

Dr. Tohru Hirawake,
Editor of *Biogeosciences*,
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Hokkaido, 040-0821 Japan

15 March 2016

Dear Dr. Hirawake,

We would like to submit our revised manuscript entitled “**Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea**” by Nobuo Kokubun, Takashi Yamamoto, Nobuhiko Sato, Yutaka Watanuki, Alexis Will, Alexander S. Kitaysky and Akinori Takahashi. We attached the revised manuscript (Kokubun et al. Revised_ms.pdf) and the letter to the reviewers (Kokubun et al. Revised_Response to the reviewers.pdf). We included the marked-up manuscript version at the end of the letter to the reviewers. We would like to draw your attention that the title was changed from “Foraging segregation of two congeneric diving seabird species (common and thick-billed murre) breeding on St. George Island, Bering Sea” to “Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea”, after discussing with co-authors.

We hope that the paper will be considered suitable for publication as a research article in the special issue “Catastrophic reduction of sea ice in the Arctic Ocean – its impact on the marine organisms and ecosystems in the polar region” in *Biogeosciences*. However, we would of course be happy to make any further changes that you think necessary.

Sincerely yours,

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RESPONSE TO THE REVIEWERS

We are grateful to Prof. George Hunt and Dr. David Ainley for their helpful comments and suggestions. We expressed our thanks to them in the acknowledgements. We showed our response to the reviewers by **red color**.

Prof. Hunt G. L. Jr.

General Comment

Kokubun et al examine ecological segregation of two closely related seabirds by providing a thorough analysis of their diving behavior. They find that the common murre, with smaller wings, was more agile underwater and brought larger fish to its young than the thick-billed murre, with larger wings and a heavier body. Prey choice resulted in common murre foraging at a higher trophic level than thick-billed murre. They suggest that the greater underwater agility of common murre allows them to be more flexible in the marine habitats that they inhabit. The paper has two themes, neither of which is developed in much depth. On the one hand is ecological segregation, a concept that two species cannot inhabit the same ecological niche. The second theme is that climate change will challenge species to be flexible in their behaviors as new opportunities emerge and old resources decline. The first theme is investigated thoroughly using recording devices that document the details of underwater behavior of the birds, and stable isotope analyses to document differences in trophic levels. The methods used here are state of the art, and the results are compelling. Fig. 2 is particularly effective in showing the diving behavior over the daily cycle, whereas Fig. 3 shows how the dives of the two species differed. In the diet analyses, it was good to have observations of foods brought to chicks as well as stable isotope analyses of red blood cells from adult birds that provide an indication of foods used by the adults. That said, they do not place their results in the broader context of where this field has gone. The discussion of the relevance of the differences in foraging behavior to adaptability to climate change seemed to be an afterthought tacked on at the end. This theme of the paper is probably of more general interest than the ecological segregation analysis, as many people are interested in predicting which species will be winners or losers in a world with a warming climate. I would have liked to see this theme developed in the Introduction, with the aim of exploring the characteristics that might improve adaptability

and then asking if one of the two murre species was likely to thrive more than the other. For advancing this theme, it would have been valuable to: 1) describe the observation that common murre cope with environmental variability better than thick-billed murre; 2) evaluate how the eastern Bering Sea ecosystem responds to years with late ice retreat and warm water temperatures and how the prey field likely available to the murre would change; and 3) hypothesize that the common murre are more flexible in their foraging because they can dive deeper, turn faster, and take a wider size range of fish.

We are very grateful for the helpful comments provided by Prof. George Hunt. We recognize that we do not have enough evidence for evaluating how foraging COMU and TBMU respond to changes in Bering Sea ecosystem due to limited data from only one field season. According to the suggestions, we have modified the introduction and now mentioned what was our initial expectation about inter-specific difference in foraging behavior between COMU and TBMU deduced from previous literatures (L. 62-66, L. 108-111). We have also developed the discussion on implications of our results (despite limited) about how inter-specific difference in foraging behavior relates to response to environmental changes in the southeastern Bering Sea (L. 522-537).

Specific comments:

Abstract- There is a big jump from the first sentence on environmental change to the second on what you did to look at murre foraging behavior. Do you have ideas about what changes are expected and what impacts they might have on predators?

We have modified the first sentence accordingly (L. 20-22).

Page 18153, line 22-24: What are the differences in the responses of these two species to long term changes, or do you mean predict how they might respond? I think that you can do a better job of setting up the question and/or hypotheses up front, and then telling us what to do and what you found. It would then be good to finish off with your take on why this research is important and/or your predictions.

We could not provide a clear hypothesis due to limited information available, nevertheless we modified the related sentences in Introduction (L. 63-66, L. 108-114).

Page 18154, line 2: There are more recent USFWS reports.

We added the reference (L. 51).

Page 18154, line 6: Add Hunt et al., 2011

We added the reference (L. 53).

Page 18154, line 14: Is this driven by ocean temperature directly, or by something that ocean temperature affects?

We now added more explanation (L. 56-60).

Page 18154, lines around line 25: There are several Hunt group papers that deal with prey difference in the two murre species at St. Paul and St. George Islands. Also, the nest sites preferred by the two murre species are quite different.

Now we added the references (L. 71, L. 77-79).

Page 18155, line 7: Again, cite papers on murre prey use at the Pribilof Islands.

Now we added the reference (L. 86).

Page 18155, line 25 - 27: Can you propose this as a hypothesis?

Now we modified the last section of Introduction (L. 108-114).

Page 18157, line 14: ? should this be m^{-2} ? I am not sure.

