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Resource partitioning between sympatric seabird species increases during chick-rearing

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Abstract. Partitioning of resources by competing species of seabirds may increase during periods of food shortages and elevated energy demands. Here, we examined whether food resource partitioning (differential use of foraging habitat or the consumption of different prey species) between common murres (COMU, *Uria aalge*) and thick-billed murres (TBMU, *U. lomvia*) breeding on the same colony in the Bering Sea increases with a predictable increase in energy demands between the incubation and chick-rearing stages of reproduction. We assessed the seasonal dynamics of food availability via corticosterone (CORT) levels and examined adult diet (via stable isotope analysis of nitrogen and carbon, SI) and chick diets (based on nest observations). We compared chick provisioning patterns and examined the characteristics of parental foraging habitat via deployment of bird-borne temperature-depth recorders. We found that CORT levels remained low and similar between the species and reproductive stages, reflecting relatively stable and favorable foraging conditions for both murre species during the study period. Comparisons of SI between murres and their potential prey indicated that diets were similar between the species during incubation and diverged during chick-rearing. Chick-rearing common and thick-billed murres also used different foraging habitats, as reflected in travel distances to foraging areas and sea surface temperature distributions of their foraging dives. TBMUs performed shorter foraging trips, deeper dives and delivered squid to their chicks, while COMUs foraged farther from the colony, performed shallower dives, and delivered fish species to their chicks. These results suggest that food resource partitioning between murre species increased during chick-rearing under favorable foraging conditions. Whether the dietary segregation reflected species-specific differences in adults' foraging efficiency, differences in chicks' dietary requirements, or was a way of reducing competition remains unknown. Regardless of the causal mechanism(s), food resource partitioning might ameliorate interspecific competition between sympatrically breeding birds during periods of increased energy demands.

Key words: common murre; competition; diving; foraging; stable isotope; stress levels; TDRs; thick-billed murre.

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Introduction

Interspecific resource partitioning may be affected by environmental fluctuations and competition (Schoener 1974, Goldberg and Barton 1992). The ecological theory of segregation predicts that multiple species competing for a single resource cannot persist in the same region (Lack 1946, Pianka 1969), and diet partitioning—along spatial, temporal, or prey-type axes—is essential for the coexistence of ecologically similar species. Spatial (Frere et al. 2008), temporal (Navarro et al. 2013), and dietary partitioning of resources has been previously detected in colonially breeding

seabirds (Young et al. 2010, Linnebjerg et al. 2013, Navarro et al. 2013, Robertson et al. 2014). However, few seabird studies have addressed whether partitioning occurs in response to food limitations or due to the predictable increases in energy demand at certain life stages (but see Barger and Kitaysky 2012). Here, we examine whether two sister species of murres (*Uria* spp., Alcidae), breeding side by side on the same colony, engage in spatial, temporal, and/or diet partitioning, which may allow them to decrease interspecific competition during the energetically demanding chick-rearing period.

When energy availability in the environment declines, seabirds respond by increasing the secretion of the stress hormone corticosterone (CORT; e.g., Kitaysky et al. 2007, 2010, Riechert et al. 2014, Barrett et al. 2015), which in turn mediates the changes in foraging behavior (Angelier et al. 2007, 2009, Barger and Kitaysky 2012). In murres, CORT is an effective proxy for changes in prey availability: Its relative concentration in blood plasma increases during food shortages (Kitaysky et al. 2007, Benowitz-Fredericks et al. 2008, Doody et al. 2008, Barrett et al. 2015). A previous study demonstrated that stressful food shortages (years when baseline CORT was elevated) resulted in increased interspecific trophic niche partitioning between murre species during incubation; that is, stable isotopic signatures diverged between species during food-limited periods (Barger and Kitaysky 2012). Therefore, we measured CORT in chick-rearing murres to determine whether food limitation might contribute to resource partitioning during the period of rearing young.

Alternatively, when life history stages result in anticipated increases in energy demand, birds can change food resources and foraging patterns facultatively, without the trigger of nutritional stress. Increases in energy demands associated with raising young impose additional, yet predictable, constraints on parental foraging and may lead to the changes in foraging habitat, behavior, or food sources during the breeding season (Ito et al. 2010, Wilson 2010, Linnebjerg et al. 2013). The shift from incubation to chick provisioning is a common example of an expected increase in energy demands in birds (Monaghan et al. 1989, Croll 1990, Montevecchi et al. 1992, Welcker et al. 2015), which may incite behavioral responses, independent of environmentally induced food shortages.

Murres are central place foragers during the breeding season (Elliott et al. 2009), and thus, parents may adjust behavior to optimize self-foraging (Williams et al. 2008) or specific requirements of their young (Markman et al. 1999) without a nutritionally driven increase in stress hormones. These adjustments may also result in partitioning of the trophic niche. To examine the interspecific differences in spatial and temporal variability of foraging habitat use, we deployed temperature-depth recorders (TDRs) on adult murres during chick-rearing. Previous studies have shown these bird-borne data loggers to be an effective tool to detect slight differences in water mass selection and foraging behaviors between and within seabird species (Ito et al. 2010, Wilson 2010, Navarro et al. 2013, Young et al. 2015).

Common and thick-billed murres are pursuit-diving predators specializing on fish and large invertebrates (Birkhead and Nettleship 1987, Iverson et al. 2007); each foraging trip they bring back a single whole prey item (by holding it in the beak) to their chick. Adult diets might differ substantially and cannot be inferred from chick diets (Ito et al. 2010). To compare the interspecific differences in the diet composition of adult birds, we analyzed the stable isotope ratios of red blood cells and plasma (slow and fast turnover rates, respectively) and the murres' potential prey (Thompson et al. 1999, Cherel et al. 2008, Inger and Bearhop 2008). Using these values, we estimated the contribution of potential prey species to the diet of adult birds using a Bayesian mixing model (Parnell et al. 2010). To compare chick diets, we directly observed prey delivered to chicks.

The main goal of this study was to determine whether the degree of interspecific food resource partitioning (along spatial, temporal, and/or prey-type axes) changes between the incubation and chick-rearing stages of reproduction and in relation to levels of nutritional stress incurred by parent murres. Earlier observations (Paredes et al. 2012, Harding et al. 2013) suggest that during the study period, foraging conditions were favorable for seabirds breeding on our focal colony, thus potentially allowing us to disentangle the resource partitioning in response to a predictable increase in energy demand from that

induced by a food shortage. We predicted that if interspecific food resource partitioning is a facultative response to an increase in energy demands, then we would observe a change in diets and/or foraging habitats between the incubation and chick-rearing stages under the conditions of low adult nutritional stress.

