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Foraging segregation of two congeneric diving seabird species (common and thick-billed murres) breeding on St. George Island, Bering Sea

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Abstract

Sub-arctic environmental changes are expected to affect the ecology of marine top predators. We examined the characteristics of foraging behavior of two sympatric congeneric diving seabirds, common (*Uria aalge*: hereafter COMU) and thick-billed (*U. lomvia*: hereafter TBMU) murres breeding on St. George Island located in the seasonal sea-ice region of the Bering Sea. We investigated their flight duration, diel patterns of dive depth, and underwater wing strokes, along with morphology and blood stable isotopes. Acceleration-temperature-depth data loggers were attached to chick-guarding birds, and behavioral data were obtained from 7 COMU and 12 TBMU. Both species showed similar trip duration (13.21 ± 4.79 h for COMU and 10.45 ± 7.09 h for TBMU) and similar diurnal patterns of diving (frequent dives to various depths in the daytime and less frequent dives to shallow depths in the nighttime). During the daytime, dive depths of COMU had two peaks in shallow (18.1 ± 6.0 m) and deep (74.2 ± 8.7 m) depths, while those of TBMU were 20.2 ± 7.4 m and 59.7 ± 7.9 m. COMU showed more frequent wing strokes during the bottom phase of dives (1.90 ± 0.11 s^{-1}) than TBMU (1.66 ± 0.15 s^{-1}). Fishes occurred with higher proportion in the bill-loads brought back to chicks in COMU (85 %) than in TBMU (56 %). δ^{15}N value of blood was significantly higher in COMU (14.47 ± 0.27 ‰) than in TBMU (13.14 ± 0.36 ‰). Relatively small wing area (0.053 ± 0.007 m^2) of COMU compared to TBMU (0.067 ± 0.007 m^2) may make them more agile underwater and thus enable them to target more mobile prey including larger fishes that inhabit deeper depths. These differences in foraging behavior between COMU and TBMU might explain the differences in their responses to long-term marine environmental changes.

1 Introduction

The southeastern Bering Sea has one of the most productive continental shelf areas in the world's ocean, and hosts large colonies of seabirds (Sowls et al., 1978; Hunt et al., 1981). During recent decades, the area has experienced a series of warm and cold regimes that lead to different responses of plankton and nekton communities (Coyle et al., 2011), and sympatric predators (Barger and Kitaysky, 2012). Common murres (*Uria aalge*: hereafter COMU) and thick-billed murres (*U. lomvia*: hereafter TBMU) are abundant and closely related diving seabirds and often breed sympatrically in subarctic regions (Gaston and Jones, 1998). Long-term population trends on St. George Island in the Bering Sea show that COMU repeatedly increase and decrease in short periods (< 10 years), whereas TBMU gradually decreased until the late 1980 s and then recovered toward the late 2000 s (Byrd et al., 2008; Mudge et al., 2015). In addition, COMU and TBMU have different optimal ocean thermal ranges associated with their population growth (Irons et al., 2008). The linkage between their different responses to environmental changes and various components of the Bering Sea ecosystem is still not well understood.

Ecological segregation is a common mechanism that enables closely related species to coexist sympatrically (Pianka, 1981). In diving seabirds, segregation in foraging behavior has been found in horizontal, vertical and temporal dimensions (Kokubun et al., 2010a; Masello et al., 2010; Navarro et al., 2013), or in prey species (Croxall et al., 1997). Both intrinsic and extrinsic factors affect the patterns of segregation. Intrinsic factors include physiology, morphology or energy requirement in relation to breeding stages, and can influence diving depth (Mori and Boyd, 2004), flight distance (Thaxter et al., 2010) or foraging habitat use (Linnebjerg et al., 2013). Extrinsic factors include oceanographic conditions and prey availability, and may affect the degree of inter-specific competition for food resources (Lynnes et al., 2002; Barger and Kitaysky, 2012). Potential effects of climate or human-induced environmental changes may appear differently among species with different foraging characteristics (Kitaysky and Golubova, 2000; Trivelpiece et al., 2011). Therefore, it is important to understand the foraging segregation and its underlying processes among closely related marine predators.

Ecological segregation between morphologically similar COMU and TBMU has been studied mostly by the observation of chick diet. Several studies have pointed out that COMU use fish almost exclusively, whereas TBMU use divergent prey (Barrett et al., 1997; Bryant et al., 1998; Barger et al., 2015). Whether/how, their foraging behavior contributes to these prey differences is, however, not well known. Several studies have revealed inter- or intra-specific differences in the foraging behavior of COMU and TBMU from the aspects of morphology (Paredes et al., 2015) and breeding ecology (Barger et al., 2015). Paredes et al. (2015) revealed that within TBMU populations, smaller birds are adapted to fly longer and dive shallower whereas larger birds are adapted to fly shorter and dive deeper reflecting their body mass and wing loading. The overlap in horizontal and vertical foraging habitats and/or in prey species are greater during the incubation period than the chick-rearing period, possibly to avoid potential inter-specific competition during energy-demanding chick-rearing period (Barger et al., 2015). In addition, presence or absence of inter-sexual differences in the diel patterns of diving behavior has been reported (Jones et al., 2002; Paredes et al., 2008), depending on the geographical regions (Elliott et al., 2010). In this context, fine-scale studies of murre diving and flight behavior combined with dietary and morphological analyses would be critical to better understanding their ecological niche in the marine ecosystem. We anticipate that fine-scale studies on foraging segregation between COMU and TBMU will provide a link between their different responses to environmental change and various components of the Bering Sea ecosystem.

Here we investigate the differences in flight and diving behavior between COMU and TBMU, and discuss possible factors that may drive inter-specific differences in their foraging behaviors.

2 Materials and methods

2.1 Study site

We conducted-field work on St. George Island, one of the largest colonies of murres in the world (Sowls et al., 1978: 190 000 COMU and 1 500 000 TBMU), located in the southeastern Bering Sea. Birds were captured at High Bluffs (56°36′ N 169°39′ W) on the northern side of the island. At our study location COMU and TBMU form mixed colonies on narrow open ledges where avian predators are nearly absent, yet adults spent most of their non-foraging time at the nest attending the chick. Instruments (see below) were deployed on birds guarding chicks from 30 July to 13 August 2014. During the study period, sunrise and sunset ranged between 07:17–07:44 and 23:33–23:02 LT. The start and end of nautical twilight (when the sun is less than 12° below the horizon) ranged between 05:07–05:57 and 01:45–0:52 LT. We defined the time between sunrise and sunset as "daytime", and the time between sunset and the next sunrise as "nighttime" which includes dusk (sunset to end of nautical twilight), dark night (end of nautical twilight to start of next nautical twilight) and dawn (start of nautical twilight to sunrise).