Corrected (L. 154).

Page 18158, lines 4-7: Why put mention of the GPS data in if it was not the focus?

Now we removed this part (L. 173-175).

Page 18159, line 21: delete "following"

Corrected (L. 226).

Page 18160, lines 19-23: In thinking about enrichment values, ^{13}C values vary on and off the shelf, and with rates of primary production. Also, in summer, micro-zooplankton play a very important trophic role and can bounce ^{15}N values up by a trophic level. If all of your murre samples were collected in the same year and at about the same date, this should not be a problem, but it is something to think about in evaluating your enrichment results.

We now added some consideration about the above matter (L. 252-258).

Page 18163, line 13 - 23: Did you expect to find differences, and if so, why?

Now we added purpose of these analyses (L. 196-202).

Page 18164, line 2: fewer rather than “less”

Corrected (L. 344).

Page 18164, line 14: Did you expect to find differences? This would make a difference between a one-tailed and a two-tailed test. What about using AIC methods to identify the dive characteristics that may differ most between species?

We used two-tailed test throughout the paper, because we did not have prior expectations which sex has larger or smaller values. We did not present the AIC value of each model to make the manuscript concise, but AIC was lowest when only the term ‘species’ was included (when significant inter-specific difference was detected).

Page 18165, line 13: When murre are bringing back meso-zooplankton (and maybe squid), higher quality prey may be scarce. Historical data might show whether, in years when squid were common in murre diets, growth rates of young were lower.

We are grateful to the suggestion. Now we add a reference regarding it in the discussion (L. 526-529).

Page 19165, line 21: Because of, not “according to”

Corrected (L. 394).

Page 18166, lines 5 – 11: why look at CORT? Did you expect one of the murre to be working harder to feed its young? I do not recall you mentioning stress or CORT in either the Abstract or the Introduction.

We now added brief explanation about stress hormone analyses, in Abstract and Introduction (L. 27, L. 107-108).

Page 18166, line 14 – 16: Why do you conclude that they use similar foraging areas? One could be going off the shelf and the other toward the middle shelf.

Now we added some explanation (L. 415-419).

Page 18166, line 19: How did you determine their ages?

Now we added an explanation (L. 423).

Page 18166, line 24: Why? I am a bit confused by this whole sentence. Could thick-billed murrelets be switching more to fish when in the chick-rearing period? What do you mean by isotopic distance? Between what and what?

Sorry for the confusing description. Now we provided detailed explanation (L. 427-432).

Page 18167, line 6: Can you test this with your data?

We could not test this with our data, due to the lack of simultaneous records of feeding events.

Page 18168, line 10-13: There is an old Hunt et al. paper that discusses the impact of living in a larger colony.

We added the reference (L. 486-489).

Page 18169, lines 18- 29 and top page 18170: This is really the first that you have brought this up. If prey niche breadth and foraging behavior breadth are tied to better performance in a variable climate or a poor one, then highlight this in the Introduction as an hypothesis.

We could not provide a clear hypothesis due to limited information available, nevertheless we modified the related sentences in Introduction (L. 63-66, L. 108-114) and Discussion (L. 522-537).

Fig 2: Do you have any idea as to the depth at which light is sufficient for visual predators? Are prey bioluminescent?

According to Regular et al., 2011 Plos One, it seems that both COMU and TBMU foraged under light levels higher than ambient moonlight, which means they mostly use visual cue during diving. We have no evidence that the prey observed in this study was bio-luminescent. As we considered that this was out of scope of this study, we omitted these descriptions in the manuscript.

Fig. 3. Are there differences in wing stroke characteristics in the upper water column in day and

night? Do the murrelets work as hard or harder at night?

Now we added some explanation about the above matter in Discussion (L. 369-371).

Dr. Ainley D. G.

General Comment

Other than perhaps some editing here and there so that in places it conforms better to proper English, the paper is suitable for publication. I would think that the two English-speaking co-authors could correct this. Otherwise, in fact, it is a very interesting synthesis of morphology with ecology and foraging behavior, and thus a very valuable contribution to our understanding of the ecology of marine birds. Thus I recommend its publication. The one issue that I might mention, and it is a minor one, revolves around what is said at line 15, p 18155, in regard to species attempting to avoid competition. It is competition for a resource that drives the separation of abilities among individuals, eventually leading to differing adaptations between species that allow access to the resource in question. Without competition, there would be no between-species divergence. Adaptations are a way to solve competition, not necessarily avoid it.

We are very grateful for the positive comments provided by Dr. David Ainley. We have now modified the sentence accordingly (L. 98-99).

Marked-up manuscript version

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

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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) murre 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 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 ± 7.095 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 ± 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). Fish occurred more frequently in the bill-loads of COMU ~~Fishes occurred with higher proportion in the bill loads brought back to chicks in COMU~~ (85%) than in TBMU (56%). $\delta^{15}\text{N}$ value of blood was significantly higher in COMU (14.47 ± 0.275 ‰) than in TBMU (13.14 ± 0.36 ‰). Relatively small wing area (0.053 ± 0.007 m²) of COMU compared to TBMU (0.067 ± 0.007 m²) may facilitate their increased agility while foraging and allow them to capture more mobile prey such as larger fishes that inhabit deeper depths ~~make them more agile underwater and thus enable them to target more mobile prey including 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 ~~foraging~~

~~behavior between COMU and TBMU might explain the differences in their responses to long-term marine environmental changes.~~

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 ~~that lead to different~~which result in contrasting responses of plankton and nekton communities (Coyle et al., 2011; [Hunt et al., 2011](#)), and ~~sympatric~~-predators (Barger and Kitaysky, 2012). Common murre (*Uria aalge*: hereafter COMU) and thick-billed murre (*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). ~~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 1980s and~~

~~then recovered toward the late 2000s (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). 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). 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 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 ~~appear~~ [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 ~~its~~ [underlying processes](#) ~~among closely related~~ [in](#) marine predators.