Methods

Study site and field methods

This study was conducted on Bogoslof Island (53°55′38″ N 168°02′04″ W) in 2009. Bogoslof Island is located ~40 km north of the Aleutian Islands in the Bering Sea. Incubating (COMU n = 11, TBMU n = 10) and chick-rearing (COMU n = 31, TBMU n = 36) birds were captured (with telescopic noose poles) at their nesting sites in mixed colonies of common and thick-billed murres (for details of bird capture methods, see Benowitz-Fredericks et al. 2008). In 2009, murres arrived in the vicinity of Bogoslof Island in early April (Orben et al. 2012), laid eggs in late June (incubation ~26–39 d), hatched chicks in early August (Ainley et al. 2002), and fledged their chicks by early September (C. P. Barger, *personal observation*). Incubating birds were captured from 26 June to 30 June, while chick-rearing birds were captured from 26 July to 25 August. During sampling, all birds were banded with US Fish and Wildlife metal bands, and no individuals were sampled twice. Blood samples were collected from the brachial vein within three minutes of capture, with the capture time defined as the second the bird had contact with the monofilament noose. Samples collected within this time frame reflect baseline CORT levels (Romero and Reed 2005, Kitaysky et al. 2007). During chick-rearing, we placed TDRs (diameter: 8 mm, length: 30 mm, weight in air: 2.7 g; Cefas G5, Cefas Technology, Lowestoft, UK) on common (n = 11) and thick-billed murres (n = 28).

Blood sampling and hormone analysis

Blood samples of COMU and TBMU were collected using a heparinized syringe or heparinized needles and microhematocrit tubes, transferred to 0.5-mL microcentrifuge tubes, and stored on ice until centrifugation, usually no more than 8 h postcollection. Whole blood samples were centrifuged for 5 min to separate the plasma and red blood cells. The plasma was removed and stored frozen until CORT assays. Plasma concentrations of CORT were determined via radioimmunoassay as previously described (Kitaysky et al. 2007). Inter- and intra-assay CVs were less than 6% and 2%, respectively.

Stable isotope analysis

Red blood cells and plasma from common and thick-billed murres were used for stable carbon and nitrogen isotope analysis. Of these two major constituents of blood tissues, plasma has a faster turnover rate than the red blood cells (Hobson and Clark 1993). Thus, stable isotope signatures of red blood cells of birds sampled at incubation represent their diet during the two months prior to blood sampling, which in our case corresponds to the period of birds' arrival at the colony (late April; Orben et al. 2015). Stable isotope signatures of plasma reflect current diets (i.e., the week prior to blood sampling) of birds at incubation (late June) and chick-rearing (late July–August). Sampling and stable carbon and nitrogen isotope analyses of murre prey species, which represent similar sizes of prey consumed by murres and were collected in murre foraging areas near the colony, have been reported earlier (Barger and Kitaysky 2012). Briefly, concurrent with sampling of birds at the colony, all potential prey species were collected during systematic fish trawl surveys in the vicinity of the colony and stable isotope analyses of lipid-extracted whole body tissue of prey were determined (following the procedures described in Williams et al. 2007).

Prior to the stable isotope analysis, the plasma samples were delipidated via the extraction of 20 μL of plasma in 800 μL of 20:80 methanol–chloroform solution. This procedure effectively reduced the plasma lipid content so that the carbon/nitrogen ratio of samples more closely resembled pure protein (carbon/nitrogen ratio was reduced from more than 4 to less than 3.5 in delipidated plasma samples). Carbon/nitrogen ratio of red blood cells was low (< 3.5); thus, lipid extraction was not needed. Freeze-dried plasma and red blood cell samples were weighed (0.100–0.600 mg) and placed in a tin capsule, sealed, and deposited in an elemental analyzer (EA) autosampler. The stable isotope data were obtained using continuous-flow isotope ratio mass spectrometry (CF-IRMS). The instrumentation used was a

Delta+XP isotope ratio mass spectrometer (Thermo Electron, Waltham, Massachusetts, USA) interfaced with an EA Costech ECS 4010. Stable isotope ratios are reported in delta notation as parts per thousand (‰) deviation from the international standards $\delta^{13}C_{PDB}$ and $\delta^{15}N_{air}$, as follows: $\delta X = [(R_{sample}/R_{standard}) - 1]‰$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Replicate measures of internal laboratory standard (Peptone) indicated measurement errors to be ±0.16‰ N and ±0.13‰ for C. Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility.

Chick diet and parental time budgets

Murres typically forage for themselves and then bring a single prey item back to the colony for their chick (Birkhead and Nettleship 1987). Prey delivered to chicks are held in the beak and are usually visible for identification (Birkhead and Nettleship 1987). We conducted two 18-h observation periods for common murres and three similar observation periods for thick-billed murres. In each study plot, 12–15 pairs were marked with a nontoxic cattle dye such that we could observe specifically marked individuals and distinguish between the parents at a single nest. During nest watches, each pair was observed continuously and prey items were photographed and identified to the lowest taxonomical level possible.

Data logger deployment and analysis

Temperature-depth recorders (G5, Cefas Technology) were set to record temperature and pressure (depth) at 2-s intervals with a temperature and depth resolution of 0.1°C and 0.1 m, respectively. In order to reduce the instrument impacts on flight and diving behavior, the loggers were attached to the keel feathers with Tesa tape (Tremblay et al. 2003, Takahashi et al. 2008, Ito et al. 2010). Birds with data loggers had a blood sample drawn at the initial capture, were banded and measured, and were released within 10 min. Upon recapture of the bird, the logger was removed and diving and temperature data were downloaded to a computer using G5 Host, Cefas Technology.

The analyses of diving profiles were conducted using Igor Pro software (Wave Metrics, Portland, Oregon, USA). Maximum depth was measured for each dive, sea surface temperature (SST) for each dive bout, and trip duration for each trip. Foraging trip duration was determined from the timing of the temperature drop associated with colony departure to a return to temperature indicative of presence at the colony (equal or higher than 15°C). To estimate the duration of flight from the foraging ground, we extracted flight times from the end of last dive until an individual's return to the colony. Sea surface temperatures were calculated by using a custom-written script (developed by Ito et al. 2010) in Igor Pro that calculated the SST during the long postdive surface times at the end of a bout of diving.