2.2 Deployment of data loggers

We used acceleration–temperature–depth data loggers to record behavioral and environmental data during the foraging trips of adult birds. The loggers (ORI-380 D3GT: housed in a cylindrical container, 12 mm diameter, 45 mm length, mass 10 g, Little Leonardo, Tokyo, Japan) were deployed on 13 COMU and 15 TBMU. Weight of the logger corresponds to 1.1 ± 0.1 % and 1.0 ± 0.1 % of body mass for COMU and TBMU, respectively. We captured chick-rearing birds with a 5 m noose pole, weighed them to the nearest 5 g by a Pesola® balance, and then attached a logger alongside their keel with strips of Tesa® tape, and cyanoacrylate glue (Loctite® 401) to secure the end of the tape. Handling time for each bird was less than 9 min. The loggers were set to record tri-axial acceleration (heave, surge and sway) at a rate of 20 Hz (every 0.05 s), as well as depth (at a resolution of 0.1 m) and temperature (at a resolution of 0.1 °C) every second.

The birds were recaptured between 1 to 6 days after deployment. The loggers were removed and the data were downloaded to a laptop computer. Upon logger retrieval, blood samples were taken for stable isotope analyses, and body size (body mass and wing area) were measured. The wing area of each bird was analyzed following Pennycuick (2008). We put the bird's right wing extended on a white flat board with a black colored 5 cm × 5 cm square as reference, and took pictures of the wing from the above. The wings were then traced on the digital picture and the pixels of the wing trace counted using IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA). The pixel number was converted in the area (m^2) using the reference square with known area, and the total wing area was calculated by doubling the area for one wing including "root chord" (Pennycuick, 2008). Wing loading ($N\,m^2$) was calculated from body mass (kg) $\times g$ (gravity acceleration: $9.8\,m\,s^{-2}$) divided by wing area (m^2).

2.3 Foraging trip and dive parameters

During the chick-rearing period, parent murres alternate foraging at sea with guarding their chicks at the colony. We defined the duration of foraging trips (to the nearest second) as the time between departure and return to the colony. This transition was clearly marked by a rapid change in bird's body angle associated with a rapid shift in temperature (Takahashi et al., 2008). We classified the behavior of the birds during foraging trips into diving, flight, or sitting on the water, using acceleration, depth, and temperature (Watanuki et al., 2006). The timing and duration of flight events was determined from the heaving acceleration. Foraging trips consisted of several series of dives separated by flight events (Falk et al., 2000). Because the birds move among the foraging locations by flying, we defined the series of dives as "dive bouts" (Takahashi et al., 2008). We also estimated the potential maximum distance from the colony by calculating total flight duration during foraging trips. We used a regression between time spent in flight (h) and maximum distance from the colony (km) during foraging trips, obtained from GPS-tracked TBMU with time-depth recorders attached to their leg ($n = 17$ foraging trips: maximum distance from the colony (km) = 27.284 (regression coefficient) × total flight duration (h): $R^2 = 0.787$). The regression analyses using GPS track was not the main focus of this study, thus the GPS-tracked birds did not carry accelerometers. The GPS data were collected concurrently to this study, and are reported in Yamamoto et al. (2015).

For each dive we determined dive depth, dive duration, bottom time (the time between the start and end of the time when birds showed depth change of 0 m), descent and ascent time (the time between the start of the dive and the start of the bottom phase, and the time between the end of the bottom phase and the end of the dive, respectively). A dive was considered to occur when dive depth exceeded 0.5 m (Watanuki et al., 2001; Takahashi et al., 2008). We calculated the number of wing strokes per unit time during the descent, bottom and ascent phases using the heaving (dorso-ventral) acceleration, as an index of their underwater activity (Watanuki et al., 2003, 2006). We applied a high-pass filter 1 Hz to heaving acceleration such that active body movements induced by wing strokes were highlighted. Peaks in the filtered acceleration exceeding a threshold amplitude ($0.2 \times 9.8\,\mathrm{m\,s^{-2}}$) were counted within a 1.0 s time window, and summed during diving descent, bottom and ascent phases of each dive, then divided by descent, bottom and ascent duration to calculate the wing stroke frequency in each phase. The analyses on wing strokes were made with the analysis software Igor Pro version 6.0 (Wave Metrics Inc., Lake Oswego, OR, USA).

2.4 Environmental parameters

We used four ocean thermal parameters at the bird's foraging locations as indices of environmental use (Kokubun et al., 2010b). Sea surface temperature (SST), thermocline depth, thermocline intensity and water temperature at depth > 40 m were recorded by the loggers. Vertical temperature profiles were determined for each dive bout, using data from the deepest dive of the bouts (only dives > 20 m were used). Because the temperature sensor had a slow response time, we corrected the temperature data for the response time following Daunt et al. (2003) and Takahashi et al. (2008). We defined thermocline depth as the depth where dT/dD was the maximum (T: temperature, D: depth) only when dT/dD was $> 0.25\,^\circ$C (Takahashi et al., 2008). We defined thermocline intensity as the difference between averaged temperatures above and below the thermocline (Kokubun et al., 2010b). The averaged water temperature below 40 m was assumed as water temperature at depth because the thermocline depth was shallower than 40 m for most dives in the study area (Kokubun et al., 2010b).

2.5 Diet

Chick diet was recorded from direct observation of adult birds (both with and without data loggers) carrying prey items to their nest. Prey items were visually identified to their lowest taxonomic level possible during observation or later from photographs.

We collected blood samples ($n = 14$ COMUs and 18 TBMUs, including 7 COMUs and 7 TBMUs with successful recordings of acceleration-temperature-depth data) upon retrieval of data loggers to analyze carbon and nitrogen stable isotope ratios to investigate inter-specific differences in trophic levels between COMU and TBMU (Hobson et al., 2002). We followed Barger and Kitaysky (2012) for the sampling and analyses procedures. Blood samples were collected by heparinized syringes, transferred to 1.5 mL microtubes, and stored cool until centrifugation (usually no more than 8 h after collection). Whole blood samples were centrifuged for 5 min to separate plasma and red blood cells. The red blood cells were stored frozen until following stable isotope analysis (SIA) in the laboratory for ^{13}C and ^{15}N. A small portion of freeze-dried samples (0.100–0.400 mg) were placed in a tin capsule, sealed and deposited in an EA autosampler. The stable isotope data was obtained using continuous-flow isotope ratio mass spectrometry (CFIRMS). The instrumentation used was a Delta +XP interfaced with a Costech ESC 4010 elemental analyzer. Stable isotope ratios are reported in δ(Delta) notation as parts per thousand (‰) deviation from the international standards $\delta^{13}\mathrm{C}_{\mathrm{PDB}}$ and $\delta^{15}\mathrm{N}_{\mathrm{air}}$ according to $\delta X = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$, where X

is ^{13}C and ^{15}N, R_{sample} and R_{standard} are the corresponding ratio ^{13}C/^{12}C or ^{14}N/^{15}N of samples and international standards. Replicate measurement of an internal laboratory standard (Peptone) indicated measurement errors to be ±0.16 ‰ for N and ±0.13 ‰ for C. Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility.