~~Ecological-Foraging~~ 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-a~~

variety of prey ([Hunt et al., 1981a](#); Barrett et al., 1997; Bryant et al., 1998; [Barger et al., 2016](#)~~Barger et al., in review~~). Whether/how, their foraging behavior contributes to these prey differences is, however, not well known. ~~Several~~ 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](#)~~Barger et al., in review~~). Paredes et al. (2015) ~~revealed~~ showed that, within TBMU ~~populations~~ colonies, smaller ~~birds~~ individuals are adapted ~~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 ~~larger birds are adapted to fly shorter and dive deeper 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~~ the overlap in horizontal and vertical foraging habitats and/or in prey species ~~are~~ is greater during ~~the incubation period~~ than the chick-rearing period, possibly to enhance resource partitioning between the species during the energy-demanding chick-rearing

~~period~~ avoid potential inter-specific competition during energy-demanding chick-rearing period (Barger et al., 2016; Barger et al., in review). 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, a fine-scale study of murre diving and flight behavior combined with dietary and morphological analyses ~~would be critical~~ is needed to better understanding the differences in the ecological niches of these closely related species. ~~their ecological niche in the marine ecosystem.~~ We anticipate that fine-scale studies on foraging segregation between COMU and TBMU will provide insight into whether/how their responses to environmental change in the Bering Sea ecosystem may differ. ~~a link between their different responses to environmental change and various components of the Bering Sea ecosystem.~~

Here we investigated the differences in foraging behavior between COMU and TBMU with depth-temperature-acceleration data loggers. Stable isotope analyses, observation of prey delivered to chicks, and stress hormone analyses were used to examine inter-specific differences in diet and consequent nutritional stress.

Based on results of previous studies, we predicted that COMU would consume higher trophic level prey and show more specialized foraging behavior on fish prey compared to TBMU, which might be also associated with inter-specific differences in wing morphology. We combine detailed foraging behavior, diet, and morphology to discuss how inter-specific differences in the foraging behavior may affect the responses of two murre species to environmental change in the southeastern Bering Sea. 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, southeastern Bering Sea, home to one of the largest murre colonies ~~of murre~~ 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~~ colony, where avian predators are nearly absent, COMU and TBMU form mixed colonies on narrow open ledges ~~where avian predators are nearly absent, yet~~

and adults spent most of their non-foraging time at the nest ~~attending brooding~~ the chick.

Instruments (see below) were deployed on chick-rearing birds ~~guarding chicks~~ from

30th July to 13th August 2014. During the study period, sunrise and sunset ranged

between 07:17-07:44 and 23:33-23:02 ~~local time~~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).~~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. 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~~depth-temperature-~~depth~~-acceleration 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. ~~The Weight-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 and stress hormone 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 x 5 cm square as reference, and took pictures of the wing from ~~the~~-above. The wings were then traced ~~on~~-in the digital picture and the pixels of the wing trace were counted using IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA). The pixel number was converted ~~in~~-to area (m²) 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) × *g* (gravity acceleration: 9.8 m s⁻²) divided by wing area (m²).

2.3 Foraging trip and dive parameters

During the chick-rearing period, parent murrelets alternate foraging at sea with ~~guarding~~-brooding 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) \times total flight duration (h): $R^2 = 0.787$). ~~The regression analyses using GPS track was not the main focus of this study, thus the~~ The GPS-tracked birds did not carry accelerometers. ~~The~~ the GPS data were collected concurrently to this study, and the detailed results are reported in Yamamoto et al. (~~submitted to this issue~~ 2015).

For each dive we determined dive depth, dive duration, bottom time (the time

between the start and end of the time period when birds showed depth change of 0 m no change in the diving depth), 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; Watanuki et al., 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 ($0.2 \times 9.8 \text{ ms}^{-2}$) 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~~ calculated four ~~ocean thermal~~ parameters from temperature data obtained from bird-borne data loggers to characterize at the bird's thermal environment of murre's foraging locations: as indices of environmental use (Kokubun et al., 2010b).

~~S~~sea surface temperature (SST), thermocline depth, thermocline intensity and water temperature at depth >40 m (Kokubun et al., 2010b). These parameters are known to vary spatially in the southeastern Bering Sea continental shelf (Coachman, 1986). In the vicinity of the Pribilof Islands, the areas close to the islands are expected to have lower sea surface temperature, higher temperature at depth and less intense or no thermoclines due to tidal mixing, whereas areas far from the islands are expected to show the reversed pattern: higher SST, lower temperature at depth and a more intense thermocline due to heating of the sea surface (Kinder et al., 1983; Takahashi et al., 2008). ~~were recorded by the loggers. Vertical temperature profiles were determined for each dive bout, using the temperature~~ 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 the maximum and~~ was $>0.25^{\circ}\text{C}$ (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 $\delta^{13}\text{C}_{\text{PDB}}$ and $\delta^{15}\text{N}_{\text{air}}$ according to $\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1,000$, where X is ^{13}C and ^{15}N , R_{sample} and R_{standard} are the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{14}\text{N}/^{15}\text{N}$ of samples and international standards. Replicate measurement of an internal laboratory standard

(Peptone) indicated measurement errors to be $\pm 0.16\%$ for N and $\pm 0.13\%$ 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. (~~in review~~2016). This approach allows for simultaneous analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and quantifies the uncertainty of the contributions of multiple sources to the diet of the birds. The model combines the likelihoods for the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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., ~~submitted in this issue~~2015). Because both murre species 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively

following Barger et al. (~~in review~~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~~added to~~

~~the data~~ 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~~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 was collected within three minutes of capture.