Statistical analyses

To assess the diet differences by species from arrival to incubation, carbon and nitrogen signatures in the red blood cells and plasma (sampled at incubation) were compared using Kruskal–Wallis tests, as the values were not normally distributed. To address the diet differences by species between the incubation and chick-rearing stage, linear models were run with either carbon or nitrogen plasma signature as the response variable and date (incubation and chick-rearing dates) and species as predictors. We used a general linear model (GLM) to determine whether baseline CORT changed between species as the breeding season progressed from incubation through chick-rearing. Baseline CORT data were log-transformed to meet the assumptions for parametric statistical comparisons. To assess the differences in chick diets between the species, we used chi-squared tests. We compared attendance (time spent at the colony), foraging trip durations, and chick-feeding rates obtained from chick-rearing TDR deployments using normal linear mixed models, with species as a fixed factor, individual as a random factor, and Julian date as a covariate. For the comparisons of diving data, we used separate normal linear mixed models to test whether birds were using different water masses (SST per dive), dive depths, trip durations (a time period between departure and the subsequent return of an individual to the colony), and flight times from the end of last foraging bout to arriving at the colony. For each model, species was included as a fixed factor and individual identity was included as a random factor. To test how the usage of different water masses (as reflected in the SST of each diving bout) and diving depths changed over the course of the day, time of day was included in those models as a

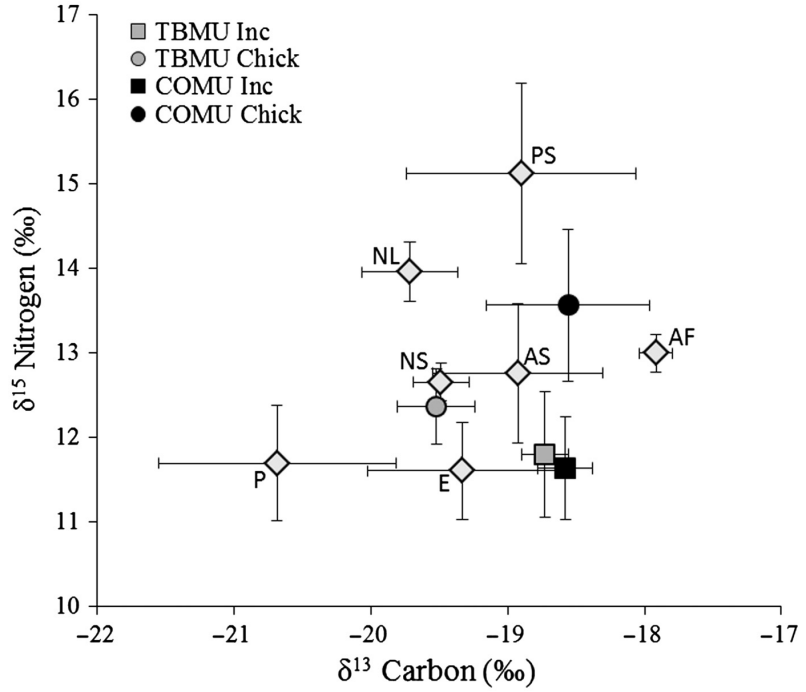

Fig. 1. Mean ± SD $\delta^{13}C$ and $\delta^{15}N$ plasma values for common murres (COMU) and thick-billed murres (TBMU) during incubation and chick-rearing. Prey species $\delta^{13}C$ and $\delta^{15}N$ have been adjusted by a trophic enrichment factor of −0.08‰ (C) and 2.25‰ (N) and are coded as follows: arctic squid (AS), arrowtooth flounder (AF), northern lampfish (NL), northern smoothtongue (NS), Pacific smelt (PS), walleye pollock (P), and euphausiids (E).

continuous variable. To assess the temporal partitioning, we used the Kolmogorov–Smirnov two-sample test on frequencies of dives performed by individuals over time of the day. We compared diving frequencies between species during the night- and daytime periods using a *t*-test on proportions of dives performed by each individual during the nighttime period. We determined the night- and daytime periods based on the direct observations of the colony attendance behavior of chick-rearing murres. As we have never observed murres arriving at the colony after mid-night and prior to 07:00 in the morning, we deemed it as the "nighttime" and the remaining part of the day as the "daytime" period. Our definition of the nighttime and daytime periods also corresponds to the timing of sunset (24:39–01:21) and sunrise (09:15–09:53) in the study region from 25 July to 16 August (www.NOAA.gov). All statistical analyses were performed using R (v.2.11.1, R Foundation for Statistical Computing, Vienna, Austria). Data are presented as means ± SE unless otherwise specified.

Dietary analysis based on stable isotope ratios

We used the SIAR package (Parnell et al. 2010) in R (version 3.1.2), to infer murre diet composition based on the stable isotope signatures of blood plasma and those of seven potential prey species caught in the vicinity of the colony concurrent with sampling of chick-rearing birds (Whitman 2010, see table in appendix 1.1 and 1.2 as reported in Barger and Kitaysky 2012).

The means for the seven potential prey species were assigned as noninformative independent priors. The mean and precisions for the priors of the enrichment factors (Fig. 1) were determined using (1) for N, we calculated an enrichment factor for TBMU chick plasma sampled during the same year based on their squid prey (mean = 2.25, SD = 0.50) and (2) for C, the enrichment factor reported in Caut et al. (2009) for plasma (mean = −0.08, SD = 0.38). The N enrichment factor we estimated is similar to the enrichment factors reported for plasma in Caut et al. (2009) and Cherel et al. (2005*a*, *b*). For whole

blood, Williams et al. (2007) reported a fractionation factor of 2.28‰ for $\delta^{15}N$ and −0.50‰ for $\delta^{13}C$ for tufted puffins (*Fratercula cirrhata*) that belong to the same family, Alcidae, as our focal species. We modeled the vector of the seven prey sources for a given year and bird species as coming from a Dirichlet distribution and ran a Markov chain Monte Carlo (MCMC) for 500,000 iterations. We discarded the first 50,000 samples as a burn-in period, resulting in a total of 450,000 samples for calculating the posterior statistics.

