. The 25%, 50% and 75% UD are represented by continuously lighter shades, and the lightest solid line represents the 95% UD. The Bering Sea ice edge (5% contour) at the end of each month is shown in light blue.

south-east Bering Sea, the Western Subarctic Gyre (WSG) and along the northern edge of the BLKI distribution (Fig. 1). Both species remained in the Pribilof region until late September. Although there were no significant differences in the maximum range, departure or arrival date between species, the ranges of individual RLKIs were further west and significantly smaller than those of BLKIs (see Appendix S2). The furthest locations of males were further to the west than those of females, but no other significant effects of sex were observed.

High densities of BLKIs were consistently present in the central subarctic North Pacific (Fig. 2). In February, BLKIs were highly dispersed, with a distribution that spanned the North Pacific from the Kuril Islands to the California coast. A total of 23 BLKIs (68%) travelled to the WSG. Overall BLKIs spent minimal time in the Gulf of Alaska, with three birds (8%) travelling to the California Current system in February (6 February ± 6 days), where they remained for 30 ± 8 days until departure in March (9 March ± 5 days). In contrast, 82% of RLKIs remained in the eastern Bering Sea through December, largely foraging over the shallow shelf, north to the Chukchi Peninsula. In November, two RLKIs (12%) flew to the northern Kuril Islands. By January, the remaining birds left the eastern Bering Sea as the sea ice extended south, and rapidly crossed the basin or moved south along the coast of Kamchatka, where high densities occurred into February (Fig. 2). By this time, all RLKIs had briefly visited the western subarctic and, when the birds began returning north, four birds made brief forays into the Sea of Okhotsk.

The total area occupied during the non-breeding period appeared to approach saturation (i.e. an asymptote) with the number of birds tracked; for RLKIs, an asymptote was reached at a lower sample size, indicating little variation between individuals (Fig. 3). The species differed significantly in spatial extent, with BLKIs using a larger area (Fig. 3). The species' distributions showed significantly less overlap than occurred randomly at both the core and range scales (50% UD, 10% overlap; 95% UD, 68.5% overlap; P < 0.001). BLKIs originating from the two study colonies showed significantly less overlap than occurred at random, indicating spatial differences (50% UD, 17% overlap, P < 0.001; 95% UD, 67% overlap, P = 0.022). There was less overlap between sexes than occurred at random in BLKIs for the 50% UD (14% overlap, P = 0.002) but not the 95% UD (59% overlap, P = 0.065); for RLKIs, there was less overlap for both the 50% UD (10% overlap, P < 0.001) and 95% UD (69%
The physical characteristics of the habitats used by RLIKIs and BLKIs in their core areas differed significantly for all environmental variables except mean sea level pressure and SSH (Table 1). RLIKIs encountered, on average, significantly colder water and air temperatures and lower humidity, whereas BLKIs encountered higher winds and more cloud and precipitation. BLKIs experienced more hours of daylight but fewer hours of twilight. RLIKIs were closer to the sea-ice edge; however, not all core areas were associated with sea ice. Core areas of RLIKIs had higher EKE; this difference reflected the pelagic portion of the respective distributions, as satellite remote-sensing limits the measurement of EKE to off-shelf regions. RLIKIs remained closer to the Pribilof Islands and the coast, and hence in shallower water.

### Daily activity patterns

BLKIs actively foraged more than RLIKIs throughout the non-breeding period; RLIKIs spent more time in flight or roosting in October–December and more time on the water in December–January than BLKIs (Fig. 4; percentage of 24 h). Both species engaged in their most active foraging in October (RLKIs 15%, BLKI 25.3%) and the least in January (RLKIs 11.5%, BLKI 19.1%). The majority of the night was spent sitting on the water (BLKI 84.8 ± 8.5%, RLKI 91.1 ± 1.4%, $F_{1.46} = 4.66, P = 0.036$), with <5% of darkness spent in flight; however, BLKIs spent a higher percentage of the night engaged in active foraging behaviour than RLIKIs (BLKI 10.3 ± 4.1%, RLKI 6.1 ± 2.1%, $F_{1.45} = 21.54, P < 0.001$).