We ~~conducted~~ used DNA ~~extracted from sex determination of~~ red blood cells to genetically sex our study birds using (see Griffiths ~~(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 these~~ cases ~~that the genetic sex information was not available,~~ 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 ~~was is~~ 80%. We considered that the morphologically determined sex ~~data from 3 out of the 5 in three~~ TBUMs 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 software (R Development Core Team, 2014) for GLMs and GLMMs. Data are presented as mean values \pm 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: 945.76 ± 44.85 g,

TBMU: ~~1022.9~~1023 ± ~~64.4~~64 g, one-way ANOVA, $F_{1,17} = 7.8$, $P = 0.013$), ~~had~~-smaller wing area ~~than TBMU~~ (COMU: 0.053 ± 0.007 m², TBMU: 0.067 ± 0.007 m², one-way ANOVA, $F_{1,17} = 16.4$, $P = 0.001$), and ~~had~~-greater wing loading than TBMU (COMU: ~~175.9~~176 ± ~~26.4~~ N m⁻², TBMU: ~~151.1~~151 ± ~~19.7~~20 N m⁻², one-way ANOVA, $F_{1,17} = 5.6$, $P = 0.031$). There were no significant differences in these morphological parameters 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 (~~2.1~~ ± ~~0.7~~3 h for males and ~~1.0~~ ± ~~0.28~~3 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 <200m: Yamamoto et al., [this issue 2015](#)).

3.3 Environmental use

The sea surface temperature (SST) where the dive bouts occurred did not differ between COMU and TBMU (Fig. 1 A, B: COMU: $11.9 \pm 0.4^\circ\text{C}$, TBMU: $11.8 \pm 0.7^\circ\text{C}$, 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. 1 C, D: COMU: $4.8 \pm 0.9^\circ\text{C}$, TBMU: $4.9 \pm 0.7^\circ\text{C}$, 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 ($5.4 \pm 1.1^\circ\text{C}$ for COMU and $5.3 \pm 1.1^\circ\text{C}$ 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~~-fewer dives with shallow depths in the nighttime (Fig. 1). Proportion of the daytime and nighttime dives did not differ between the species ($62.0 \pm 21.5\%$ and $63.1 \pm 28.7\%$ for daytime, and $38.0 \pm 21.5\%$ and $37.0 \pm 28.7\%$ 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: $58.0 \pm 25.7\%$ and $42.4 \pm 16.4\%$ for shallow dives, $42.0 \pm 25.7\%$ and $57.6 \pm 16.4\%$ 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: $88.9 \pm 8.5\%$ and $86.5 \pm 8.8\%$ for shallow dives, $11.1 \pm 8.5\%$ and $13.5 \pm 8.8\%$ 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, the shallow diving depth (<40 m) did not differ between the species (Fig. 3 C, 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~~ However, the deep diving depth (>40 m) was deeper for COMU (74.2 ± 8.7 m) compared to TBMU (59.7 ± 7.9 m: Fig. 3 C, 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. 3 G, 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. 3 E, 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. 3 I, J: 1.84 ± 0.07 s⁻¹ for COMU and 1.57 ± 0.21 s⁻¹ for TBMU: GLMM with LRT, $\chi^2 = 6.545$, $P = 0.011$). The number of wing strokes during the bottom phase of the dive was slightly higher during the daytime for both COMU (GLMM with LRT, $\chi^2 = 8.551$, $P = 0.003$) and TBMU (GLMM with LRT, $\chi^2 = 20.052$, $P < 0.001$). The number of wing

strokes during the dive ~~On the other hand, the number of wing strokes during diving~~

descent phase did not differ between the species either in the daytime ($2.29 \pm 0.07 \text{ s}^{-1}$ for COMU and $2.18 \pm 0.21 \text{ s}^{-1}$ for TBMU: GLMM with LRT, $\chi^2 = 3.301$, $P = 0.069$) or the nighttime ($2.23 \pm 0.11 \text{ s}^{-1}$ for COMU and $2.19 \pm 0.16 \text{ s}^{-1}$ 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~~ either species (GLMM with LRT, $P > 0.05$).

3.5 Diet

We observed 20 and 39 prey items ~~for delivered by parent~~ COMU and TBMU to feed their chicks, respectively. The proportion of fishes (consisting of 6 walleye pollock (*Gadus chalcogrammus*), 1 sculpin (*Cottidae*), 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-squid (*Gonatidae*) for COMU, 12 ~~cephalopods-squids~~ and 1

unidentified ~~meso-zooplankton~~crustacean for TBMU₇) 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. $\delta^{15}\text{N}$ was higher in COMU than in TBMU (Fig. 4: $14.47\text{--}5 \pm 0.273\text{‰}$ for COMU and $13.14 \pm 0.364\text{‰}$ for TBMU: one-way ANOVA, $F_{1,30} = 134.84$, $P < 0.001$). $\delta^{13}\text{C}$ was also slightly higher for COMU compared to TBMU (Fig. 4: $-19.36\text{--}4 \pm 0.20\text{‰}$ for COMU and $-19.76\text{--}8 \pm 0.172\text{‰}$ 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~~Because ~~of~~ 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 $\delta^{15}\text{N}$ value (~~13.77‰ for both males~~ 4‰ ~~and~~ 13.65‰) compared to those of females ($13.07\text{--}1 \pm 0.32\text{‰}$, ranging $12.37\text{--}4$ to 13.798‰), while $\delta^{13}\text{C}$ value of males (-19.667‰ and -19.778‰) was similar to those of females ($-19.77\text{--}8 \pm 0.18\text{‰}$, ranging $-20.03\text{--}0$ to -19.354‰).