Results

Corticosterone (CORT) analysis

Baseline CORT levels were relatively low (COMU: 4.86 ± 0.58 ng·mL^{-1}; TBMU: 3.63 ± 0.33 ng·mL^{-1}) and similar between the species ($F_{1,115} = 2.35$, $P = 0.128$) and stages ($F_{1,114} < 0.001$, $P = 0.978$). The species × stage interaction term was not significant ($F_{1,114} = 0.50$, $P = 0.479$), and the Julian date effect was also not significant ($F_{1,114} = 1.82$, $P = 0.180$).

Stable isotope analysis and Bayesian model output

Diets from arrival to incubation, as measured in stable isotope signatures of red blood cells, differed between the two species (Fig. 2): Nitrogen was more enriched in thick-billed murres (Kruskal–Wallis $\chi^2 = 6.98$, df = 1, $P = 0.0082$), and carbon was more enriched in common murres (Kruskal–Wallis $\chi^2 = 10.1$, df = 1, $P = 0.0015$). However, in plasma at incubation, species did not differ in isotope signature (nitrogen: Kruskal–Wallis $\chi^2 = 0.436$, df = 1, $P = 0.51$; carbon: Kruskal–Wallis $\chi^2 = 1.44$, df = 1, $P = 0.23$). Therefore, the diets were different at arrival, but similar by the time birds were incubating.

During the chick-rearing stage, diets diverged between species (based on stable isotope signatures of their blood plasma, Fig. 2). Nitrogen increased from incubation to chick-rearing in both species, but much more strongly in common murres (date: $F_{1,67} = 61.5$, $P < 0.0001$; species: $F_{1,67} = 26.6$, $P < 0.0001$; date × species: $F_{1,67} = 19.9$, $P < 0.0001$). Carbon signatures declined from incubation to chick-rearing in thick-billed murres, while remaining the same in common murres (date: $F_{1,67} = 17.4$, $P < 0.0001$; species: $F_{1,67} = 67.5$, $P < 0.0001$; date × species: $F_{1,67} = 16.4$, $P < 0.001$).

Using the Bayesian mixing analysis, we modeled the fractional contribution (95% credible interval) of seven prey items known to contribute to diets of murres breeding on Bogoslof Island in the North Pacific (Fig. 3). The results suggest that during the incubation stage for both species of murres, arrowtooth flounder was the most important prey type (Fig. 3). During chick-rearing, arrowtooth flounder and Pacific smelt were likely the most important prey of adult common murres, while northern smoothtongue, walleye pollock, and euphausiids were likely the main prey items for adult thick-billed murres (Fig. 3).

Chick diets

A total of 184 prey items were observed between the two species and 98% were identified to genus/family. The remaining 2% were classified as unidentified because the observer's view of the prey delivered was obscured or the rate of delivery was too rapid. The proportion of fish and squid in chick diets differed between species ($\chi^2 = 13.56$, df = 2, $P < 0.001$). Common murre chicks were primarily (91%) fed schooling fish, *Osmeridae*, whereas thick-billed murre chicks received primarily squid (89%) and only a small percentage of their diet was composed of fish (Fig. 4).

Chick provisioning rates were also different between the species: Thick-billed murre chicks were fed four to five items per 18-h observational period (0.244 ± 0.008 feeds/h, $n = 113$) compared to common murre chicks that were fed only two to three items per 18-h observational period (0.156 ± 0.012 feeds/h; $n = 71$; interspecific difference: $F_{1,55} = 23.27$, $P < 0.001$).

Foraging habitat

A significant interspecific difference in the foraging trip duration was detected (Fig. 5). Direct observations of nests showed that thick-billed murres performed shorter forging trips compared with those of common murres (TBMU 174 ± 6.18 min, $n = 82$; COMU 353 ± 22.13 min, $n = 43$; $F_{1,36} = 5.67$, $P = 0.023$), and TDR data showed the same pattern ($F_{1,35} = 17.34$, $P < 0.001$; Fig. 5).

Based on the flight time from last foraging bout prior to an individual's arrival at the colony (assessed via TDR), thick-billed murres performed shorter flights than common murres (COMU:

