Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea

N. Kokubun[1, 2], T, Yamamoto[1, 3], N. Sato[2], Y. Watanuki[3], A. Will[4], A. S. Kitaysky[4], and A. Takahashi[1, 2]

[1] National Institute of Polar Research, Japan, 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan.

[2] Department of Polar Science, School of Multidisciplinary Sciences, SOKENDAI (The Graduate University for Advanced Studies), 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan.

[3] Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido, 040-0821, Japan.

[4] Institute of Arctic Biology, Department of Biology and Wildlife, University of Alaska Fairbanks, Irving 311, Alaska 99503, USA.

Correspondence to: N. Kokubun (kokubun@nipr.ac.jp)

Abstract

Sub-arctic environmental changes are expected to affect the foraging ecology of marine top predators, but the response to such changes may vary among species if they use food resources differently. 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 foraging trip and flight durations, diel patterns of dive depth, and underwater wing strokes, along with wing morphology and blood stable isotope signatures and stress hormones. Acceleration-temperature-depth loggers were attached to chick-guarding birds, and data were obtained from 7 COMU and 12 TBMU. Both species showed similar mean trip duration (13.2 h for COMU and 10.5 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, the dive depths of COMU had two peaks in shallow (18.1 m) and deep (74.2 m) depths, while those of TBMU were 20.2 m and 59.7 m. COMU showed more frequent wing strokes during the bottom phase of dives (1.90 s^{-1}) than TBMU (1.66 s^{-1}). Fish occurred more frequently in the bill-loads of COMU (85%) than those of TBMU (56%). $\delta^{15}N$ value of blood was significantly higher in COMU (14.5 ‰) than in TBMU

(13.1 ‰). The relatively small wing area (0.053 m^2) of COMU compared to TBMU (0.067 m^2) may facilitate their increased agility while foraging and allow them to capture more mobile prey such as larger fishes that inhabit deeper depths. These differences in food resource use may lead to the differential responses of the two murre species to marine environmental changes in the Bering Sea.

Keywords:

Inter-specific competition, walleye pollock, acceleration, prey distribution, murre

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., 1981b; Dragoo et al., 2015). During recent decades, the area has experienced a series of warm and cold regimes which result in contrasting responses of the plankton and nekton communities (Coyle et al., 2011; Hunt et al., 2011), and their 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 sub-arctic regions (Gaston and Jones, 1998). A range-wide comparison of COMU and TBMU population trends demonstrated that they have different favorable oceanographic temperature regimes for population growth reflecting importance of bottom-up effects of climate variability on their populations (Irons et al., 2008). However, how these two species respond to local variation in the environment, where their ranges overlap, is still not well understood (but see Barger et al., 2016, and references therein). Comparisons of foraging characteristics would provide insight into the respective ecological niche of these diving seabirds. A more narrow niche would be indicative of a species with specialist strategy which is predicted to show more sensitive responses to environmental changes than a species characterized as a generalist (Clavel

et al., 2011; Gallagher et al., 2015).

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 the use of prey species (Croxall et al., 1997; Hunt et al., 1981a). 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; Barger et al., 2016). 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). In addition, microhabitats for nesting are often segregated (Squibb and Hunt, 1983; Linnebjerg et al., 2015), which may affect allocation of time to the nest attendance vs foraging. Potential effects of climate or human-induced environmental changes may manifest differently among species with different foraging characteristics (Kitaysky and Golubova, 2000; Trivelpiece et al., 2011). Therefore, it is important to understand the mechanisms of foraging segregation and underlying processes in marine predators.

Foraging segregation between 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 a variety of prey (Hunt et al., 1981a; Barrett et al., 1997; Bryant et al., 1998; Barger et al., 2016). Whether/how, their foraging behavior contributes to these prey differences is, however, not well known. A few 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., 2016). Paredes et al. (2015) showed that, within TBMU colonies, smaller individuals tended to fly longer distances and dive shallower whereas the opposite pattern was observed in larger individuals, likely reflecting their body mass and wing loading. TBMU have also shown inter-sexual differences in the diel patterns of diving behavior (Jones et al., 2002; Paredes et al., 2008), however the presence of such habitat partitioning appear to vary by geographical region (Elliott et al., 2010). Between COMU and TBMU the overlap in horizontal and vertical foraging habitats and/or in prey species is greater during incubation than chick-rearing, possibly to enhance resource partitioning between the species during the energy-demanding chick-rearing period (Barger et al., 2016). In this context, a fine-scale study of murre diving and flight behavior combined with dietary and morphological analyses is needed to better understanding the differences in the ecological

102 niches of these closely related species. We anticipate that fine-scale studies on foraging
103 segregation between COMU and TBMU will provide insight into whether/how their
104 responses to environmental change in the Bering Sea ecosystem may differ.

105 Here we investigated the differences in the foraging behavior between COMU
106 and TBMU with depth-temperature-acceleration data loggers. Stable isotope analyses,
107 observation of prey delivered to chicks, and stress hormone analyses were used to
108 examine inter-specific differences in diet and consequent nutritional stress. Based on
109 results of previous studies, we predicted that COMU would consume higher trophic level
110 prey and show more specialized foraging behavior on fish prey compared to TBMU,
111 which might be also associated with inter-specific differences in wing morphology. We
112 combine detailed foraging behavior, diet, and morphology to discuss how inter-specific
113 differences in the foraging behavior may affect the responses of two murre species to
114 environmental change in the southeastern Bering Sea.

115

116 **2 Materials and methods**

117 **2.1 Study site**

118 We conducted fieldwork on St. George Island, southeastern Bering Sea, home to
119 one of the largest murre colonies in the world (Sowls et al. 1978: 190,000 COMU and

120 1,500,000 TBMU). Birds were captured at High Bluffs (56º36’ N 169º39’W) on the
121 northern side of the island. At our study colony, where avian predators are nearly absent,
122 COMU and TBMU form mixed colonies on narrow open ledges and adults spent most of
123 their non-foraging time at the nest brooding the chick. Instruments (see below) were
124 deployed on chick-rearing birds from 30th July to 13th August 2014. During the study
125 period, sunrise and sunset ranged between 07:17-07:44 and 23:33-23:02 LT. The start and
126 end of nautical twilight (when the sun is less than 12º below the horizon) ranged between
127 05:07-05:57 and 01:45-0:52 LT. We defined the time between sunrise and sunset as
128 “daytime”, and the time between sunset and the next sunrise as “nighttime” which
129 includes dusk (sunset to end of nautical twilight), dark night (end of nautical twilight to
130 start of next nautical twilight) and dawn (start of nautical twilight to sunrise).
131
132 **2.2 Deployment of data loggers**
133 We used depth-temperature-acceleration data loggers to record behavioral and
134 environmental data during the foraging trips of adult birds. The loggers (ORI-380 D3GT:
135 housed in a cylindrical container, 12 mm diameter, 45 mm length, mass 10 g, Little
136 Leonardo, Tokyo, Japan) were deployed on 13 COMU and 15 TBMU. The weight of the
137 logger corresponds to 1.1 ± 0.1 % and 1.0 ± 0.1% of body mass for COMU and TBMU,