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~~ and 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 ± 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 murre, ~~at a fine scale~~. Both

species showed similar foraging ranges and diel patterns of diving (Table 1, Fig. 2).

~~Both species used and appeared to use~~ similar thermal environments at sea, with no significant inter-specific differences in SST, temperature at depth, thermocline depth/foraging areas (Figs. 1 and intensity (Fig. 2, Table 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-zooplankton (Figs. 4, 5, 6 and 7). ~~Arguably, stable isotope of $\delta^{15}N$ in~~ blood cells reflect adult diet/reflects conditions during incubation and early chick-rearing, ~~according to its relatively slow turnover rate (half-life ~4 weeks: Barger et al., in review~~ 2016; Hobson and Clark 1993). A recent study suggested ~~Assuming~~ that, under good foraging conditions, the dietary differences between sympatrically breeding

COMU and TBMU isotopic distance becomes greater in during the chick-rearing period rather than compared to the incubation or pre-laying period (Barger et al., ~~in~~ review 2016).; Therefore, it is likely we anticipate that in this study the differences in the the inter-specific difference in trophic levels between level is also applicable to the chick-rearing COMU and TBMU were even greater than suggested from our results based on stable isotope analysis of red blood cells period.

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

daytime probably to capture larger fishes.

Larger fast-swimming 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).

Accordingly, we observed the deeper diving depths in the daytime and more frequent wing strokes during the bottom phase of COMU dives, ~~combined~~ Combined with higher trophic levels of their prey, these data 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/ similarities 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.

Croll and McLaren (1993) suggested that ~~According to a previous study,~~ resting or diving metabolic rates are expected ~~not to be~~ similar between COMU and TBMU ~~(Croll and McLaren, 1993)~~. On the other hand, ~~COMU and~~ TBMU at ~~the~~ our

study colony ~~had larger~~~~differed morphologically in~~ body mass, larger 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. According to previous studies~~ ~~(-Thaxer et al., 2010; Linnebjerg et al., 2013),~~ alcid species with larger body mass are expected to dive deeper, and that with smaller wing loading are expected to fly farther. However, these predictions were not supported in our~~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. 3 E, F, I, J), are possibly due to pursuing larger fishes, and may support the observation by Spring (1971) ~~and reflect that~~ their small wing-size enables them to chase down large fast-moving juvenile fish~~morphological~~ ~~characteristics.~~

This study was conducted during the chick-rearing period of both species when ~~their~~ the energy ~~demand for~~demands of 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., ~~in review~~2016) and post- or pre-breeding

periods (Linnebjerg et al., 2013). In addition, one member of a pair of COMU consistently guarded their chicks like during incubation 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). suggesting that the food conditions of the study year were favorable for both species (Kitaysky et al. 2007; Kitaysky et al. 2010; Barrett et al. 2015). In addition, the~~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 murrelets: 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 communications, 2015). Although seabirds breeding on St. George Island may be prone to experience food shortage due to high bird density (Hunt et al., 1986), murrelets were not food-limited during the study period, and the inter-specific foraging niche partitioning occurred under favorable foraging condition. Barger et al. (2016-Barger et al. (in review) suggested that the resource partitioning proactively increases during this period of elevated energetic needs without apparent food limitations. This-Our study provides further support that also suggests the resource partitioning during the chick-rearing period between COMU and TBMU breeding on St. George Island proactively partition resources 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 frequency. Inter-sexual foraging 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., in review2016). Barger et al. (in review2016) 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 ~~divergent~~ 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 ~~TBMU's~~ their morphology differs at a regional scale.

It has been reported that, in other regions, ~~COMUs~~ COMU prefer larger, more mobile fish including walleye pollock and capelin (*Mallotus villosus*), whereas TBMU use more ~~divergent~~ various prey including benthic fishes, cephalopods and meso-zooplankton (Hunt et al. 1981a; Barrett et al., 1997; Bryant et al., 1998; Barger et al., in review 2016). 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 i~~
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), . During warm regimes, distribution of age-0 walleye pollock shifts northwards, their abundance increases over the southeastern Bering Sea shelf and their lipid content decreases (Wyllie-Echeverria and Wooster, 1998; Hunt et al., 2011). A recent study suggests that breeding success of TBMU was higher in years when parents fed more on on-shelf fish species including walleye pollock, rather than oceanic fish (myctophids) or invertebrates (Renner et al., 2014). possibly enabling COMU to capitalize on their foraging behavior in cold years. Although rReproductive success was similar between the species at the study colony in 2014 (0.61 for COMU and 0.55 for TBMU) and it was higher than long-term averages (Mudge et al., 2015). This is supported by the relatively low level of 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.), 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 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 ~~had~~ have smaller wings ~~that~~ which potentially enables ~~to~~ the pursuit of 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. These differences in food resource use ~~Such ecological segregation~~ may lead to the differential responses of the two murre ~~closely related~~ species to ~~respond to~~ local marine environmental change ~~differently~~ 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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References

Barger, C. P., and Kitaysky, A. S.: Isotopic segregation between sympatric seabird species increases with nutritional stress, *Biol. Lett.*, 8, 442-445, 2012.