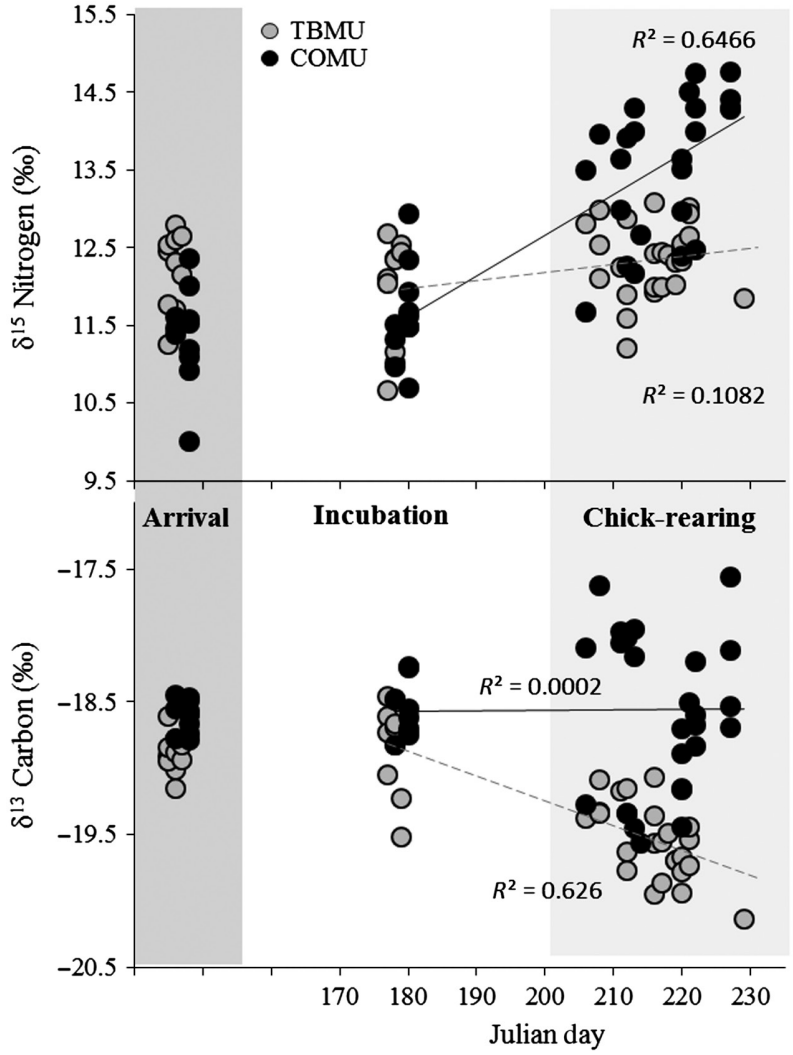

Fig. 2. Seasonal changes in stable isotope signatures of adult common (black circles: COMU) and thick-billed (gray circles: TBMU) murres breeding on Bogoslof Island in 2009: top $\delta^{15}N$ and bottom $\delta^{13}C$. "Arrival" values are signatures of RBC collected during incubation. Lines represent linear regressions for common (solid line; $\delta^{15}N$: $R^2 = 0.65$, $\delta^{13}C$: $R^2 < 0.01$) and thick-billed (dashed line; $\delta^{15}N$: $R^2 = 0.11$, $\delta^{13}C$: $R^2 = 0.63$) murres. Julian dates before 206 represent the incubation stage and thereafter the chick-rearing stage.

50.1 ± 5.4 min, n = 31; TBMU: 15.5 ± 1.6 min, n = 122; $F_{1,36} = 5.67$, $P = 0.023$). Assuming that individuals traveled directly from the location of their last foraging place back to the colony at a speed of 65 km·h^{-1} (Benvenuti et al. 1998, Takahashi et al. 2008), their estimated average travel distances were ~54 km from the colony for common and ~17 km for thick-billed murres.

Sea surface temperatures differed by time of day for common and thick-billed murres (time of day × species; $F_{1,15515} = 56.19$, $P < 0.001$). Common murres foraged in warmer waters at night and colder waters during daytime compared with thick-billed murres (Fig. 6, lower panel).

Diving depths were not significantly different between the species ($F_{1,37}$ = 5.31, P = 0.337), but diving depth differed with the time of day ($F_{1,23032}$ = 1,115.19, P < 0.001). The temporal dynamics of diving depths were different between the species (time of day × species; $F_{1,23032}$ = 115.57, P < 0.001) with common murres diving shallower during daytime and deeper at

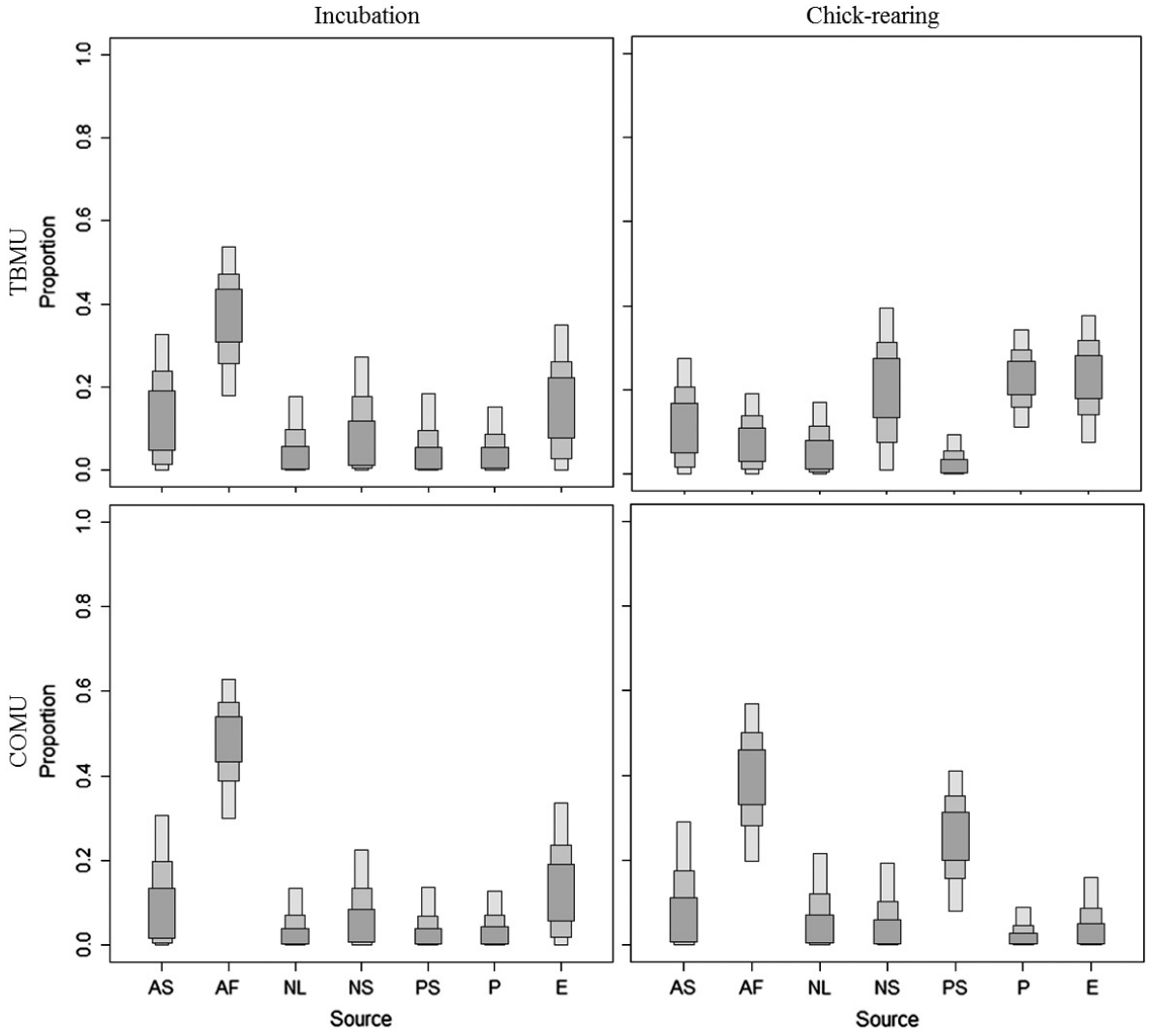

Fig. 3. Diet compositions of incubating and chick-rearing common (COMU) and thick-billed murres (TBMU) as estimated by SIAR. Figure shows posterior means and 95%, 75%, and 25% credible intervals of the fractional contribution (proportion) of arctic squid (AS), arrowtooth flounder (AF), northern lampfish (NL), northern smoothtongue (NS), Pacific smelt (PS), walleye pollock (P), and euphausiids (E) sampled in the vicinity of the breeding colony in 2009.

nighttime compared with thick-billed murres (Fig. 6, middle panel).