A Bayesian Mixing Model approach was used to infer murre diet compositions based on the stable isotope signatures of bird red blood cells and those of their potential prey, following Parnell et al. (2010) and Barger et al. (2015). This approach allows for simultaneous analysis of δ^{13}C and δ^{15}N and quantifies the uncertainty of the contributions of multiple sources to the diet of the birds. The model combines the likelihoods for the observed δ^{13}C and δ^{15}N data from the sources ($N = 7$ potential prey species) caught in the vicinity of the colony (< 100 km). In this process, we had 2 constraints. First, we did not sample the sources in the study year, and so used source samples caught in 2009 instead (methods of SI analyses of prey previously reported in Barger and Kitaysky, 2012). Second, there were no available source samples of age-1 walleye pollock (*Gadus chalcogrammus*) within 100 km from the colony, a distance in which birds are more likely to forage (Yamamoto et al., 2015). Because both murres are known to deliver walleye pollock to their offspring (and thus may consume them as well) we used data from outside the 100 km range (133 to 161 km distant, $n = 6$ source samples, located on the shelf, northwest of the study colony). The enrichment factors were set to −0.19 and 2.25 ‰ for δ^{13}C and δ^{15}N respectively following Barger et al. (2015). The enrichment factors were added to the data prior to the analysis. The analyses were conducted using the “SIAR” package in R® 3.1.1 software (R Develop Core Team, 2014).

2.6 Stress hormone and sexing

We measured circulating levels of baseline corticosterone (CORT) in the plasma samples to infer the level of nutritional stress of parents ($n = 11$ COMUs and 22 TBMUs).

All birds were sampled according to a standardized technique (Benowitz-Fredericks et al., 2008), with a blood sample collected within three minutes of capture.

We conducted DNA sex determination of red blood cells (Griffith et al., 1998) using the blood samples. However in some cases, we did not collect blood samples from the instrumented birds ($n = 5$ TBMU). In the cases that the genetic sex information was not available, we employed linear discriminant analysis (LDA: cf. Niizuma et al., 1999) using external traits (bill length, bill depth, head-bill length, tarsus length and wing length) with known sex ($n = 53$ TBMU), previously collected at the study colony (N. Kokubun, unpublished data). The efficiency of the discriminant function was 80 %. We considered that the morphologically determined sex data from 3 out of the 5 TBMUs was reliable, because their posterior classification probability was larger than 80 %. We used "MASS" package in R® 3.1.1 software (R Development Core Team, 2014) for LDA analysis.

2.7 Statistics

Morphology (body mass, wing area and wing loading), foraging trip parameters (trip duration, total flight duration, number of dive bouts per trip and bout duration), baseline CORT and stable isotopic values were compared between the species by one-way ANOVA. The proportion of different prey types was compared between the species by a χ^2 test. The proportion of daytime/nighttime dives, or deep/shallow dives were compared between the species by generalized linear models (GLM). A binomial error distribution was used for GLMs. Sea surface temperature (SST), temperature at depth (> 40 m), thermocline depth and thermocline intensity where dive bouts occurred were compared between the species by generalized linear mixed models (GLMM). Also, dive depth and number of wing strokes were compared between the species by GLMMs. In the GLMMs, species was set as a fixed factor, and bird identity was included as a random factor. In the analyses of number of wing strokes, we included the dive depth as a fixed factor, as dive depth can affect buoyancy and wing stroke frequency (Watanuki et al., 2006). In the GLMMs, a Gamma error distribution was used, and the models with and without the effect of fixed factors (species) were compared using a Likelihood Ratio Test (LRT). We compared the foraging parameters between the sexes if applicable. We used Minitab® v. 14 for one-way ANOVA and χ^2 tests, and the "lme4" package in R® 3.1.1 software (R Development Core Team, 2014) for GLMs and GLMMs. Data are presented as mean values ± standard deviation (SD), with significance set at the 0.05 level.

3 Results

3.1 Data recovery

We recaptured 11 of 13 instrumented COMUs and all of 15 instrumented TBMUs. The remaining 2 COMUs were not observed after the planned timing of retrieval. Among the retrieved data loggers, 4 from COMU and 3 from TBMU did not record data properly due to memory malfunctions. Overall, we analyzed behavioral data from 7 COMU (consisting of 4 males and 3 females) and 12 TBMU (consisting of 3 males, 7 females and 2 unknown sexes). These data covered 14 and 21 foraging trips that included 64 and 79 dive bouts, for COMU and TBMU, respectively (Table 1).

COMU had smaller body mass than TBMU (COMU: 945.7 ± 44.8 g, TBMU: 1022.9 ± 64.4 g, one-way ANOVA, $F_{1,17} = 7.8$, $P = 0.013$), had smaller wing area than TBMU (COMU: $0.053 \pm 0.007\,\mathrm{m}^2$, TBMU: $0.067 \pm 0.007\,\mathrm{m}^2$, one-way ANOVA, $F_{1,17} = 16.4$, $P = 0.001$), and had greater wing loading than TBMU (COMU: $175.9 \pm 26.1\,\mathrm{N\,m}^{-2}$, TBMU: $151.1 \pm 19.7\,\mathrm{N\,m}^{-2}$, one-way ANOVA, $F_{1,17} = 5.6$, $P = 0.031$). There were no significant differences between the sexes in either the COMU or TBMU morphological data (one-way ANOVA, $P > 0.05$).

3.2 Trip parameters

Foraging trip duration, total flight duration and dive bout duration did not differ between COMU and TBMU (Table 1). There was no significant difference in trip and bout duration between the sexes in COMU and TBMU (one-way ANOVA, $P > 0.05$). The total flight duration of male COMU were longer than those of females (2.11 ± 0.73 h for males and 1.02 ± 0.28 h for females: one-way ANOVA, $F_{1,12} = 13.7$, $P = 0.003$). There was no significant difference between the sexes in TBMU total flight duration (one-way ANOVA, $P > 0.05$). The maximum distance from the colony during foraging trips estimated by total flight duration was 42.6 ± 21.1 km (ranging 12.8–81.2 km) for COMU and 38.1 ± 21.9 km (ranging 4.4–76.4 km) for TBMU, respectively. With these small foraging ranges, both COMU and TBMU probably foraged on the continental shelf (bottom depth < 200 m: Yamamoto et al., 2015).