Barger, C. P., Young, R. C., Cable, J. M., Ito, M., and ~~Alexander S.~~ Kitaysky, A. S.: Resource partitioning between sympatric seabird species increases during chick rearing. [Ecosphere, in press, 2016.](#)~~In review.~~

Barrett, R. T., Asheim, M., and Bakken, V.: Ecological relationships between two sympatric congeneric species, common murres and thick-billed murres, *Uria aalge* and *U. lomvia*, breeding in the Barents Sea, *Can. J. Zool.*, 75, 618-631, 1997.

[Barrett, R. T., Erikstad, K. E., Sandvik, H., Myksvoll, M., Jenni-Eierlmann, S., Kristensen, D. L., Moum, T., Reiertsen, T. K., and Vikebø, F.: The stress hormone corticosterone in a marine top predator reflects short-term changes in food availability, *Ecol. Evol.*, 5, 1306-1317, 2015.](#)

Benowitz-Fredericks, Z. M., Shultz, M. T., and Kitaysky, A. S.: Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. *Deep Sea Res. Pt. II*, 55, 1868–1876, 2008.

Bryant, R., Jones, I. L., and Hipfner, J. M.: Responses to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador, Can. J. Zool., 77, 1278-1287, 1998.

~~Byrd, G. V., Renner, H., and Renner, M.: Distribution patterns and population trends of breeding seabirds in the Aleutian Islands, Fish. Oceanogr., 14, 139-159, 2005.~~

~~Byrd, G. V., Schmutz, J. A., and Renner, H. M.: Contrasting population trends of piscivorous seabirds in the Pribilof Islands: A 30-year perspective, Deep Sea Res. Pt. II, 55, 1846-1855, 2008.~~

Clavel, J., Julliard, R., and Devictor, V.: Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ., 9, 222-228, 2011.

Coachman, L. K.: Circulation, water masses and fluxes on the southeastern Bering Sea Shelf, Cont. Shelf Res., 5, 23-108, 1986.

Croll, D. A., and McLaren, E.: Diving metabolism and thermoregulation in common and thick-billed murres, Comp. Physiol., 163, 160-166, 1993.

Croxall, J. P., Prince, P. A., and Reid, K.: Dietary segregation of krill-eating South Georgia seabirds, J. Zool., 242, 531-556, 1997.

Coyle, K. O., Eisner, L. B., Mueter, F. J., Pinchuk, A. I., Janout, M. A., Cieciel, K. D., Farley, E. V., and Andrews, A. G.: Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis, *Fisher. Oceanogr.*, 20, 139-156, 2011.

Daunt, F., Peters, G., Scott, B., Gremillet, D., and Wanless, S.: Rapid-response recorders reveal interplay between marine physics and seabird behaviour, *Mar. Ecol. Prog. Ser.*, 255, 283–288, 2003.

[Dragoo, D. E., Renner, H. M., and Irons, D. B.: Breeding status and population trends of seabirds in Alaska, 2014, U.S. Fish and Wildlife Service Report AMNWR 2015/03, Homer, Alaska, 2015.](#)

Elliott, K. H., Woo, K., Gaston, A. J., Benvenuti, S., Dall'Antonia, L., and Davoren, G. K.: Seabird foraging behaviour indicates prey type. *Mar. Ecol. Prog. Ser.* 233, 89-103, 2008.

Elliott, K. H., Gaston, A. J., and Crump, D.: Sex-specific behavior by a monomorphic seabird represents risk partitioning, *Behav. Ecol.*, 21, 1024-1032, 2010.

Falk, K., Benvenuti, S., Dall'Antonia, L., Kampp, K., and Ribolini, A.: Time allocation

and foraging behaviour of chick rearing Brünnich's guillemots *Uria lomvia* in high-arctic Greenland, *Ibis*, 143, 82-92, 2000.

Gallagher, A. J., Hammerschlag, N., Cooke, S. J., Costa, D. P., and Irschick, D. J.:

Evolutionary theory as a tool for predicting extinction risk. *Trends Ecol. Evol.* 30, 61-65, 2015.

Gaston, A. J., and Jones, I. L. *The Auks: Alcidae*. Oxford University Press, Oxford, London, 1998.

Griffiths, R., Double, M. C., Orr, K., and Dawson, R. J. G.: A DNA test to sex most birds. *Mol. Ecol.*, 7, 1071–1075, 1998.

Harding, A., Paredes, R., Suryan, R., Roby, D., Irons, D., Orben, R., Renner, H., Young, R., Barger, C., Dorresteijn, I., and Kitaysky, A.: Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea 2013. *Deep Sea Res. Pt. II*, 94, 178-191, 2013.

Hobson, K. A., and Clark, R. G.: Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk*,

110, 638-641, 1993.

Hobson, K., A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J-M., and Fortier, M.: A stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants, Deep Sea Res. Pt. II, 49, 5131-5150, 2002.

Hunt, G. L. Jr., Burgeson, B., and Sanger, G. A.: Feeding ecology of seabirds of the eastern Bering Sea, In: Hood, D., and Calder, J., A. (Eds.) The Eastern Bering Sea shelf: oceanography and resources. Juneau, AK: Office of Marine Pollution Assessment, National Oceanographic and Atmospheric Administration, pp. 629-648, 1981a.