Temporal changes in frequencies of foraging dives were different between the species (Kolmogorov–Smirnov $D = 43.77$, $P < 0.001$; Fig. 6, upper panel). Thick-billed murres performed a higher proportion of dives at nighttime ($t_{31} = 3.62$, $P < 0.001$) and a lower proportion of dives during daytime when compared with common murres.

Discussion

Animals with a large ecological niche overlap, such as common and thick-billed murres, are expected to increase the partitioning of their foraging resources when experiencing an energy deficit, induced by either food shortages (resulting in less energy available from the environment, i.e., Barger and Kitaysky 2012) or an increase in organismal energy demands

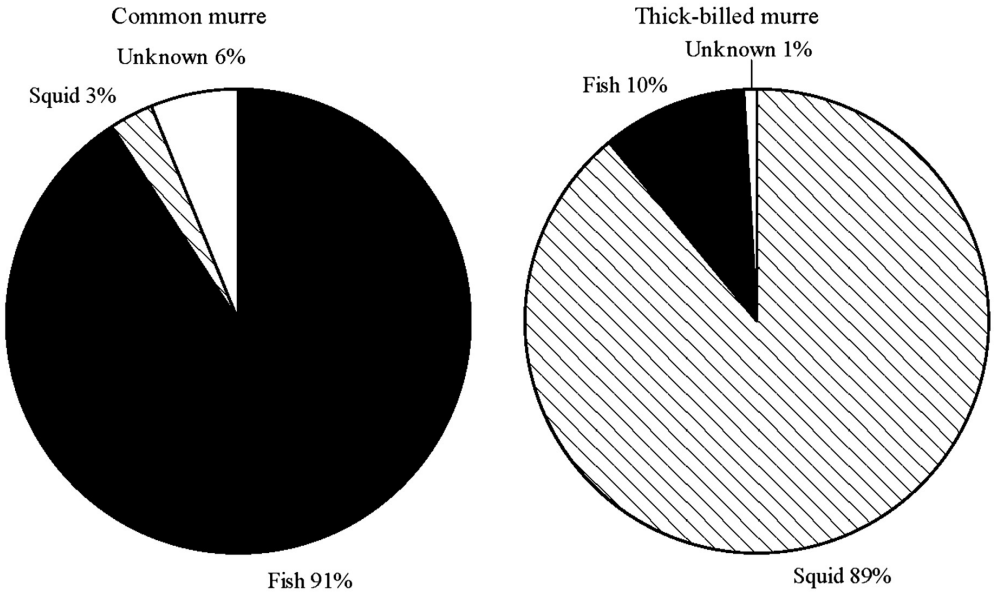

Fig. 4. Diet compositions of common and thick-billed murre chicks (based on the direct observations of prey delivered). Fish were the primary item in common murre chick diets compared to squid in thick-billed murre chick diets.

(presented here). In this study, we examined how these two closely related species partitioned available food resources during incubation and chick-rearing. We found that the diets of common and thick-billed murres were dissimilar when they arrived at the breeding colony, converged during incubation and then diverged during chick-rearing. Chick-rearing murres used different foraging habitats and pursued different foraging strategies: Thick-billed murres foraged in close proximity to the colony and primarily delivered squid to their young, while common murres foraged farther from the colony and fed their chicks with schooling fish. This apparent partitioning of foraging resources, at a spatial, temporal, and prey-type level, was not influenced by food limitations experienced by breeding birds, as nutritional stress levels of parents remained low in both species and did not change throughout the breeding season. Similar results have been recently obtained for resource partitioning by chick-rearing common and thick-billed murres on a different colony (St. George I. the Pribilofs) in the southeastern Bering Sea (Kokubun et al. 2015), which indicates a potential generality of our findings.

Adult diets

Murres breeding on Bogoslof Island in 2009 appeared to utilize a variety of prey species for chick provisioning and self-feeding. During incubation, adults of both species had similar plasma isotopic signatures, suggesting their reliance on similar prey resources and habitats. Bayesian modeling predicted that incubating birds (both species) fed on a broad spectrum of available prey species dominated by the arrowtooth flounder. However, as parents transitioned from incubation to chick-rearing, a concurrent shift in adult diets occurred in both species: Common murres were consuming mostly arrowtooth flounder and Pacific smelt, while thick-billed murres were consuming northern smoothtongue, euphausiids, and walleye pollock (Fig. 3). The trend of increasing $\delta^{15}N$ signatures of chick-rearing common murres (Fig. 2) also suggests that parents, especially common murres, switched from lower trophic-level prey (probably euphausiids) during incubation to higher trophic-level prey during chick-rearing. Enrichment of $\delta^{15}N$ values can occur when food shortages result in starvation and metabolism of body proteins (Oelbermann and Scheu 2002). However, this was not supported by our