138 respectively. We captured chick-rearing birds with a 5 m noose pole, weighed them to the
139 nearest 5 g by a Pesola® balance, and then attached a logger alongside their keel with
140 strips of Tesa® tape, and cyanoacrylate glue (Loctite ®401) to secure the end of the tape.
141 Handling time for each bird was less than 9 min. The loggers were set to record tri-axial
142 acceleration (heave, surge and sway) at a rate of 20 Hz (every 0.05 s), as well as depth (at
143 a resolution of 0.1 m) and temperature (at a resolution of 0.1^{o}C) every second.

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

156

157 **2.3 Foraging trip and dive parameters**

158 During the chick-rearing period, parent murres alternate foraging at sea with
159 brooding their chicks at the colony. We defined the duration of foraging trips (to the
160 nearest second) as the time between departure and return to the colony. This transition
161 was clearly marked by a rapid change in bird's body angle associated with a shift in
162 temperature (Takahashi et al., 2008). We classified the behavior of the birds during
163 foraging trips into diving, flight, or sitting on the water, using acceleration, depth, and
164 temperature (Watanuki et al., 2006). The timing and duration of flight events was
165 determined from the heaving acceleration. Foraging trips consisted of several series of
166 dives separated by flight events (Falk et al., 2000). Because the birds move among the
167 foraging locations by flying, we defined the series of dives as 'dive bouts' (Takahashi et
168 al., 2008). We also estimated the potential maximum distance from the colony by
169 calculating total flight duration during foraging trips. We used a regression between time
170 spent in flight (h) and maximum distance from the colony (km) during foraging trips,
171 obtained from GPS-tracked TBMU with time-depth recorders attached to their leg (n =
172 17 foraging trips: maximum distance from the colony (km) = 27.284 (regression
173 coefficient) × total flight duration (h): R^2 = 0.787). The GPS-tracked birds did not carry

174 accelerometers, the GPS data were collected concurrently to this study, and the detailed
175 results are reported in Yamamoto et al. (2015).

176 For each dive we determined dive depth, dive duration, bottom time (the time
177 between the start and end of the period when birds showed no change in the diving depth),
178 descent and ascent time (the time between the start of the dive and the start of the bottom
179 phase, and the time between the end of the bottom phase and the end of the dive,
180 respectively). A dive was considered to occur when dive depth exceeded 0.5 m (Watanuki
181 et al., 2001; Takahashi et al., 2008). We calculated the number of wing strokes per unit
182 time during the descent, bottom and ascent phases using the heaving (dorso-ventral)
183 acceleration, as an index of their underwater activity (Watanuki et al., 2003; Watanuki et
184 al., 2006). We applied a high-pass filter 1 Hz to heaving acceleration such that active body
185 movements induced by wing strokes were highlighted. Peaks in the filtered acceleration
186 exceeding a threshold amplitude (0.2×9.8 ms^{-2}) were counted within a 1.0 s time
187 window, and summed during diving descent, bottom and ascent phases of each dive, then
188 divided by descent, bottom and ascent duration to calculate the wing stroke frequency in
189 each phase. The analyses on wing strokes were made with the analysis software Igor Pro
190 version 6.0 (Wave Metrics Inc., Lake Oswego, OR, USA).

191

192 **2.4 Environmental parameters**

193 We calculated four parameters from temperature data obtained from bird-borne
194 data loggers to characterize the thermal environment of murre's foraging locations: sea
195 surface temperature (SST), thermocline depth, thermocline intensity and water
196 temperature at depth >40 m (Kokubun et al., 2010b). These parameters are known to vary
197 spatially in the southeastern Bering Sea continental shelf (Coachman, 1986). In the
198 vicinity of the Pribilof Islands, the areas close to the islands are expected to have lower
199 sea surface temperature, higher temperature at depth and less intense or no thermoclines
200 due to tidal mixing, whereas areas far from the islands are expected to show the reversed
201 pattern: higher SST, lower temperature at depth and a more intense thermocline due to
202 heating of the sea surface (Kinder et al., 1983; Takahashi et al., 2008). Vertical
203 temperature profiles were determined for each dive bout, using the temperature data from
204 the deepest dive of the bouts (only dives > 20 m were used). Because the temperature
205 sensor had a slow response time, we corrected the temperature data for the response time
206 following Daunt et al. (2003) and Takahashi et al. (2008). We defined thermocline depth
207 as the depth where d*T*/d*D* (T: temperature, D: depth) was the maximum and >0.25ºC
208 (Takahashi et al., 2008). We defined thermocline intensity as the difference between
209 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 stable isotope analysis 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 $\delta^{13}C_{PDB}$ and $\delta^{15}N_{air}$ according to $\delta X = [(R_{sample}/R_{standard})\text{-}1] \times 1{,}000$, where X is ^{13}C or ^{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. (2016). This approach allows for simultaneous analysis of $\delta^{13}C$ and $\delta^{15}N$ and quantifies the uncertainty of the contributions of multiple sources to the diet of the birds. The model combines the likelihoods for the observed $\delta^{13}C$ and $\delta^{15}N$ data from the sources ($N = 7$ potential prey species) caught in the vicinity of the colony (<100 km). In this process, we had two 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 $\delta^{13}C$ and $\delta^{15}N$ respectively following Barger et al. (2016). We recognize that prey stable isotope signatures may vary spatially (Jones et al., 2014: between on-shelf and off-shelf) and/or temporally (among years). However, we are primarily interested in comparing COMU and TBMU diets within the same season at the same breeding location, and thus use these source values as a proxy to compare the relative trophic position and obtain insights on potential inter-specific differences in prey composition (e.g. Fig. 6). The enrichment factors were subtracted from the isotope values of red blood cells prior to the analysis. The analyses were conducted using the "SIAR" package (Parnell et al., 2010) 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 parents experiences as a result of foraging conditions (n = 11 COMUs and 22 TBMUs). All birds were sampled according to a standardized technique (Benowitz-Fredericks et al., 2008), with a blood sample was collected within three minutes of capture.