3.3 Environmental use

The sea surface temperature (SST) where the dive bouts occurred did not differ between COMU and TBMU (Fig. 1a, B: COMU: 11.9 ± 0.4 °C, TBMU: 11.8 ± 0.7 °C, GLMM with LRT, $\chi^2 = 0.01$, $P = 0.91$). The temperature at depth (> 40 m) where the dive bouts occurred did not differ between COMU and TBMU (Fig. 1c and d: COMU: 4.8±0.9 °C, TBMU: 4.9±0.7 °C, GLMM with LRT, $\chi^2 = 0.02$, $P = 0.90$). The thermocline depth (19.6 ± 2.2 m for COMU and 21.1 ± 4.3 m for TBMU) and thermocline intensity (5.4 ± 1.1 °C for COMU and 5.3 ± 1.1 °C for TBMU) where the dive bouts occurred did not differ between the species (GLMM with LRT, $P > 0.05$). There were no significant differences between the sexes in either the COMU or TBMU environmental use data (GLMM with LRT, $P > 0.05$).

3.4 Dive parameters

Both COMU and TBMU showed a diel diving pattern that indicated more dives with divergent depths in the daytime and less dives with shallow depths in the nighttime (Fig. 1). Proportion of the daytime and nighttime dives did not differ between the species (62.0 ± 21.5 % and 63.1 ± 28.7 % for daytime, and 38.0 ± 21.5 % and 37.0 ± 28.7 % for nighttime, for COMU and TBMU respectively, GLM, $t = 0.528$, $P = 0.605$). During the daytime, birds dove to both shallow (< 40 m) and deep (> 40 m) depths in regard to the maximum thermocline depth (Fig. 3a–d: 58.0 ± 25.7 % and 42.4 ± 16.4 % for shallow dives, 42.0 ± 25.7 % and 57.6 ± 16.4 % for deep dives, for COMU and TBMU respectively: GLM, $t = 1.952$, $P = 0.068$). In the nighttime, both COMU and TBMU dove almost exclusively to shallow (< 40 m) depths (Fig. 3 g, H: 88.9 ± 8.5 % and 86.5 ± 8.8 % for shallow dives, 11.1 ± 8.5 % and 13.5 ± 8.8 % for deep dives, for COMU and TBMU respectively: GLM, $t = 1.193$, $P = 0.254$). There were no significant differences in the proportion of daytime and nighttime dives or shallow and deep dives between the sexes in either COMU or TBMU (GLM, $P > 0.05$).

During the daytime, shallow diving depth (< 40 m) did not differ between the species (Fig. 3c and d: 18.1 ± 6.0 m for COMU and 20.2 ± 7.4 m for TBMU: GLMM with LRT, $\chi^2 = 0.30$, $P = 0.581$). On the other hand, the deep diving depth (> 40 m) was deeper for COMU (74.2 ± 8.7 m) compared to TBMU (59.7 ± 7.9 m: Fig. 3c and d: GLMM with LRT, $\chi^2 = 7.04$, $P = 0.008$). In the nighttime, the depth of shallow dives (< 40 m) did not differ between the species (Fig. 3g and h: 15.4 ± 4.0 m for COMU and 19.1 ± 6.2 m for TBMU: GLMM with LRT, $\chi^2 = 1.12$, $P = 0.289$). There were no significant differences between the sexes in either COMU or TBMU dive depths (GLMM with LRT, $P > 0.05$).

The number of wing strokes during the bottom phase of day and night dives was higher in COMU than in TBMU (Daytime: Fig. 3e and f: 1.95 ± 0.16 s^{-1} for COMU and 1.68 ± 0.20 s^{-1} for TBMU: GLMM with LRT, $\chi^2 = 5.978$, $P = 0.014$ and Nighttime: Fig. 3i and j: 1.84 ± 0.07 s^{-1} for COMU and 1.57 ± 0.21 s^{-1} for TBMU: GLMM with LRT, $\chi^2 = 6.545$, $P = 0.011$). On the other hand, the number of wing strokes during diving descent phase did not differ between the species either in the daytime ($2.29 \pm 0.07\,\mathrm{s}^{-1}$ for COMU and $2.18 \pm 0.21\,\mathrm{s}^{-1}$ for TBMU: GLMM with LRT, $\chi^2 = 3.301$, $P = 0.069$) or the nighttime ($2.23 \pm 0.11\,\mathrm{s}^{-1}$ for COMU and $2.19 \pm 0.16\,\mathrm{s}^{-1}$ for TBMU: GLMM with LRT, $\chi^2 = 1.387$, $P = 0.239$). There were no significant differences between the sexes in the number of wing strokes in COMU or TBMU (GLMM with LRT, $P > 0.05$).

3.5 Diet

We observed 20 and 39 prey items for COMU and TBMU respectively. The proportion of fishes (consisting of 6 walleye pollock (*Gadus chalcogrammus*), 1 sculpin (*Cottoidae*), 1 flatfish (*Pleuronectidae*) and 9 unidentified fishes for COMU, and 9 walleye pollock, 2 sculpins, 1 prickleback (*Stichaeidae*) and 10 unidentified fishes for TBMU) was higher for COMU compared to TBMU (χ^2 test, $\chi^2 = 6.108$, $P = 0.047$). Conversely, the proportion of invertebrates (consisting of 1 cephalopod (*Gonatidae*) for COMU, 12 cephalopods and 1 unidentified meso-zooplankton for TBMU,) was higher for TBMU compared to COMU.

The stable isotope analysis for red blood cells showed differences in the potential adult diet between the species. δ^{15}N was higher in COMU than in TBMU (Fig. 4: 14.47 ± 0.27 ‰ for COMU and 13.14 ± 0.36 ‰ for TBMU: one-way ANOVA, $F_{1,30} = 134.84$, $P < 0.001$). δ^{13}C was also slightly higher for COMU compared to TBMU (Fig. 4: -19.36 ± 0.20 ‰ for COMU and -19.76 ± 0.17 ‰ for TBMU: one-way ANOVA, $F_{1,30} = 37.71$, $P < 0.001$). There were no significant differences among the sexes in COMU stable isotope data (one-way ANOVA, $P > 0.05$). According to an inequality in number of male and females ($n = 2$ males and 16 females) in TBMU, the effect of sex could not be analyzed, but males generally showed higher δ^{15}N value (13.74 and 13.65 ‰) compared to those of females (13.07 ± 0.32 ‰, ranging 12.37 to 13.79 ‰), while δ^{13}C value of males (−19.66 and −19.77 ‰) was similar to those of females (-19.77 ± 0.18 ‰, ranging −20.03 to −19.35 ‰).