For the linear models relating active foraging (percentage of 24 h) to environmental characteristics, the inclusion of a temporal autocorrelation term improved the AIC scores. For RLIKIs, the best-fit model included six significant factors (Table 2); air temperature and combined daylight and twilight length were all positively related to active foraging, while SST, distance to the sea ice, cloud cover and wind speed were negatively related. For BLKIs, the best-fit model included seven significant factors (Table 2); active foraging was related positively to SST, mean sea level pressure, air

![Figure 3](https://example.com/figure3.png)
Figure 4 Activity budgets of red-legged kittiwakes (RLKIs), Rissa brevirostris (grey), and black-legged kittiwakes (BLKIs), Rissa tridactyla (black), for the non-breeding period, October–February, in the subarctic North Pacific. Percentages are of 24-h periods. Months when species are not significantly different, as determined by monthly linear mixed effects models with individual as a random effect, are indicated by a horizontal line. An asterisk indicates differences between sexes within a species. Means ± SD.

Table 2 Summary statistics for linear mixed models of environmental influences on time spent actively foraging for red-legged kittiwakes (RLKIs), Rissa brevirostris (n = 17, observations = 1927), and black-legged kittiwakes (BLKIs), Rissa tridactyla (n = 32, observations = 4202), in the subarctic North Pacific. All models include a temporal correlation term [corCAR1(form = ~date|id)]. Akaike information criterion (AIC), change in AIC relative to the best-fit model (ΔAIC) and marginal $R^2$ [$R^2(m)$] and conditional $R^2$ [$R^2(c)$] values are presented. For both species, AIC indicated that model 4 (in bold) was the best-fit model.

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SST, sea surface temperature; d2ice, distance to sea-ice edge; cloud, cloud cover; wind, wind speed; BP, mean sea level pressure; air, air temperature; moon, moonlight; humid, humidity; bathy, bathymetry.

Stable isotope analysis

Compared with BLKIs, the head feathers of RLKIs had higher $\delta^{15}N$ ($F_{1,62} = 27.29, P < 0.001$), lower $\delta^{13}C$ ($F_{1,62} = 10.38, P = 0.002$) and less variance for both $\delta^{15}N$ ($F_{42,18} = 11.91, P < 0.001$) and $\delta^{13}C$ ($F_{42,18} = 3.14, P = 0.011$; Fig. 5). $\delta^{15}N$ of body feathers was higher for RLKIs ($F_{1,62} = 9.41, P = 0.003$); neither $\delta^{13}C$ nor variances of body feathers were significantly different, but variance was higher between body feathers than head feathers for both species (Fig. 5). $\delta^{15}N$ of body feathers was higher than head feathers of BLKIs ($t = -2.56, P = 0.032$) but not RLKIs ($t = -1.774, P = 0.093$). There was a significant difference in $\delta^{13}C$ of head feathers of individual RLKIs sampled in two consecutive years (2010, $-18.56 \pm 0.32^{\circ} \text{C}; 2011, -18.34 \pm 0.21^{\circ} \text{C}; t = -2.2$, n = 17, $P = 0.043$) but not in those of individual BLKIs (2010, $14.94 \pm 0.96^{\circ} \text{C}; 2011, 14.32 \pm 1.50^{\circ} \text{C}; t = 2.73$, n = 37, P = 0.011) within individuals, there were no significant differences between years in $\delta^{15}N$ of head feathers and $\delta^{13}C$ and $\delta^{15}N$ of body feathers.

**Discussion**

We found that both kittiwake species made long-distance migrations and showed a substantial degree of spatial and dietary niche partitioning during the non-breeding period. Contrary to expectations, RLKIs were more coastal whereas BLKIs migrated to more pelagic areas and therefore experienced very different physical environmental conditions. Overall, BLKIs foraged more actively, more active at night and foraged more in moonlight. The lower variance in stable isotope ratios suggested that RLKIs tended to be dietary specialists during the late winter, whereas BLKIs were
Figure 5 Stable carbon and nitrogen isotope values from subarctic North Pacific red-legged kittiwakes (RLKIs), Rissa brevirostris (red, n = 19), and black-legged kittiwakes (BLKIs), Rissa tridactyla (black, n = 49), from head feathers (triangles) and body feathers (circles). Error bars are ± SD and lighter shaded markers indicate values of individual birds.

generalists. Our data suggest that RLKIs are particularly adapted to exploitation of the Bering Sea ecosystem, and that changes in the oceanographic regime here will more strongly influence population trends of this species.