We used DNA extracted from red blood cells to genetically sex our study birds using (see Griffiths et al., 1998). However, in some cases, we did not collect blood samples from the instrumented birds (n = 5 TBMU). In these cases we employed a 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 is 80%. We considered that the morphologically determined sex in three TBMUs was reliable, because their posterior classification probability was larger than 80%, but we could not determine sex of the other two individuals with posterior classification probability lower 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

299 software (R Development Core Team, 2014) for GLMs and GLMMs. Data are presented
300 as mean values ± standard deviation (SD), with significance set at the 0.05 level.
301
302 **3 Results**
303 **3.1 Data recovery**
304 We recaptured 11 of 13 instrumented COMUs and all of 15 instrumented
305 TBMUs. The remaining 2 COMUs were not observed after the planned timing of retrieval.
306 Among the retrieved data loggers, 4 from COMU and 3 from TBMU did not record data
307 properly due to memory malfunctions. Overall, we analyzed behavioral data from 7
308 COMU (consisting of 4 males and 3 females) and 12 TBMU (consisting of 3 males, 7
309 females and 2 unknown sexes). These data covered 14 and 21 foraging trips that included
310 64 and 79 dive bouts, for COMU and TBMU, respectively (Table 1).
311 COMU had smaller body mass (COMU: 946 ± 45 g, TBMU: 1023 ± 64 g, one-
312 way ANOVA, $F_{1,17} = 7.8$, $P = 0.013$), smaller wing area (COMU: 0.053 ± 0.007 m^2,
313 TBMU: 0.067 ± 0.007 m^2, one-way ANOVA, $F_{1,17} = 16.4$, $P = 0.001$), and greater wing
314 loading than TBMU (COMU: 176 ± 26 N m^{-2}, TBMU: 151 ± 20 N m^{-2}, one-way ANOVA,
315 $F_{1,17} = 5.6$, $P = 0.031$). There were no significant differences in these morphological
316 parameters between the sexes in either COMU or TBMU (one-way ANOVA, P> 0.05).

317

318 **3.2 Trip parameters**

319 Foraging trip duration, total flight duration and dive bout duration did not differ
320 between COMU and TBMU (Table 1). There was no significant difference in trip and
321 bout duration between the sexes in COMU and TBMU (one-way ANOVA, $P > 0.05$). The
322 total flight duration of male COMU were longer than those of females (2.1 ± 0.7 h for
323 males and 1.0 ± 0.3 h for females: one-way ANOVA, $F_{1,12} = 13.7$, $P = 0.003$). There was
324 no significant difference between the sexes in TBMU total flight duration (one-way
325 ANOVA, P> 0.05). The maximum distance from the colony during foraging trips
326 estimated by total flight duration was 42.6 ± 21.1 km (ranging 12.8 - 81.2 km) for COMU
327 and 38.1 ± 21.9 km (ranging 4.4 - 76.4 km) for TBMU, respectively. With these small
328 foraging ranges, both COMU and TBMU probably foraged on the continental shelf
329 (bottom depth <200m: Yamamoto et al., 2015).

330

331 **3.3 Environmental use**

332 The sea surface temperature (SST), where the dive bouts occurred, did not differ
333 between COMU and TBMU (Fig. 1 A, B: COMU: 11.9 ± 0.4°C, TBMU: 11.8 ± 0.7°C,
334 GLMM with LRT, $\chi^2 = 0.01$, $P = 0.91$). The temperature at depth (>40 m) did not differ

between COMU and TBMU (Fig. 1 C, D: COMU: 4.8 ± 0.9ºC, TBMU: 4.9 ± 0.7ºC, 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 ± 1.1ºC for COMU and 5.3 ± 1.1 ºC for TBMU) 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 fewer 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. 3 A, B, C, 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%

353 for shallow dives, 11.1 ± 8.5% and 13.5 ± 8.8% for deep dives, for COMU and TBMU
354 respectively: GLM, t = 1.193, P = 0.254). There were no significant differences in the
355 proportion of daytime and nighttime dives or shallow and deep dives between the sexes
356 in either COMU or TBMU (GLM, P> 0.05).
357 During the daytime, the shallow diving depth (<40 m) did not differ between the
358 species (Fig. 3 C, D: 18.1 ± 6.0 m for COMU and 20.2 ± 7.4 m for TBMU: GLMM with
359 LRT, χ^2 = 0.30, P = 0.581). However, the deep diving depth (>40 m) was deeper for
360 COMU (74.2 ± 8.7 m) compared to TBMU (59.7 ± 7.9 m: Fig. 3 C, D: GLMM with LRT,
361 χ^2 = 7.04, P = 0.008). In the nighttime, the depth of shallow dives (<40 m) did not differ
362 between the species (Fig. 3 G, H: 15.4 ± 4.0 m for COMU and 19.1 ± 6.2 m for TBMU:
363 GLMM with LRT, χ^2 = 1.12, P = 0.289). There were no significant differences between
364 the sexes in either COMU or TBMU dive depths (GLMM with LRT, P> 0.05).
365 The number of wing strokes during the bottom phase of day and night dives was
366 higher in COMU than in TBMU (Daytime: Fig. 3 E, F: 1.95 ± 0.16 s^{-1} for COMU and
367 1.68 ± 0.20 s^{-1} for TBMU: GLMM with LRT, χ^2 = 5.978, P = 0.014 and Nighttime: Fig.
368 3 I, J: 1.84 ± 0.07 s^{-1} for COMU and 1.57 ± 0.21 s^{-1} for TBMU: GLMM with LRT, χ^2 =
369 6.545, P = 0.011). The number of wing strokes during the bottom phase of the dive was
370 slightly higher during the daytime for both COMU (GLMM with LRT, χ^2 = 8.551, P =

371 0.003) and TBMU (GLMM with LRT, χ^2 = 20.052, P < 0.001). The number of wing
372 strokes during the dive descent phase did not differ between the species either in the
373 daytime (2.29 ± 0.07 s^{-1} for COMU and 2.18 ± 0.21 s^{-1} for TBMU: GLMM with LRT, χ^2
374 = 3.301, P = 0.069) or the nighttime (2.23 ± 0.11 s^{-1} for COMU and 2.19 ± 0.16 s^{-1} for
375 TBMU: GLMM with LRT, χ^2 = 1.387, P = 0.239). There were no significant differences
376 between the sexes in the number of wing strokes in either species (GLMM with LRT, P>
377 0.05).
378
379 **3.5 Diet**
380 We observed 20 and 39 prey items delivered by parent COMU and TBMU to
381 feed their chicks, respectively. The proportion of fishes (consisting of 6 walleye pollock
382 (*Gadus chalcogrammus*), 1 sculpin (*Cottoidae*), 1 flatfish (*Pleuronectidae*) and 9
383 unidentified fish for COMU, and 9 walleye pollock, 2 sculpins, 1 prickleback
384 (*Stichaeidae*) and 10 unidentified fish for TBMU) was higher for COMU compared to
385 TBMU (χ^2 test, χ^2 = 6.108, P = 0.047). Conversely, the proportion of invertebrates
386 (consisting of 1 squid (*Gonatidae*) for COMU, 12 squids and 1 unidentified crustacean
387 for TBMU) was higher for TBMU compared to COMU.
388 The stable isotope analysis for red blood cells showed differences in the potential