Based on the Bayesian Mixing Analysis for estimating potential food sources, COMU were inferred to have fed on more fishes such as age-1 walleye pollock or age-0 flounder, whereas TBMU were inferred to have fed on more invertebrates such as euphausiids and squids (Figs. 6 and 7).

3.6 Stress hormone

The baseline CORT did not differ between the species (log transformed mean = $0.43 \pm 0.25\,\text{ng}\,\text{mL}^{-1}$ for COMU and $0.37 \pm 0.27\,\text{ng}\,\text{mL}^{-1}$ for TBMU: one-way ANOVA, $F_{1,31} = 0.35$, $P = 0.559$). There was no significant difference between the sexes in COMU baseline CORT (one-way ANOVA, $P > 0.05$). Baseline CORT of males (log transformed mean $= 0.17 \pm 0.31\,\text{ng}\,\text{mL}^{-1}$) was slightly lower than that of females ($0.44 \pm 0.23\,\text{ng}\,\text{mL}^{-1}$) in TBMU (one-way ANOVA, $F_{1,20} = 4.92$, $P = 0.038$).

4 Discussion

This study investigated the differences in foraging behavior between two closely related seabirds, common and thick-billed murres, at a fine scale. Both species showed similar diel patterns of diving and appeared to use similar foraging areas (Figs. 1 and 2, Table 1). However, COMU dove to deeper depths in the daytime and showed more frequent underwater wing strokes during dive bottom time, compared to TBMU (Fig. 3). In addition, COMU used higher trophic level prey, presumably consisting of larger fishes such as age-1 walleye pollock, whereas TBMU used lower trophic level prey, which possibly includes squids and meso-zooplankton (Figs. 4–7). Arguably, stable isotope of red blood cells reflects conditions during incubation and early chick-rearing, according to its relatively slow turnover rate (half life ∼ 4 weeks: Barger et al., 2015; Hobson and Clark, 1993). Assuming that the isotopic distance becomes greater in the chick-rearing period rather than incubation or pre-laying (Barger et al., 2015), we anticipate that the inter-specific difference in trophic level is also applicable to the chick-rearing period.

Larger fishes including age-1 walleye pollock are distributed at deeper depths in the daytime compared to smaller age-0 pollock, and migrate up to thermocline depths at night (Lang et al., 2000; Schabetsberger et al., 2000). Furthermore, juvenile pollock swim faster as they grow (Hurst, 2007). Diving seabirds are considered to feed mostly during the diving bottom phase (Elliott et al., 2008). The deeper diving depths in the daytime and more frequent wing strokes during the bottom phase of COMU dives, combined with higher trophic levels of prey, suggests that COMU tended to forage on more mobile prey such as large fishes, compared to TBMU. There are several possible factors affecting the inter-specific differences in foraging behavior between closely related COMU and TBMU, such as (1) physiology and morphology, (2) breeding stages and nest attendance, and (3) prey availability.

According to a previous study, resting or diving metabolic rates are expected not to differ between COMU and TBMU (Croll and McLaren, 1993). On the other hand, COMU and TBMU at the study colony differed morphologically in body mass, wing area and wing loading. TBMU which had smaller wing loading and larger body mass are expected to fly further and dive deeper than COMU (cf. Thaxer et al., 2010; Linnebjerg et al., 2013), but this was not the case in this study. A morphological study pointed out that the smaller wings of COMU enables them to swim more agilely than TBMU (Spring, 1971). COMU's more frequent wing strokes during the dive bottom phase (Fig. 3e, f, i, j), possibly due to pursuing larger fishes, may support the observation by Spring (1971) and reflect their morphological characteristics.

This study was conducted during the chick-rearing period of both species when their energy demand for parents are highest (Ricklefs, 1983). High energy demands may force both COMU and TBMU to forage closer to the colony, compared to during incubation (Barger et al., 2015) and post- or pre-breeding periods (Linnebjerg et al., 2013). In addition, one member of a pair consistently guarded their chicks on the narrow open ledges at the study colony. This aspect was different from COMU at other locations where nests are more protected, and parents can leave their chicks alone and spend more time foraging (Linnebjerg et al., 2015). Potential foraging range and the diel patterns of diving were similar between COMU and TBMU at the study colony (Table 1, Fig. 2), which may reflect the necessity to guard chicks, along with the similar nest attendance patterns.

There are few available data on local food availability during the study period. In terms of nutritional stress, both COMU and TBMU showed lower concentrations of stress hormone in the study year, compared to those reported in other years on St. George Island (Harding et al., 2013; Paredes et al., 2015) and elsewhere (Barger and Kitaysky, 2012). Although birds breeding on St. George Island maybe prone to experience food shortage due to high bird density, which is an order of magnitude larger than nearby colonies (St. George Island: 190 000 COMU and 1 500 000 TBMU: Sowls et al., 1978; St. Paul Island: 39 000 COMU and 115 000 TBMU: Sowls et al., 1978; Bogoslof Island: 41 400 murres: Byrd et al., 2005) the food condition of the study year appeared to be good for both species. In addition, abundance of age-0 pollock in the eastern Bering Sea (in the 150 km radius around Pribilof Islands) measured within the upper 15 m of the water column was high in 2014 compared to other years since 2003 (W. Strasburger, Ted Stevens Marine Research Institute Juneau, Alaska, personal communication, 2015). Barger et al. (2015) suggested that the resource partitioning proactively increases during this period of elevated energetic needs without apparent food limitations. This study also suggests the resource partitioning during the chick-rearing period between COMU and TBMU breeding on St. George Island when food conditions are relatively good.

Overall, at the study colony, chick-rearing COMU and TBMU foraged in similar foraging ranges with a similar diel pattern of diving. Inter-sexual differences were not clear compared to other colonies (cf. Paredes et al., 2008; Linnebjerg et al., 2015). Segregation in prey species with different vertical distribution and mobility may allow the use of similar foraging ranges of these closely related species, and may possibly reflect inter-specific morphological differences. Other studies have found similar patterns of prey segregation in other regions, however horizontal and/or vertical foraging segregation have also been reported between chick-rearing COMU and TBMU (e.g. Barger et al., 2015). Barger et al. (2015) reported chick-rearing COMU and TBMU used different foraging habitats, as reflected in travel distances to foraging areas and sea-surface temperature distributions of their foraging dives. TBMU performed shorter foraging trips, deeper dives and fed their chicks squid, while COMU foraged farther from the colony, performed shallower dives, and delivered fish to feed their chicks. TBMU populations exhibit divergent behavioral patterns, which may be due to inter-regional differences in morphology (Paredes et al., 2015). Thus segregation patterns between COMU and TBMU may differ among regions partly because TBMU's morphology differs at a regional scale.