Hunt, G., L., Jr., Eppley, Z., Drury W., H.: Breeding distribution and reproductive biology of marine birds in the eastern Bering Sea, In: Hood, D., and Calder, J., A. (Eds.) The Eastern Bering Sea shelf: oceanography and resources. Juneau, AK: Office of Marine Pollution Assessment, National Oceanographic and Atmospheric Administration, pp. 649-687, 1981**b**.

Hunt, G. L. Jr., Eppley, Z. A., and Schneider, D. C.: Reproductive performance of seabirds: the importance of population and colony size, Auk, 103, 306-317, 1986.

Hunt, G. L. Jr., Coyle, K. O., Eisner, L. B., Farley, E. V., Heintz, R., A., Mueter, F., Napp, J. M., Overland, J. E., Ressler, P. H., Salo, S., and Stabeno, J.: Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis, ICES J. Mar. Sci., 68, 1230-1243, 2011.

Hurst, T., P.: Thermal effects on behavior of juvenile walleye pollock (*Theragra chalcogramma*): implications for energetics and food web models, Can. J. Fish. Aquat. Sci., 64, 449-457, 2007.

Ianelli, J., N., Barbeaux, S., Honkalehto, T., Kotwicki, S., Aydin, K., and Williamson, N.: Assessment of the walleye pollock stock in the Eastern Bering Sea. In: Stock Assessment and Fishery Evaluation Report of the Groundfish Resources of the Bering Sea / Aleutian Islands Regions. Anchorage: North Pacific Fisheries Management Council, section 1, 49–148, 2009.

Irons, D., B., Anker-Nilssen, T., Gaston, A., J., Byrd, G., V., Falk, K., Gilchrist, G., Hario, M., Hjernquist, M., Krasnov, Y., V., Mosvech, A., Olsen, B., Peterson, A.,

Reid, J. B., Robertson, G. J., Strøm, H., and Wohl, K. D.: Fluctuations in circumpolar seabird—— populations linked to climate oscillations, *Glob. Change Biol*, 14, 1455-1463, 2008.

Jones, I. L., Rowe, S., Carr, S. M., Frazer, G., and Taylor, P.: Different patterns of parental effort during chick-rearing by female and male thick-billed murre (*Uria lomvia*) at a low-arctic colony, *Auk*, 119, 1064-1074, 2002.

[Jones, N. M., Hoover, B. A., Heppel, S. A., and Kuletz, K.: A cross-shelf gradient in \$\delta^{15}\text{N}\$ stable isotope values of krill and pollock indicates seabird foraging patterns in the Bering Sea, *Deep Sea Res. II*, 109, 241-250, 2014.](#)

[Kinder, T. H., Hunt, G. L. Jr., Schneider, D., and Schumacher, J. D.: Correlations between seabirds and oceanic fronts around the Pribilof Islands, Alaska, *Estuar. Coast. Shelf Sci.*, 16, 309-319, 1983.](#)

Kitaysky, A. S., and Golubova, E. G.: Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids, *J. Anim. Ecol.*, 69, 248–262, 2000.

[Kitaysky, A. S., Piatt, J. F., and Wingfield, J.C.: Stress hormones link food availability](#)

and population processes in seabirds, Mar. Ecol. Prog. Ser., 352, 245-258, 2007.

Kitaysky, A. S., Piatt, J. F., Hatch, S. A., Kitaiskaiya, E. V., Benowitz-Frederics, Z. M.,

Shultz, M. T., and Wingfield, J. C.: Food availability and population processes:

severity of nutritional stress during reproduction predicts survival of long-lived

seabirds, Func. Ecol., 24, 625-637, 2010.

Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., and H-C., Shin.; Comparison of diving behavior and habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica, Mar. Biol., 157, 811-825, 2010a.

Kokubun, N., Takahashi, A., Ito, M., Matsumoto, K., Kitaysky, A., S., and Watanuki, Y.:

Annual variation in the foraging behaviour of thick-billed murrelets in relation to

upper-ocean thermal structure around St. George Island, Bering Sea, Aquat. Biol., 8,

289-298, 2010b.

Lang, G., M., Brodeur, R., D., Napp, J., M., and Schabetsberger, R.: Variation in

groundfish predation on juvenile walleye Pollock relative to hydrographic structure

near the Pribilof Islands, Alaska, ICES J. Mar. Sci., 57, 265-271, 2000.

Linnebjerg J., F., Guilford, T., Reuleaux, A., Mosbech, A., and Fredirixsen, M.:

Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle, *Plos One*, 8, e72987, 2013.

Linnebjerg, J. F., Reuleaux, A., Mouritsen, K. N., and Frederiksen, M.: Foraging ecology of three sympatric breeding alcids in a declining colony in southwest Greenland, *Waterbirds*, 38, 143-152, 2015.

Lynnes, A. S., Reid, K., Croxall, J. P., and Trathan, P. N.: Conflict or coexistence? Foraging distribution and competition for prey between Adélie and chinstrap penguins, *Mar. Biol.*, 141, 1165-1174, 2002.

Masello, J. F., Hundry, R., Poisbleau, M., Demongin, L., Voigt, C. C., Wiekelski, M., and Quillfeldt, P.: Ecosphere Diving seabirds share foraging space and time within and among species, *Ecosphere*, 1, 1-28, 2010.

Mori, Y., and Boyd, I.: Segregation of foraging between two sympatric penguin species: does rate maximization make the difference? *Mar. Ecol. Prog. Ser.*, 275, 241–249, 2004.