389 adult diet between the species. $\delta^{15}N$ was higher in COMU than in TBMU (Fig. 4: 14.5 ±
390 0.3 ‰ for COMU and 13.1 ± 0.4 ‰ for TBMU: one-way ANOVA, $F_{1,30}$ = 134.84, P
391 <0.001). $\delta^{13}C$ was also slightly higher for COMU compared to TBMU (Fig. 4: -19.4 ±
392 0.2 ‰ for COMU and -19.8 ± 0.2‰ for TBMU: one-way ANOVA, $F_{1,30}$ = 37.71, P
393 <0.001). There were no significant differences among the sexes in COMU stable isotope
394 data (one-way ANOVA, P> 0.05). Because of an inequality in number of male and
395 females (n = 2 males and 16 females) in TBMU, the effect of sex could not be analyzed,
396 but males generally showed higher $\delta^{15}N$ value (13.7‰ for both males) compared to those
397 of females (13.1 ± 0.3‰, ranging 12.4 to 13.8‰), while $\delta^{13}C$ value of males (-19.7‰ and
398 -19.8‰) was similar to those of females (-19.8 ± 0.2‰, ranging -20.0 to -19.4‰).
399 Based on the Bayesian Mixing Analysis for estimating potential food sources,
400 COMU were inferred to have fed on more fishes such as age-1 walleye pollock and age-
401 0 flounder, whereas TBMU were inferred to have fed on more invertebrates such as
402 euphausiids and squids (Figs. 6 and 7).
403
404 **3.6 Stress hormone**
405 The baseline CORT did not differ between the species (log transformed mean =
406 0.43 ± 0.25 ng ml^{-1} for COMU and 0.37 ± 0.27 ng 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 ± 0.31 ng ml^{-1}) was slightly lower than that of females (0.44 ± 0.23 ng ml^{-1}) in TBMU (one-way ANOVA, $F_{1,20}$ = 4.92, P = 0.038).

4 Discussion

This study investigated the fine-scale differences in foraging behavior between two closely related seabirds, common and thick-billed murres. Both species showed similar foraging ranges and diel patterns of diving (Table 1, Fig. 2). Both species used similar thermal environments at sea, with no significant inter-specific differences in SST, temperature at depth, thermocline depth and intensity (Fig. 1). Thus the two species appeared to forage in similar stratified water masses, presumably in the middle- or outer shelf domains around St. George Is. (Kinder et al., 1983; Takahashi et al., 2008). However, despite similarities in geographic location, 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, as estimated from SIAR models, whereas TBMU used lower trophic level prey, which possibly includes squids and meso-

425 zooplankton (Figs. 4, 5, 6 and 7). Red blood cells reflect adult diet during incubation and
426 early chick-rearing (half-life ~4 weeks: Barger et al., 2016; Hobson and Clark 1993). A
427 recent study suggested that, under good foraging conditions, the dietary differences
428 between sympatrically breeding COMU and TBMU becomes greater during the chick-
429 rearing period compared to the incubation or pre-laying period (Barger et al. 2016).
430 Therefore, it is likely that in this study the differences in the trophic levels between chick-
431 rearing COMU and TBMU were even greater than suggested from our results based on
432 stable isotope analysis of red blood cells.

433 Several studies have shown horizontal segregation of foraging habitat between
434 sympatric, closely related, diving seabirds (e.g. Lynnes et al., 2002; Barger et al., 2016),
435 whereas few studies have reported vertical segregation in spatially overlapped foraging
436 areas (but see Mori and Boyd, 2004). Mori and Boyd (2004) found that smaller macaroni
437 penguins dove to shallower depths than larger gentoo penguins, and suggested that
438 differences in diving capacity based on body mass contributed to the observed vertical
439 segregation. The effect of body mass on vertical segregation is not clear in our study,
440 because the smaller COMU dove to deeper depths below the thermocline (>40 m) in the
441 daytime than the larger TBMU (Fig. 3). Contrary to expected relatively poor diving
442 capacity of COMU compared to TBMU, COMU foraged at deeper depths in the daytime

443 probably to capture larger fishes.

444 Larger fast-swimming fishes, including age-1 walleye pollock, are distributed at
445 deeper depths in the daytime compared to smaller age-0 pollock, and migrate up to
446 thermocline depths at night (Lang et al., 2000; Schabetsberger et al., 2000; Hurst, 2007).
447 Diving seabirds are considered to feed mostly during the diving bottom phase (Elliott et
448 al., 2008). Accordingly, we observed the deeper diving depths in the daytime and more
449 frequent wing strokes during the bottom phase of COMU dives. Combined with higher
450 trophic levels of their prey, these data suggests that COMU tended to forage on more
451 mobile prey such as large fishes, compared to TBMU. There are several possible factors
452 affecting the inter-specific differences/ similarities in foraging behavior between closely
453 related COMU and TBMU, such as 1) physiology and morphology, 2) breeding stages
454 and nest attendance, and 3) prey availability.

455 Croll and McLaren (1993) suggested that resting or diving metabolic rates are
456 expected to be similar between COMU and TBMU. On the other hand, TBMU at our
457 study colony had larger body mass, larger wing area and smaller wing loading than
458 COMU. According to previous studies (Thaxter et al., 2010; Linnebjerg et al., 2013),
459 alcid species with larger body mass are expected to dive deeper, and that with smaller
460 wing loading are expected to fly farther. However, these predictions were not supported

461 in our study. A morphological study pointed out that the smaller wings of COMU enables
462 them to swim more agilely than TBMU (Spring, 1971). COMU's more frequent wing
463 strokes during the dive bottom phase (Fig. 3 E, F, I, J), are possibly due to pursuing larger
464 fishes, and may support the observation by Spring (1971) that their small wing-size
465 enables them to chase down large fast-moving juvenile fish.