It has been reported that, in other regions, COMUs prefer larger, more mobile fish including walleye pollock and capelin (*Mallotus villosus*), whereas TBMU use more divergent prey including benthic fishes, cephalopods and meso-zooplankton (Barrett et al., 1997; Bryant et al., 1998; Barger et al., 2015). Spring (1971) and Ogi (1979) suggested that COMU's more slender bill and palate, along with their corneous tongue, reflects their more piscivorous tendencies, whereas the wider bill and palate, and less corneous tongue of the TBMU reflects their invertebrate feeding habits. If the segregation in the prey types was consistent over different years, the effect of annual fish availability on COMU may be stronger compared to those on TBMU. Recent Arctic environmental changes may affect the two species differently through their different foraging characteristics. COMU showed the highest population growth rate at a lower ocean thermal range, compared to those of TBMU throughout the Arctic and sub-arctic regions (Irons et al., 2008). The ecological factors affecting such different responses are still not well understood, but in the Bering Sea, recruitment of age-1 walleye pollock remained high during cold regimes whereas it fell during warm regimes (Ianelli et al., 2009; Coyle et al., 2011), possibly enabling COMU to capitalize on their foraging behavior in cold years. Although reproductive success was similar between the species at the study colony in 2014 (0.61 for COMU and 0.55 for TBMU), the long-term population trend shows larger annual variation with short term (< 10 years) changes in COMU and smaller annual variation with longer term (~ 20 years) changes in TBMU (Byrd et al., 2008; Mudge et al., 2015). We hypothesize that these differences are partly explained by the different foraging behaviors of these two species, through COMU's higher reliance on fishes and TBMU's use of divergent prey. Inter-annual comparison of foraging behavior of COMU and TBMU, with varying environmental conditions and prey availability are required to test this hypothesis.

In conclusion, inter-specific comparison of foraging behavior between closely related common and thick-billed murres in the Bering Sea showed that both species foraged in similar foraging ranges with a similar diel pattern of diving. However, common murres dove to deeper depths below the thermocline (> 40 m) in the daytime, showed more frequent underwater wing strokes during the bottom phase of dives and used higher trophic level prey, compared to thick-billed murres. Common murres had smaller wings that potentially enables to pursuit more mobile prey, compared to thick-billed murres. These results suggest that common and thick-billed murres segregated prey species in relation to differences in their morphology. Such ecological segregation may lead the closely related species to respond to local environmental change differently.

Author contributions. N. Kokubun, A. Takahashi, A. S. Kitaysky and Y. Watanuki designed and coordinated the research project. N. Kokubun, T. Yamamoto and N. Sato conducted the field study on St. George Island, Alaska. A. Will and A. S. Kitaysky performed stable isotope and stress hormone analyses in the laboratory. N. Kokubun, T. Yamamoto and N. Sato analyzed the behavioral data. N. Kokubun wrote the manuscript with contributions from all of the co-authors.

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works were conducted following the Federal Fish and Wildlife Permit issued by the U.S. Fish and Wildlife Service (permit # MB70337A-3) and the Scientific Permit issued by the State of Alaska (permit # 14-109).

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Table 1. Trip parameters of common murres (COMU) and thick-billed murres (TBMU) breeding on St. George Island, Bering Sea.

Species	No. of birds	No. of trips	No. of dive bouts	No. of dive bouts per trip	Duration (h) Trip	Total flight	Dive bouts
Common murre (COMU)	7	14	64	4.57 ± 2.71	13.21 ± 4.79	1.56 ± 0.77	1.79 ± 3.74
Thick-billed murre (TBMU)	12	21	79	3.76 ± 2.86	10.45 ± 7.09	1.40 ± 0.80	1.87 ± 3.42
One-way ANOVA, *F* and *P* values				$F_{1,33} = 0.70$ $P = 0.409$	$F_{1,33} = 1.62$ $P = 0.212$	$F_{1,33} = 0.36$ $P = 0.552$	$F_{1,157} = 0.02$ $P = 0.892$

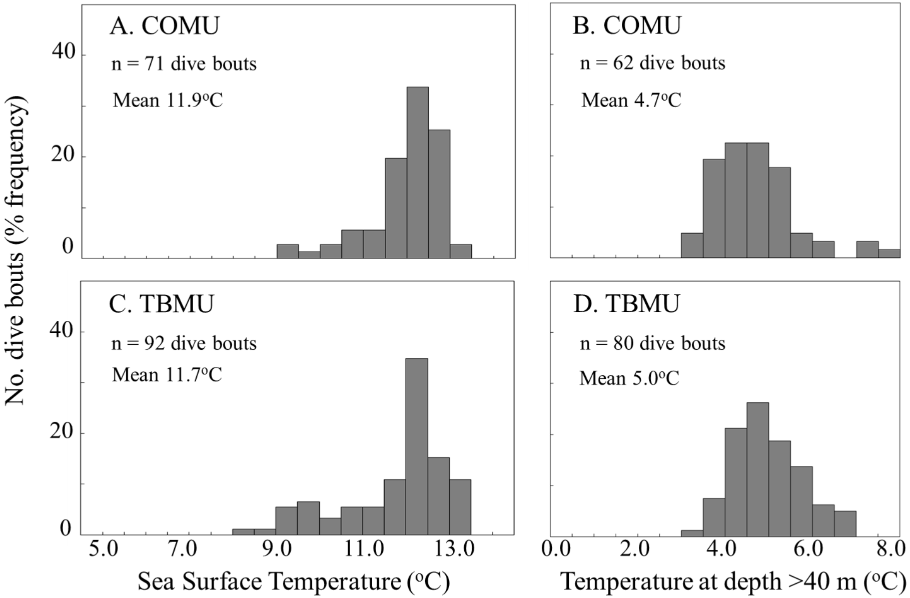

Figure 1. Frequency distribution of dive bouts in relation to **(a, c)** sea surface temperature (SST) and **(b, d)** mean temperature at depth (> 40 m) in the water column. Upper panels represent data for common murres (COMU) and lower panels represent data for thick-billed murres (TBMU).