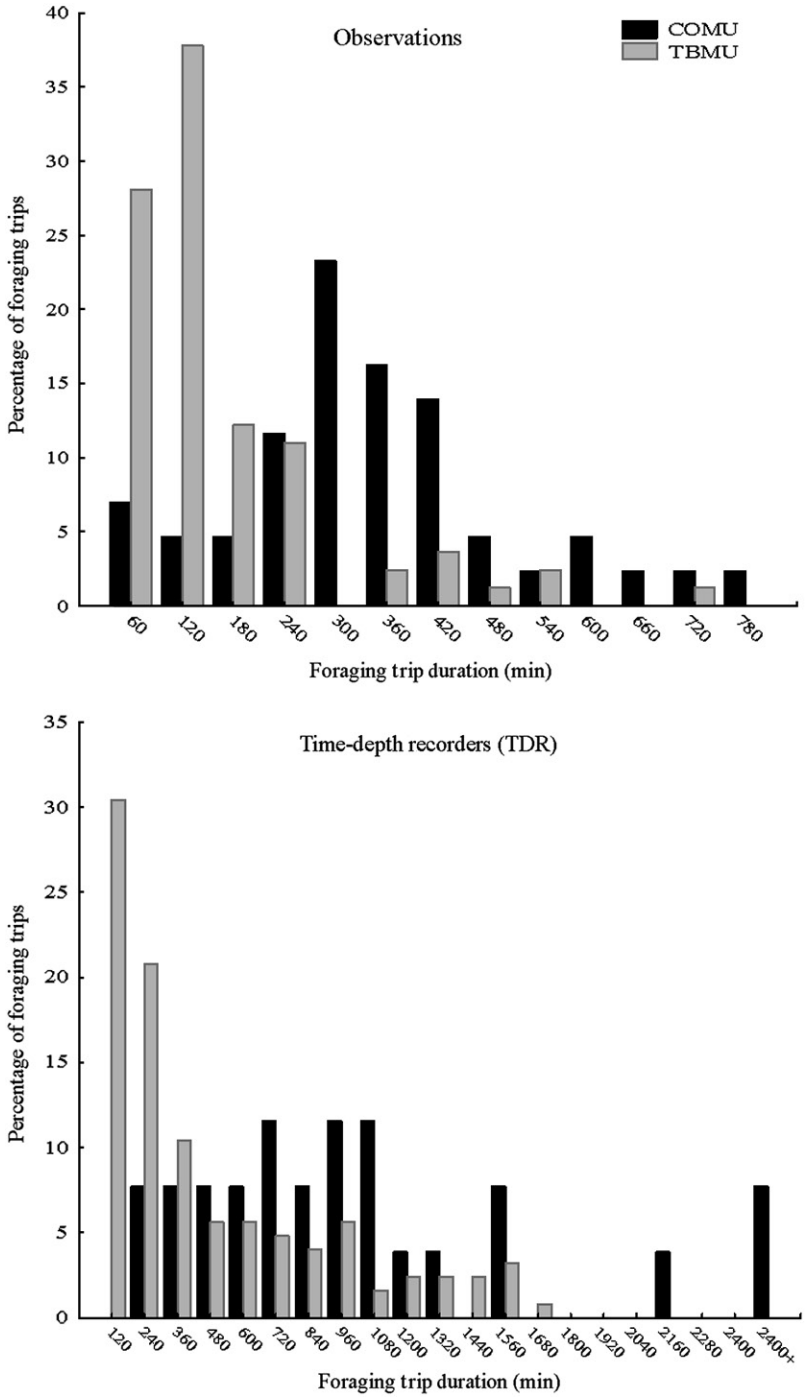

Fig. 5. Foraging trip durations of common and thick-billed murres based on the direct observations of individuals attending nest (upper panel) and obtained with bird-borne temperature-depth recorders (TDRs, lower panel). Results obtained by both techniques agreed that common murres (black bars) had longer foraging trips than thick-billed murres (gray bars). Direct observations of nests were limited to an 18-h period of daylight and thus represent only trips completed during a period that was equal or shorter than 18 h. The use of TDR loggers allowed us to record longer (overnight) foraging trips performed by breeding birds.