466 This study was conducted during the chick-rearing period of both species when
467 the energy demands of parents are highest (Ricklefs, 1983). High energy demands may
468 force both COMU and TBMU to forage closer to the colony, compared to during
469 incubation (Barger et al., 2016) and post- or pre-breeding periods (Linnebjerg et al., 2013).
470 In addition, one member of a pair of COMU consistently guarded their chicks like during
471 incubation on the narrow open ledges at the study colony. This aspect was different from
472 COMU at other locations where nests are more protected, and parents can leave their
473 chicks alone and spend more time foraging (Linnebjerg et al., 2015). Potential foraging
474 range and the diel patterns of diving were similar between COMU and TBMU at the study
475 colony (Table 1, Fig. 2), which may reflect the necessity to guard chicks, along with the
476 similar nest attendance patterns.

477 There are few available data on local food availability during the study period.
478 In terms of nutritional stress, both COMU and TBMU showed lower concentrations of

479 stress hormone in the study year, compared to those reported in other years on St. George
480 Island (Harding et al., 2013; Paredes et al., 2015) and elsewhere (Barger and Kitaysky,
481 2012), suggesting that the food conditions of the study year were favorable for both
482 species (Kitaysky et al. 2007; Kitaysky et al. 2010; Barrett et al. 2015). In addition, the
483 abundance of age-0 pollock in the eastern Bering Sea (in the 150 km radius around
484 Pribilof Islands) measured within the upper 15 m of the water column was high in 2014
485 compared to other years since 2003 (W. Strasburger, Ted Stevens Marine Research
486 Institute Juneau, Alaska, personal communications, 2015). Although seabirds breeding
487 on St. George Island may be prone to experience food shortage due to high bird density
488 (Hunt et al., 1986), murres were not food-limited during the study period, and the inter-
489 specific foraging niche partitioning occurred under favorable foraging condition. Barger
490 et al. (2016) suggested that the resource partitioning proactively increases during this
491 period of elevated energetic needs without apparent food limitations. Our study provides
492 further support that chick-rearing COMU and TBMU breeding on St. George Island
493 proactively partition resources when food conditions are relatively good.

494 Overall, at the study colony, chick-rearing COMU and TBMU foraged in similar
495 foraging ranges with a similar diel pattern of diving frequency. Inter-sexual foraging
496 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 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., 2016). Barger et al. (2016) 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. Such a spatial segregation by distance was not observed in our study (Table 1). TBMU populations exhibit various behavioral patterns, which may be due to inter-regional differences in morphology (Paredes et al. 2015). TBMU from St. Paul Island with larger body mass and wing loading performed shorter foraging trips and deeper dives, whereas TBMU from St. George Island with smaller body mass and wing loading performed longer foraging trips and shallower dives (Orben et al., 2015; Paredes et al., 2015). Thus segregation patterns between COMU and TBMU may differ among regions partly because their morphology differs at a regional scale.

515 It has been reported that, in other regions, COMU prefer larger, more mobile fish
516 including walleye pollock and capelin (*Mallotus villosus*), whereas TBMU use more
517 various prey including benthic fishes, cephalopods and meso-zooplankton (Hunt et al.
518 1981a; Barrett et al., 1997; Bryant et al., 1998; Barger et al., 2016). Spring (1971) and
519 Ogi (1979) suggested that COMU's more slender bill and palate, along with their
520 corneous tongue, reflects their more piscivorous tendencies, whereas the wider bill and
521 palate, and less corneous tongue of the TBMU reflects their invertebrate feeding habits.
522 In the Bering Sea, the recruitment of age-1 walleye pollock remained high during cold
523 regimes whereas it fell during warm regimes (Ianelli et al., 2009; Coyle et al., 2011).
524 During warm regimes, distribution of age-0 walleye pollock shifts northwards, their
525 abundance increases over the southeastern Bering Sea shelf and their lipid content
526 decreases (Wyllie-Echeverria and Wooster, 1998; Hunt et al., 2011). A recent study
527 suggests that breeding success of TBMU was higher in years when parents fed more on
528 on-shelf fish species including walleye pollock, rather than oceanic fish (myctophids) or
529 invertebrates (Renner et al., 2014). Reproductive success was similar between the species
530 at the study colony in 2014 (0.61 for COMU and 0.55 for TBMU) and it was higher than
531 long-term averages (Mudge et al., 2015). This is supported by the relatively low level of
532 stress hormones measured in our study birds which suggest that the behavioral data shown

in this study represent a year with favorable feeding conditions for both COMU and TBMU. In order for a clear prediction to be made regarding how these two species will respond to environmental change it would be necessary to determine whether the segregation patterns observed in this study persist in years with relatively unfavorable foraging conditions.

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 frequency. 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 have smaller wings which potentially enables the pursuit of more mobile prey. These results suggest that common and thick-billed murres segregated prey species in relation to differences in their morphology. These differences in food resource use may lead to the differential responses of the two murre species to marine environmental changes in the Bering Sea.

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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572
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Tables

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				$F_{1,33} = 0.70$; $P = 0.409$	$F_{1,33} = 1.62$; $P = 0.212$	$F_{1,33} = 0.36$; $P = 0.552$	$F_{1,157} = 0.02$; $P = 0.892$

784 **Figure captions**

785

786 Fig. 1. Frequency distribution of dive bouts in relation to (A, C) sea surface temperature
787 (SST) and (B, D) mean temperature at depth (>40 m) in the water column. Upper panels
788 represent data for common murres (COMU) and lower panels represent data for thick-
789 billed murres (TBMU).

790

791 Fig. 2. (A, C) Frequency distribution and (B, D) depth distribution pattern of dives in
792 relation to time of day. Left panels represent data for common murres (COMU) and right
793 panels represent data for thick-billed murres (TBMU). Means ± standard deviation (SD)
794 are shown in B, D, calculated by individual bird data. The timing of sunrise and sunset is
795 shown by marks on the top horizontal axis.

796

797 Fig. 3. (A, B) Vertical temperature profiles where foraging dive occurred with (C, D, G,
798 H) frequency distribution of dives and (E, F, I, J) number of wing strokes per diving
799 bottom phase, in relation to dive depth. Upper panels represent data for common murres
800 (COMU) and lower panels represent data for thick-billed murres (TBMU). Panels C, D,
801 E, F represent data for the daytime, and panels G, H, I, J represent data for the nighttime.