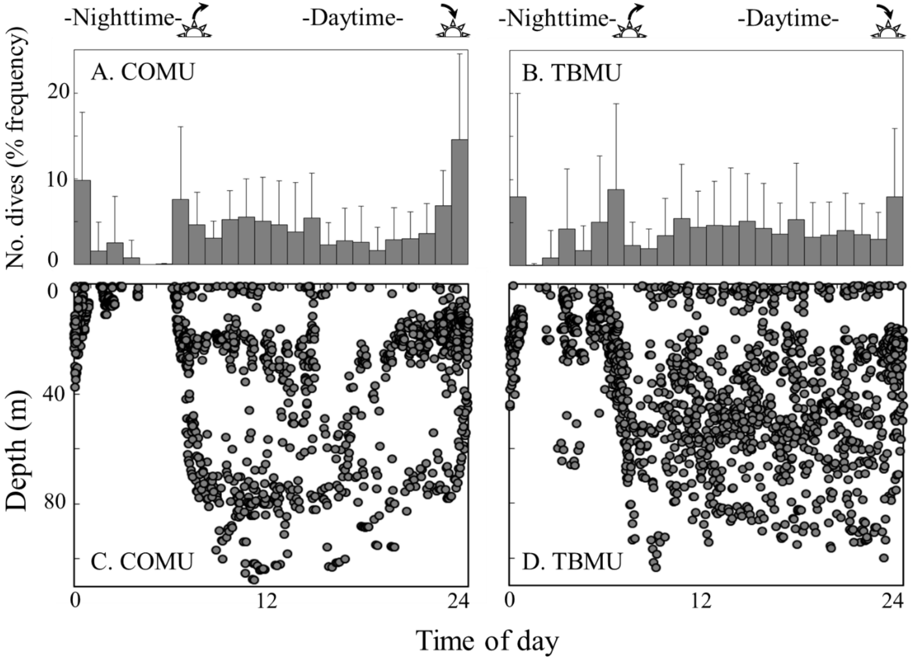

Figure 2. (a, c) Frequency distribution and **(b, d)** depth distribution pattern of dives in relation to time of day. Left panels represent data for common murres (COMU) and right panels represent data for thick-billed murres (TBMU). Means ± standard deviation (SD) are shown in **(b, d)**, calculated by individual bird data. The timing of sunrise and sunset is shown by marks on the top horizontal axis.

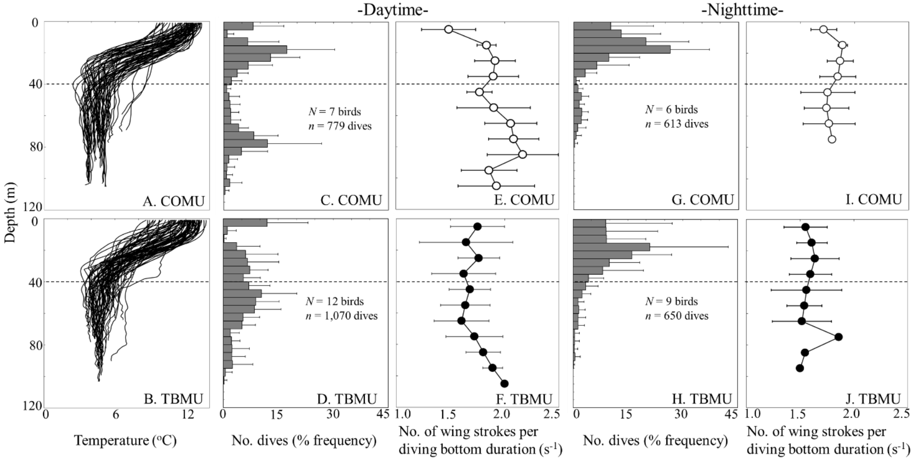

Figure 3. **(a, b)** Vertical temperature profiles where foraging dive occurred with **(c, d, g, h)** frequency distribution of dives and **(e, f, i, j)** number of wing strokes per diving bottom phase, in relation to dive depth. Upper panels represent data for common murres (COMU) and lower panels represent data for thick-billed murres (TBMU). Panels **(c–f)** represent data for the daytime, and panels **(g–j)** represent data for the nighttime. Means ± standard deviation (SD) are shown excepting for **(a, b)**, are calculated from individual bird data. Sample number of birds (*N*) and dives (*n*) are shown in **(c, d, g, h)**.

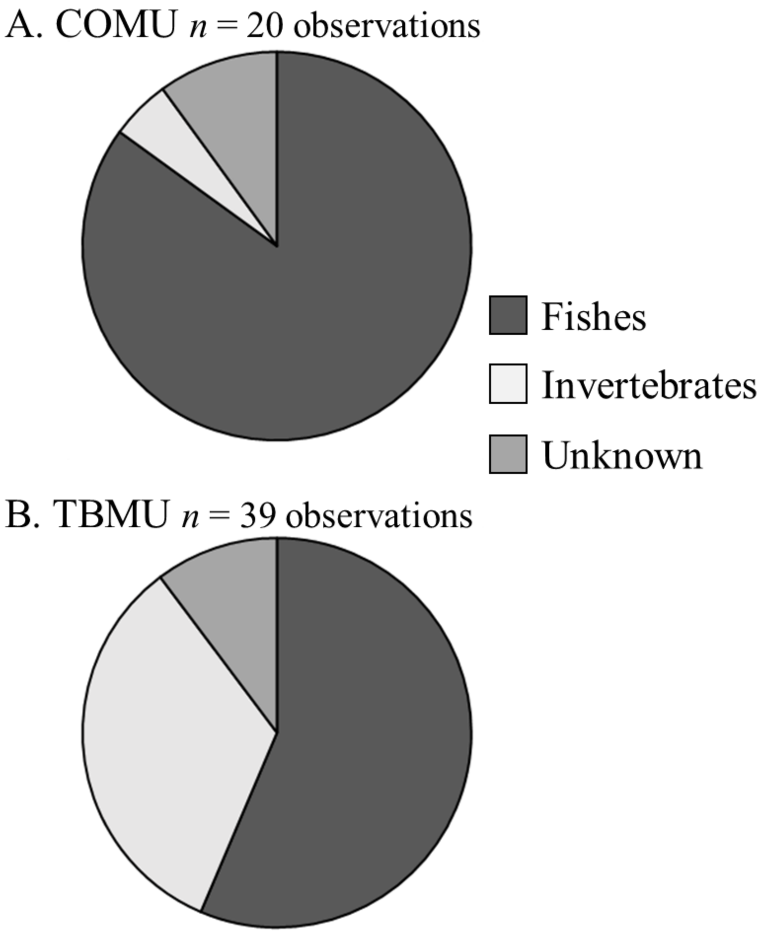

Figure 4. Diet composition of **(a)** common murres (COMU) and **(b)** thick-billed murres (TBMU) based on direct observations of prey delivered to nests.