Spatial niche

The two kittiwake species showed marked segregation in spatial distribution and associated environmental conditions during the non-breeding period, which was independent of the colony of origin (BLKIs from the two study colonies showed extensive overlap in distribution). By utilizing both the eastern and western Bering Sea, RLKIs exploited a diversity of habitats, including the shallow continental shelf, sea-ice edge and pelagic regions of high EKE. The use of the Bering Sea shelf in the autumn is supported by at-sea data (March-October), as the relative abundance of RLKIs increases over the shelf break, and to some extent over the shelf, during both the early autumn and spring, following the general trend for surface foragers in the region to move nearer to the shore during these periods (Hunt et al., 2013). The sea-ice edge is likely to be a key habitat for RLKIs, although from our large-scale geolocation data it is impossible to resolve the exact association. As well as the extensive coastal sea ice present for much of the winter, the Kamchatka Current is characterized by areas of relatively high EKE. Eddy activity may make prey more available for surface-foraging seabirds and provide predictable spatial structure for locating prey (Bost et al., 2009). Although the diversity in non-breeding habitats used by RLKIs might be expected to result in dietary shifts, our data on activity budgets, and the low variance in stable isotope ratios in feathers grown during the non-breeding season, suggest they maintain similar levels of foraging specialization throughout this period.

BLKIs showed a preference for westerly and central areas in the subarctic North Pacific and RLKIs also utilized waters of the WSG. This preference is similar to large-scale patterns observed for other marine predators, including migratory shearwaters and some cetacean species (Springer et al., 1999). It is likely that resources are more abundant or predictable here, as high primary productivity supports higher winter zooplankton biomass and a greater diversity of myctophid fishes than in the eastern North Pacific (Beamish et al., 1999; Nagasawa, 2000). None of the tracked kittiwakes utilized the Gulf of Alaska, one of the stormiest regions of the North Pacific (Wilson & Overland, 1986). Nevertheless, this is likely to be an important wintering area for a proportion of Alaskan BLKIs; birds from Prince William Sound have ranged there during some years (McKnight et al., 2011). Many kittiwakes breeding in the north-east Atlantic also cross the basin to winter in cold waters off Newfoundland and Labrador, suggesting a commonality in winter resource availability where cold waters, the Kamchatka Current (North Pacific) and Labrador Current (North Atlantic) move south (Frederiksen et al., 2012).

Behavioural niche

Both species were largely diurnal in their use of active foraging, which is similar to BLKIs tracked in the eastern North Pacific (McKnight et al., 2011). Environmental conditions were only able to explain a small portion of the variance in the percentage of time the two species spent actively foraging, reflecting the large amount of individual variation in both species. In general, BLKIs were more active, even during darkness, and, unlike RLKIs, BLKIs increased their active foraging when the Moon was fuller. Specialist predators are sometimes more efficient at catching and handling prey (Heinrich, 1976). However, it is surprising RLKIs were not more active during darkness, as suggested previously on the basis of their relatively large eyes (Storer, 1987). This does not refute the hypothesis that larger eyes are an adaptation for foraging at night, as this species could be employing a less energetically costly sit-and-wait strategy for night foraging (Jodice et al., 2003). RLKIs experienced more hours of twilight than BLKIs, but the activity patterns of both species suggest that they do not use all the daylight hours to meet their energetic needs.

Dietary niche

Our data suggest that RLKIs are foraging predominantly on higher trophic-level prey than BLKIs. Elevated $\delta^{15}N$ values do occur for other reasons, including as a result of fasting or spatial differences in baseline values. The latter are particularly important when considering large geographical ranges...
however, for head feathers grown in the late winter the geolocation data suggest both species were using off-shore resources, supporting the idea of higher trophic foraging by RLKIs. Nevertheless, higher δ¹⁵N values of body feathers from some RLKIs is probably the result of movement to the northeastern Bering Sea, as the baseline δ¹⁵N values increase 2–6‰, from south to north, whereas δ¹³C values are more spatially heterogeneous (Schell et al., 1998). Myctophids are not found in the shallow waters on the Bering Sea shelf (Beamish et al., 1999), which in itself suggests that RLKIs are able to shift their diets from the types of prey exploited during the summer. Excluding the individuals with elevated δ¹⁵N, the remaining RLKIs showed a low degree of variance in stable isotope ratios in their body feathers (δ¹⁵N variance = 0.257‰), indicating a diet specialization that is maintained for long periods.