802 Means ± standard deviation (SD) are shown excepting for A and B, are calculated from
803 individual bird data. Sample number of birds (*N*) and dives (*n*) are shown in C, D, G, H.
804
805 Fig. 4. Diet composition of (A) common murres (COMU) and (B) thick-billed murres
806 (TBMU) based on direct observations of prey delivered to nests.
807
808 Fig. 5. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopic ratio values of common murres
809 (COMU: open circles) and thick-billed murres (TBMU: closed circles) measured in red
810 blood cells. Smaller circles show individual data, and larger circles with error bars show
811 Means ± standard deviation (SD).
812
813 Fig. 6. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopic ratio values of potential food
814 samples caught around the vicinity of the study colony. Different symbols represent each
815 potential food item. **The enrichment factors -0.19‰ for $\delta^{13}C$ and 2.25‰ for $\delta^{15}N$ were
816 preliminarily applied to the bird data (open circles for common murres and closed circles
817 forthick-billed murres). Note that the potential food samples were collected in 2009, as
818 no data were available in 2014.
819

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

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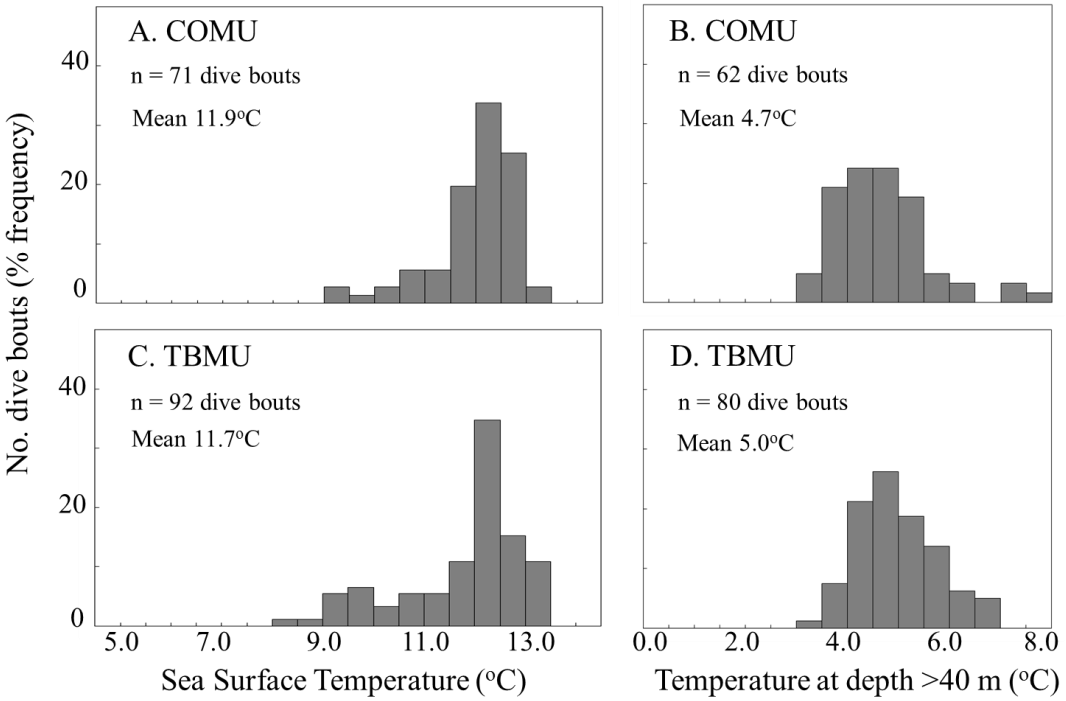

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831 Kokubun et al. Fig. 1.

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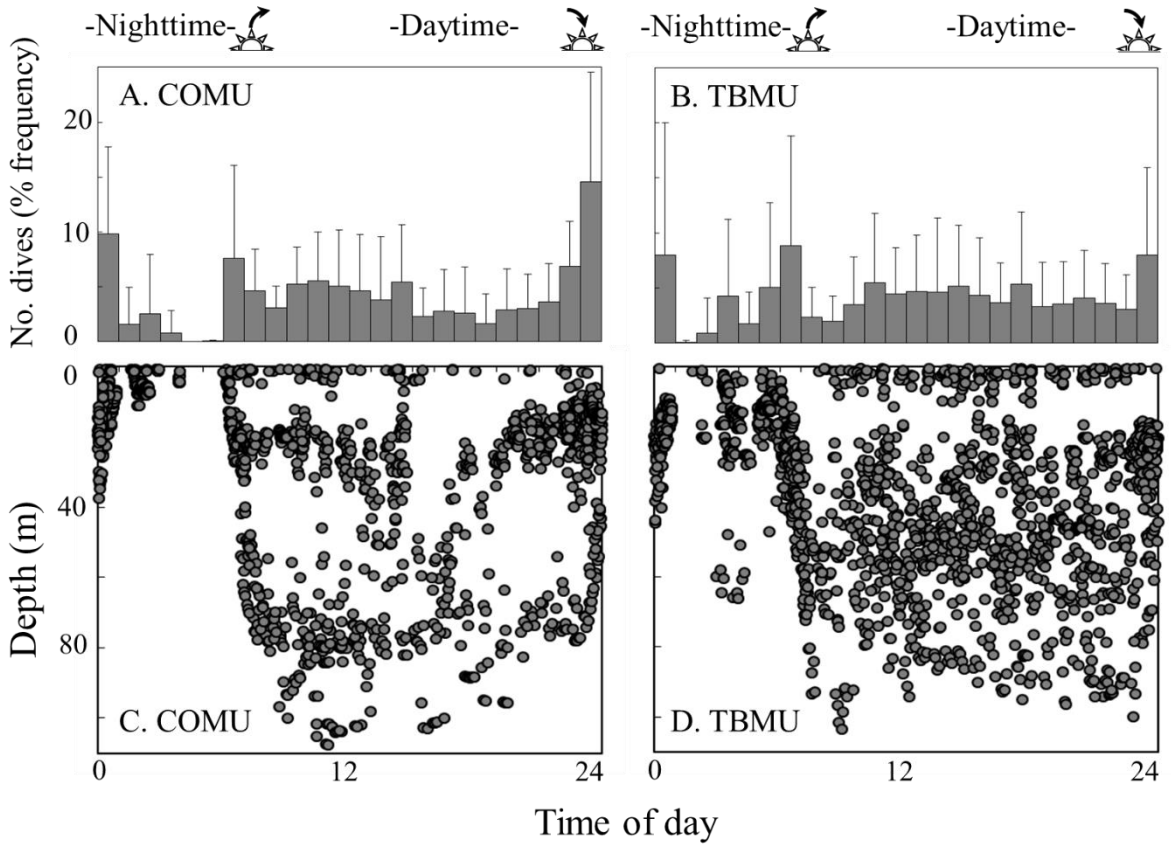

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838 Kokubun et al. Fig. 2.