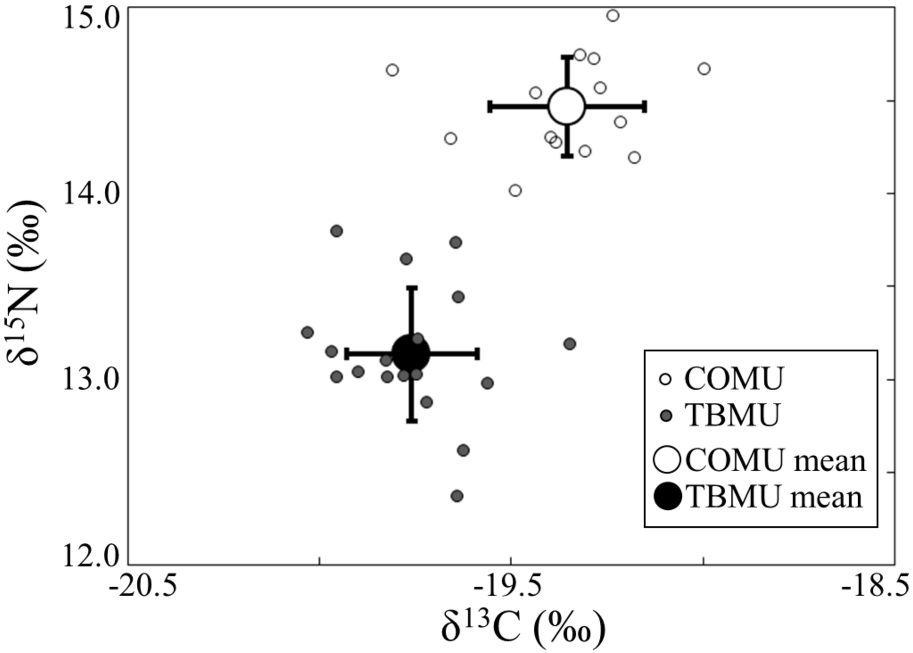

Figure 5. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopic ratio values of common murres (COMU: open circles) and thick-billed murres (TBMU: closed circles) measured in red blood cells. Smaller circles show individual data, and larger circles with error bars show Means ± standard deviation (SD).

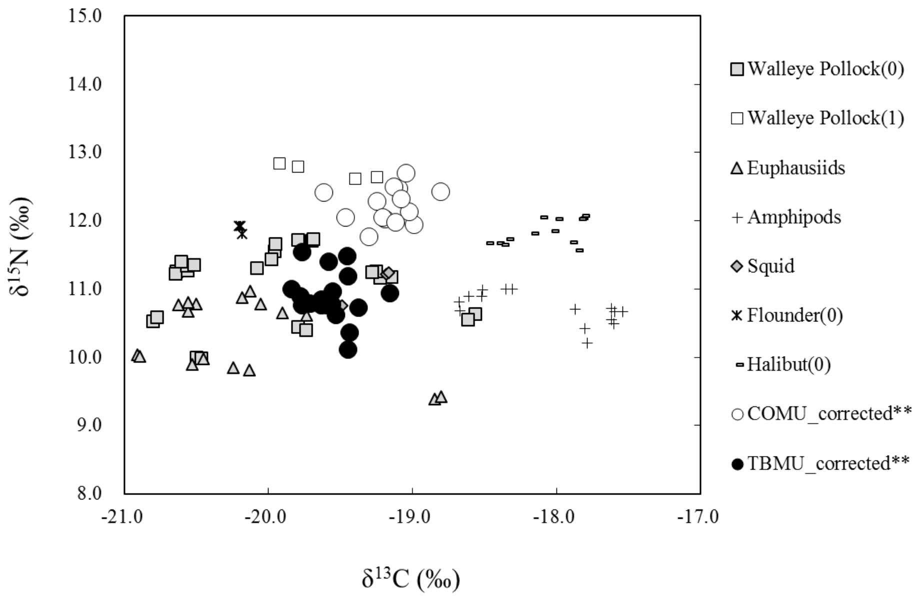

Figure 6. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopic ratio values of potential food samples caught around the vicinity of the study colony. Different symbols represent each potential food item. ** The enrichment factors −0.19 ‰ for δ^{13}C and 2.25 ‰ for δ^{15}N were preliminarily applied to the bird data (open circles for common murres and closed circles forthick-billed murres). Note that the potential food samples were collected in 2009 as no data were available in 2014.

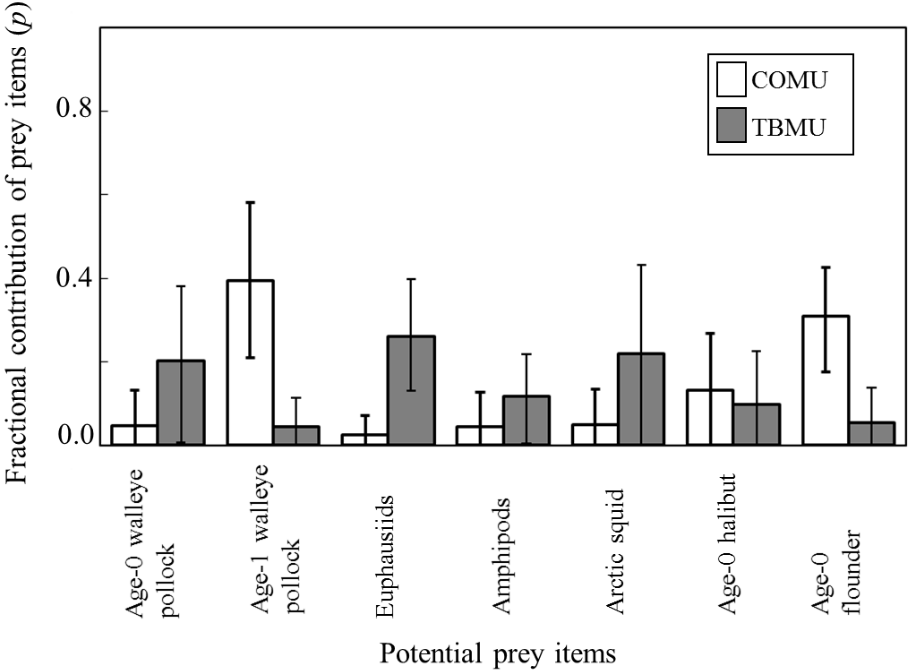

Figure 7. Diet compositions of common (COMU: open boxes) and thick-billed murres (TBMU: closed boxes) as estimated by Bayesian Mixing Analysis of stable isotope values of birds (red blood cells) and those of their potential prey items (whole body tissues). Means ± 95 % credible intervals of the fractional contribution (*p*) of seven different prey items are shown. Note that the potential food samples were collected in 2009.