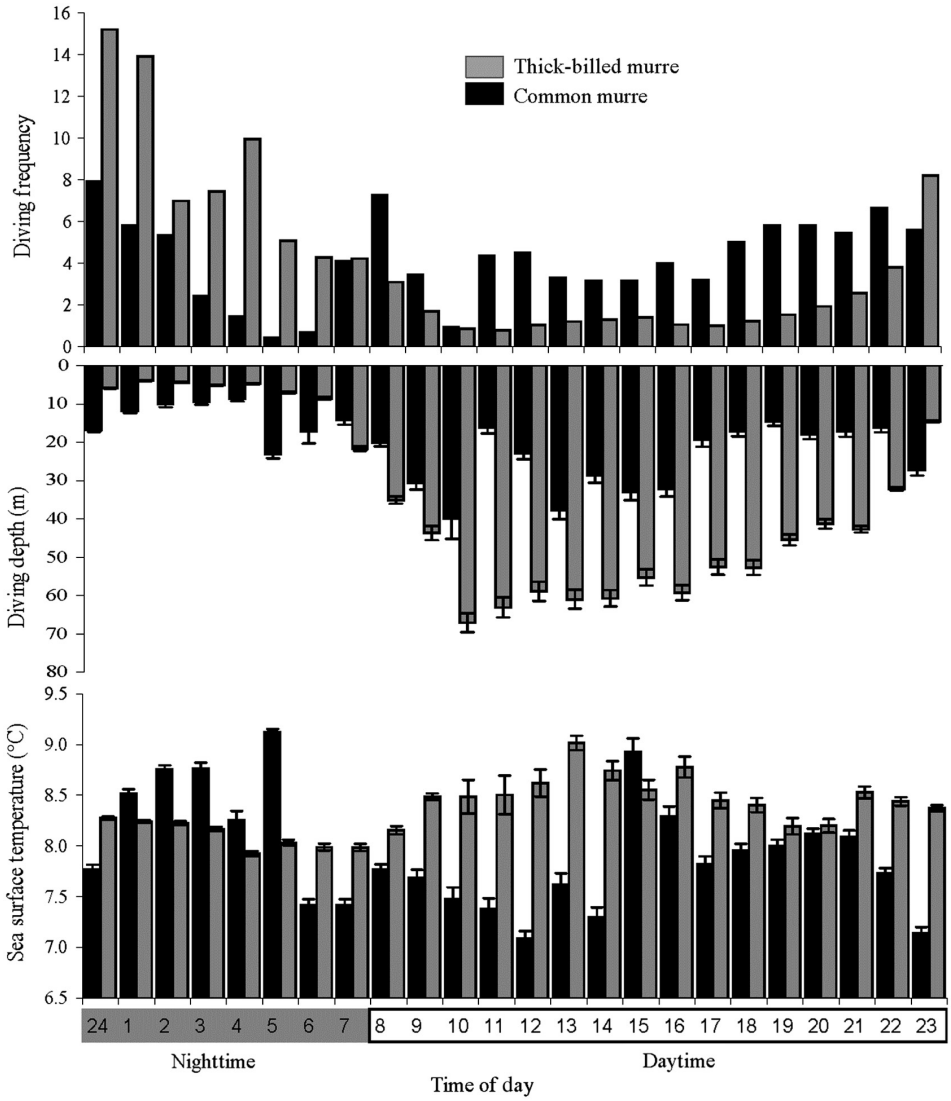

Fig. 6. Temporal variation in foraging patterns of chick-rearing murres (assessed with TDR bird-borne data loggers). Upper panel: Thick-billed (28 birds, 10,267 dives, gray bars) murres performed more of their foraging dives at nighttime (24:00–06:59) compared to common (11 birds, 5282 dives, black bars) murres (each bar represents the mean proportion of dives per time window). Middle panel: When foraging at nighttime, common murres targeted prey at deeper depths compared with thick-billed murres. Each bar represents the mean depth in that time window ±SE. Lower panel: On average, common murres foraged in colder waters (i.e., lower sea surface temperature [SST]) compared with tick-billed murres, except during nighttime hours when common murres foraged in warmer waters. Each bar represents the average maximum SST per foraging bout ±SE.

measures of physiological stress (i.e., CORT), which remained relatively low (e.g., CORT levels of common and thick-billed murres measured at the same colony in 2004 were twice as high as in 2009, see Barger and Kitaysky 2012 for interannual comparisons) and stable throughout the reproductive season in both species, indicating little nutritional limitation. Our results provide support for the hypothesis that murres differ in their prey specialization (e.g., Birkhead and Nettleship 1987, Barrett et al. 1997, Barger and Kitaysky 2012), and also indicate that foraging

preferences of both murre species may change between the incubation and chick-rearing stages of reproduction.

Spatial and temporal partitioning of foraging habitat

We found evidence that common and thick-billed murres also engage in spatial segregation of foraging habitat: (1) Murres foraged in different water masses as reflected in SST and (2) foraging trip durations and travel time between foraging grounds and the breeding colony differed between the species. We also found evidence for temporal segregation: (1) Species foraged in waters with different SST depending on the time of day and (2) thick-billed murres' diving frequency peaked during the nighttime hours, while common murres' diving frequency peaked during the daytime hours. This suggests that in response to an increase in energy demand associated with chick-rearing, the two species increased the partitioning of food resources by capturing prey in different foraging habitats.

Species-specific foraging strategies

During the breeding season, central place foragers are expected to forage optimally by balancing the length of their foraging trips with the energy content of prey delivered to young (Kacelnik 1984). In this study, we found that the focal species used two different foraging strategies to achieve this balance. Common murres took longer foraging trips farther away from the colony, while thick-billed murres took shorter trips and foraged closer to the colony. According to the predictions of optimal foraging theory, we expected that chick-rearing individuals performing longer foraging trips would deliver more energy-rich prey items to their young compared with individuals that perform shorter foraging trips. However, previous studies (Whitman 2010) have found that in the study region, the *Osmeridae* species of schooling fish (a prevalent food of common murre chicks in our study) and squid (main food of thick-billed murre chicks) are relatively similar in their energy densities per prey item (also see Cherel and Ridoux 1992, Van Pelt et al. 1997, Hedeholm et al. 2011). This observation implies that despite apparently larger foraging effort (i.e., longer traveling distances between colony and foraging grounds), common murres were not delivering more energy per trip than thick-billed murres. Thick-billed murre chicks might require the observed higher feeding rates than common murre chicks due to an additional energy expenditure associated with a squid diet. Marine fish and invertebrates differ in their salt content: Squid contain more salt (isosmotic to their environment) than fish (hyposmotic; Hodum and Hobson 2000). Because murres feed their young whole, undigested prey, thick-billed murre chicks would have to excrete excess salt they receive with squid, which is an energy-demanding physiological process (Nystrom and Pehrsson 1988, Dosch 1997, Hodum and Hobson 2000, Hedeholm et al. 2011). Thus, although common murre chicks were fed less frequently than thick-billed murre chicks, perhaps their energetically more profitable prey (i.e., that does not come with a salt excretion cost) could compensate for lower chick provisioning rates of parent common murres.

The species-specific foraging strategies that we observed during chick-rearing may also be due in part to the differences in foraging specialties of each species. Past studies suggested that common murres are potentially more adept at foraging for fish, whereas thick-billed murres are suited for capturing a variety of invertebrate and fish species (Birkhead and Nettleship 1987). Our results provided some support for this: Euphausiids were a more important prey of chick-rearing thick-billed than common murres (Fig. 2) and dive frequency and depth patterns were contrasting. Thick-billed murres dove more frequently but to shallow depths (perhaps pursuing squid) at nighttime, while common murres dove more frequently to shallower depths during the daytime (Fig. 6, upper and middle panels). It has been shown that body size may play an important role in shaping the foraging decisions of murres breeding on the same colonies (Paredes et al. 2015). For instance, large-bodied individuals (such as daytime diving TBMU; Fig. 6, middle panel) are more adept foragers on prey located at great depths, while small-bodied individuals (such as COMU) may travel long distances from breeding colonies to forage on prey available at relatively shallow depths. Morphological differences may also play a role in prey specialization; smaller, more mobile common murres may have more success capturing forage fish, which may contribute to the diel

differences in foraging patterns. Therefore, segregation of foraging habitat during chick-rearing between thick-billed and common murres may be facilitated by the morphological differences between the species (Elliott et al. 2013, Paredes et al. 2015).

Conclusions

In this study, we observed an increase in interspecific resource partitioning by chick-rearing murres. During this reproductive season, food did not appear to be limited (as reflected in low levels of nutritional stress incurred by breeding murres). This allowed us to disentangle resource partitioning due to food shortages from a predictable increase in energy demands due to a shift from incubation to chick-rearing. Our results clearly showed that resource partitioning occurred spatially, temporally, and through the selection of different prey. It is plausible that murres have adapted this foraging strategy to ameliorate interspecific competition when large energy demands of chick provisioning are anticipated. The species' chosen strategies may reflect either interspecific differences in foraging efficiencies of parents or energy demands of chicks depending on prey type (large invertebrates vs. schooling fish). Regardless of the proximate mechanism, during food shortages (Barger and Kitaysky 2012) or increased energy demands (this study), a mismatch between energy available in the environment and animal's energy demands is likely to lead to an increased partitioning of food resources by species of seabirds breeding on the same colonies.

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