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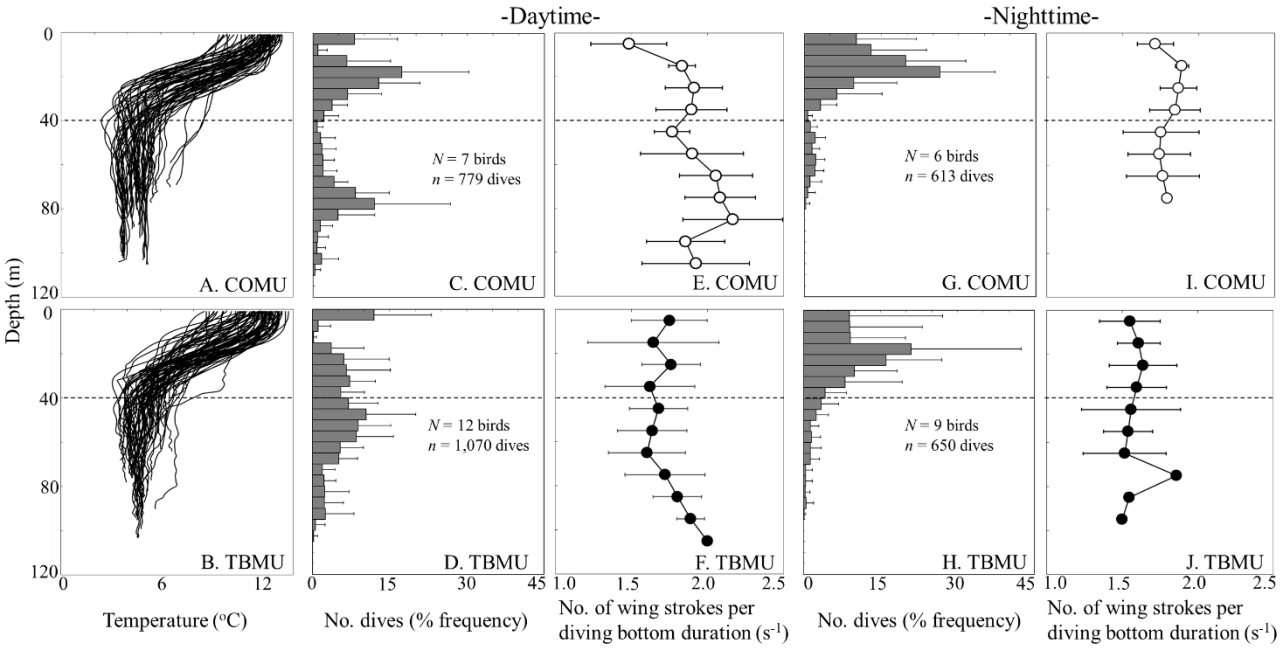

Kokubun et al. Fig. 3.

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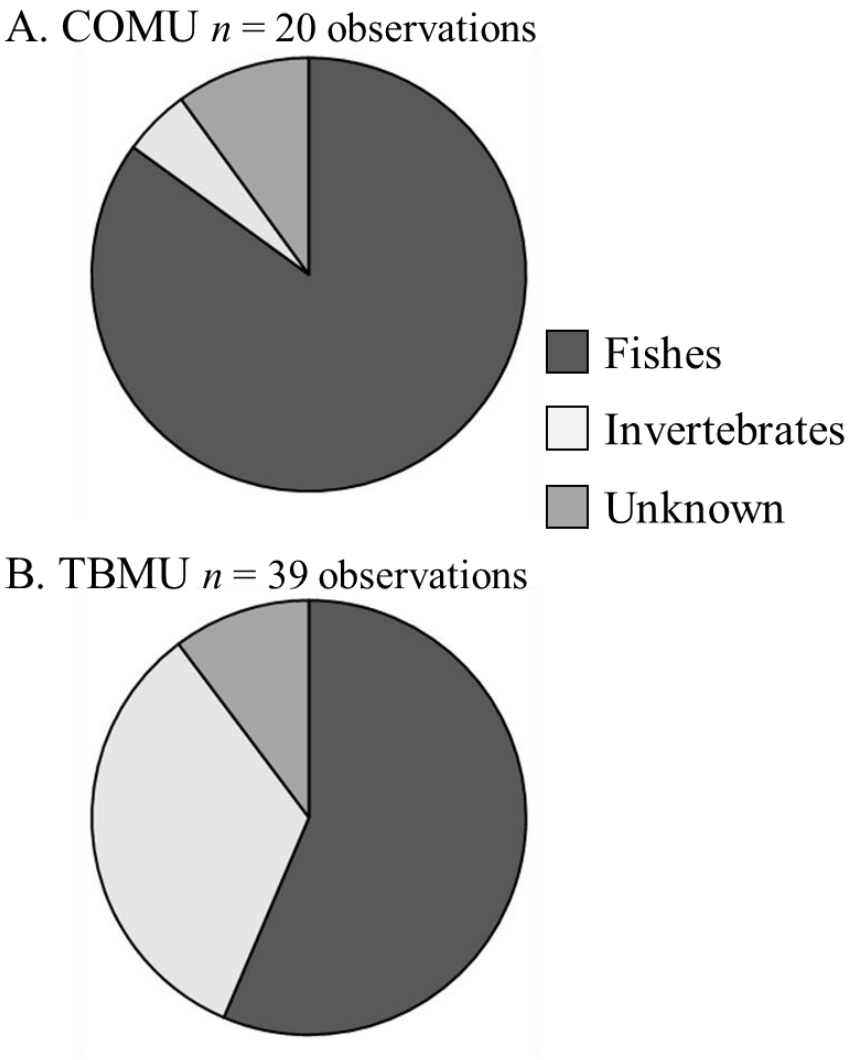

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850 Kokubun et al. Fig. 4.