Dietary specialization during the non-breeding period appears to be rare, and instead an expansion in trophic niche is more common (Cherel et al., 2007; González-Solis et al., 2011; but see Boden et al., 2013). RLKIs appear to be specialists during the pre-nuptial moult, as the variance in isotope ratios among individuals was less than 1‰ (Jaeger et al., 2009). This specialization may make them vulnerable to changes in prey populations, and indeed fluctuations in breeding success are evident at St George that relate to a negative competitive interaction with pink salmon, Oncorhynchus gorbuscha (Springer & van Vliet, 2014). How these interactions influence distributions is unknown, as we only tracked individuals during one year. However, individual RLKIs showed a slight, but significant, shift of 0.22‰, in δ¹³C in head feathers grown in consecutive years, which could relate to annual differences in spatial habitat use.

Population regulation

The striking non-breeding niche separation between these kittiwake species may help to explain the divergent population trends observed on St George, although other differences in life-history factors may also be important. Regardless, as RLKIs spent a large portion of the non-breeding period in the Bering Sea, it seems reasonable to expect that changes in year-round prey resources in this region will influence overwinter survival. Declines in RLKIs followed the 1976–77 regime shift in the Bering Sea (Hare & Mantua, 2000); however, how winter prey availability changed during this time period is unclear. Winter conditions in the Bering Sea show a high degree of annual variability, because of changes in sea-ice extent and the timing of ice retreat (Overland & Stabeno, 2004), whereas the subarctic North Pacific may provide a more stable wintering habitat (Bograd et al., 2004). Our data relate to a single year of tracking and hence the degree of annual variation in migration patterns and distributions is unknown; however, for RLKIs the lack of any significant change within individuals in the isotopic ratios of body feathers grown during consecutive winters of extensive sea ice suggests a high degree of fidelity in both habitat use and diets under these conditions.

The restricted range of the RLKI and its greater dietary specialization may make this species vulnerable to future declines in sea-ice extent, as the eastern Bering Sea is predicted to be ice-free year-round by 2050 (Wang et al., 2012). Our study highlights a close association between RLKIs and sea ice; however, it is unknown to what extent RLKIs rely on pagophilic prey. Kittiwake reproductive success is linked to sea-ice extent and timing of retreat at lagged time-scales (Zador et al., 2013); hatch dates have become progressively earlier, which is also thought to be related to prey availability and changes in sea-ice dynamics (Byrd et al., 2008). In this study, both species returned to the Pribilof Islands around the spring equinox, when there was still sea ice in the southeastern Bering Sea. Independent time series data for offspring return dates are not available, but on 8 April 1914, Hanna observed the first RLKIs returning to St George (Gabrielson & Lincoln, 1959), which hints that the reliance on springtime resources in the Bering Sea has existed for at least the last 100 years.

CONCLUSIONS

Our study provides new insights into the non-breeding distribution and ecology of two important avian predators in the Bering Sea ecosystem. Specifically, the division of range and habitat use of these two congeneric kittiwake species during this time implies that different environmental factors will influence foraging success and survival. The lower levels of activity shown by the RLKIs, as well as the high degree of similarity in stable isotope values, suggest that this species employs a specialized foraging strategy, which may increase their susceptibility to environmental change. Warming temperatures may allow BLKIs to use more of the Bering Sea during the winter, while the RLKIs' preferred habitat may shift further north. The degree of individual flexibility in migratory patterns may be an important factor in how well these two species will adapt to future climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Morphometrics of red-legged and black-legged kittiwakes.

Appendix S2 Migration characteristics of red-legged and black-legged kittiwakes.

Appendix S3 Overlap of utilization distributions between colonies and sexes of kittiwakes.

BIOSKETCH

Rachael Orben is a PhD candidate at the University of California of Santa Cruz. Her dissertation research focuses on the winter foraging ecology of Bering Sea seabirds.

Author contributions: all the authors conceived the ideas; R.A.O. and R.A.P. collected the data; R.A.O. analysed the data; and R.A.O. wrote the paper with contributions from the other authors.

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