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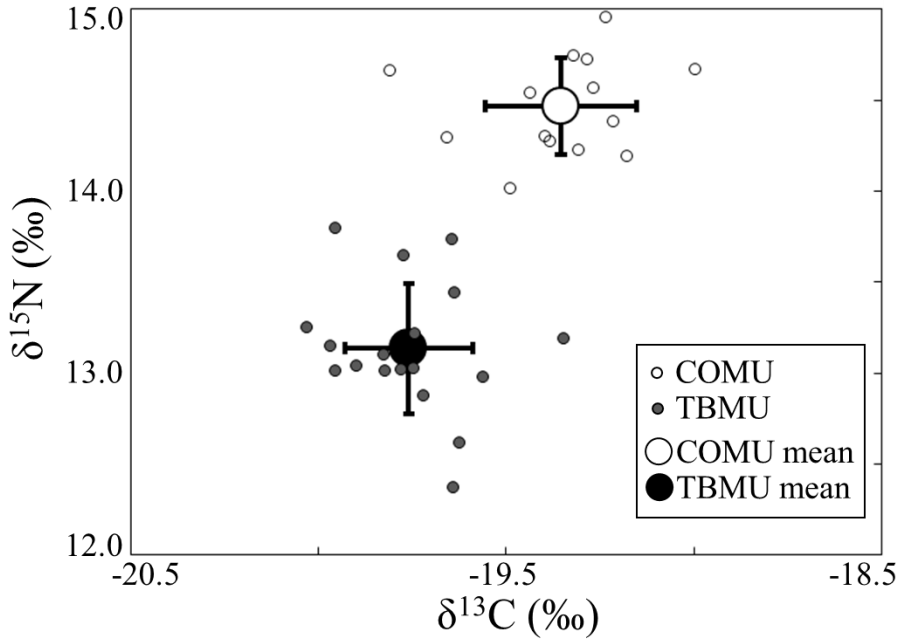

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856 Kokubun et al. Fig. 5.

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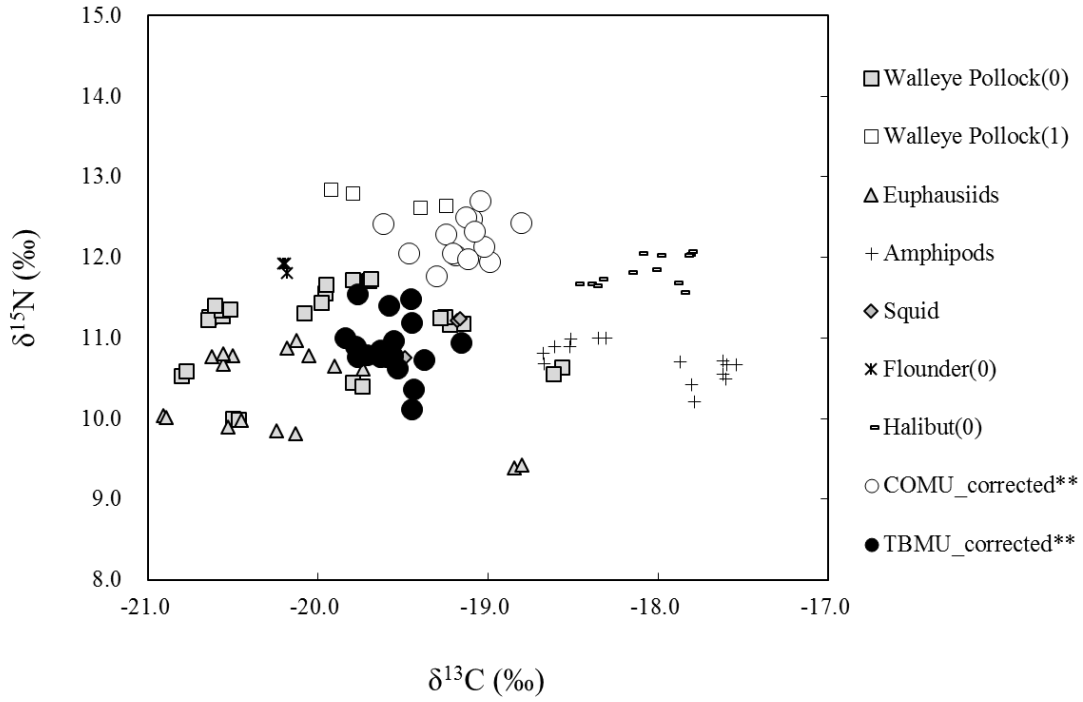

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861 Kokubun et al. Fig. 6.

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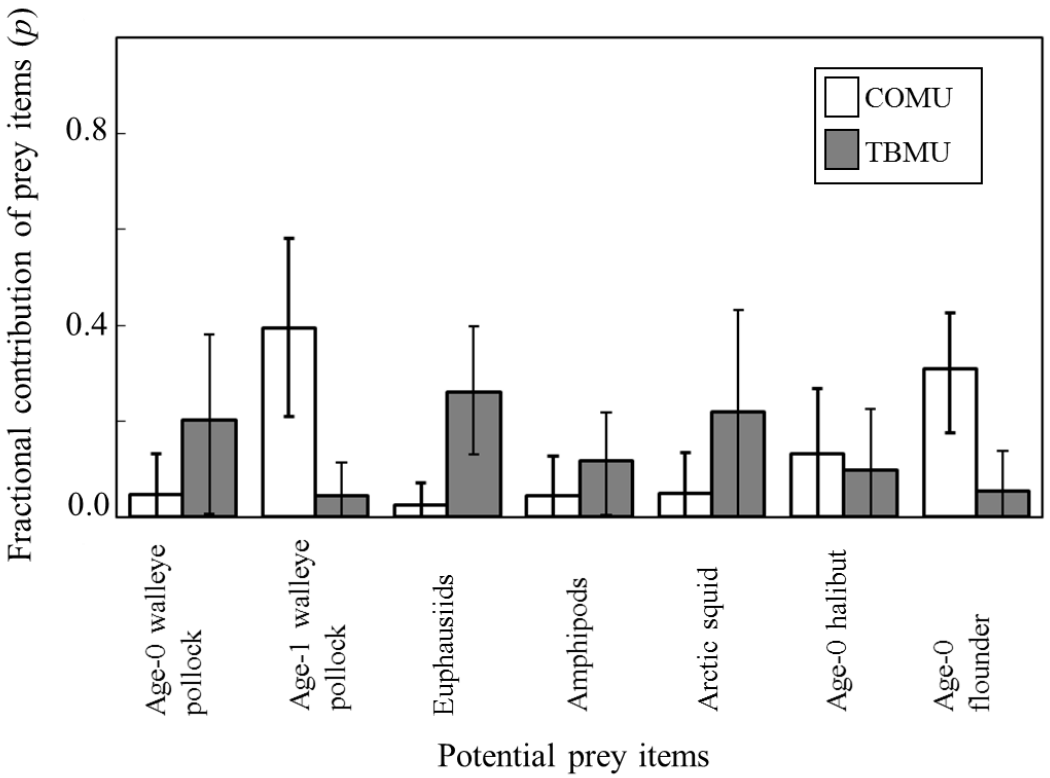

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867 Kokubun et al. Fig. 7.

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