Mudge, M. L., Pietrzak, K. W., Drummond, B. A., and Romano, M. D.: Biological monitoring at St. George Island, Alaska, in 2014, *U. S. Fish and Wildl. Serv. Rep.*,

AMNWR 2015/02. Homer, Alaska, 2015.

Navarro, J., Votier, S., C., Aguzzi, J., Chiesa, J., J., Forero, M., G., and Phillips, R., A.:

Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels, Plos One, 8, e62897, 2013.

Niizuma, Y., Takahashi, A., Kuroki, M., and Watanuki, Y.: Sexing by external

measurements of adult rhinoceros auklets breeding on Teuri island, Jpn. J. Ornithol., 48, 145-150, 1999.

Ogi, H.: Ecology of murre in subarctic Pacific regions. Aquabiology, 2, 19-26, (in

Japanese with English abstract), 1979.

Orben, R. A., Paredes, R., Roby, D. D., Irons, D. D., and Shaffer, S. A.: Body size

affects individual winter foraging strategies of thick-billed murre in the Bering Sea,

J. Anim. Ecol., 84, 1589-1599, 2015.

Paredes, R., Jones, I., L., Boness, D., J., Trembley, Y., and Renner, M.: Sex-specific

differences in diving behaviour of two sympatric Alcini species: thick-billed murre and razorbills, Can. J. Zool., 86, 610-622, 2008.

Paredes, R., Orben, R., A., Orben, Roby, D., D., Irons, D., B., Young, R., Renner, H.,

Tremblay, Y., Will, A., Harding, A., M., A., and Kitaysky, A., S.: Foraging ecology during nesting influences body size in a pursuit-diving seabird, *Mar. Ecol. Prog. Ser.*, 533, 261-276, 2015.

Parnell, [A. C.](#), Inger, R., Bearhop, S., and Jackson, A. L.: Source partitioning using stable isotopes: coping with too much variation. [PloS One, 5, e9672](#), 2010.

Pennyquick, C. J.: *Modelling the flying bird*. Academic Press, Amsterdam. 2008.

Pianka, E.: Competition and niche theory. In: May, R. M. (Ed.) *Theoretical ecology: Principles and applications*. Blackwell Scientific Publications, Oxford, London. pp. 167-196., 1981.

R Develop Core Team, R: *A language and environment for statistical computing*, Vienna: R Foundation for Statistical Computing, 2014.

[Renner, H. M., Drummond, B. A., Benson, A-M., and Paredes, R.: Reproductive success of kittiwakes and murre in sequential stages of the nesting period: Relationship with diet and oceanography, *Deep Sea Res. II*, 109, 251-265, 2014.](#)

Ricklefs, R., E: Some considerations on the reproductive energetics of pelagic seabirds, *Studies in Avian Biol.*, 8, 84-94, 1983.

Schabetsberger, R., Brodeur, R. D., Cianelli, L., Napp, J. M., and Swartzman, G. L.:

Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea, ICES J. Mar. Sci., 57, 1283-1295, 2000.

Sowls, A. L., Hatch, S. A., Lensink, C. J.: Catalog of Alaskan Seabird Colonies, U. S. Fish and Wildlife Service, Washington, DC., 1978.

Spring, L.: A comparison of functional and morphological adaptations in the common murre (*Uria aalge*) and thick-billed murre (*U. lomvia*), Condor, 74, 1-27, 1971.

Squibb, R. C., and Hunt, G. L. Jr.: A comparison of nesting-ledges used by seabirds on St. George Island, Ecology, 64, 727-734, 1983.

Takahashi, A., Matsumoto, K., Hunt, G. L. Jr., Shultz, M. T., and Watanuki, Y.:

Thick-billed murres use different diving behaviors in mixed and stratified waters, Deep Sea Res. II, 55, 1837-1845, 2008.

Thaxter, C. B., Wanless, S., Daunt, F., Harris, M. P., Benvenuti, S., Watanuki, Y.,

Grémillet, D., and Hamer, K., C.: Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills, J.

Exp. Biol., 213, 1018-1025.

Trivelpiece, W. Z., Hinke, J. T., Miller, A. K., Reiss, C. S., Trivelpiece, S. Z., and Watters, G. M.: Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica, Proc. Natl. Acad. Sci. USA., 108, 7625-7628, 2011.

Watanuki, Y., Mehlum, F., and Takakashi, A.: Water temperature sampling by Brunnich's guillemots with bird-borne data loggers, J. Avian Biol., 32, 189-193, 2001.

Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K., and Naito, Y.: Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth, Proc. R. Soc. Lond. B., 270, 483-388, 2003.

Watanuki, Y., Wanless, S., Harris, M., Lovvorn, J. R., Miyazaki, M., Tanaka, H., and Sato, K.: Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin, J. Exp. Biol., 209, 1217-1230, 2006.

[Wyllie-Echeverria, T., and Wooster, W. S.: Year-to-year variations in Bering Sea ice cover and some consequences for fish distribution, Fish. Oceanogr., 7, 159-170,](#)

1998.

Yamamoto, T., Kokubun, N., Kikuchi, D., M., Sato, N., Takahashi, A., Will, A.,

Kitaysky, A., S., and Watanuki, Y.: ~~submitted, this issue.~~ Differential responses of

seabirds to inter-annual environmental changes in the continental shelf and oceanic

habitats of southeastern Bering Sea, Biogeosciences Discuss, 2015.

Tables

Table 1. Trip parameters of common murre (COMU) and thick-billed murre (TBMU)

breeding on St. George Island, Bering Sea.

Species	No. of	No. of	No. of	No. of dive		Duration (h)	
	birds	trips	dive bouts	bouts per trip	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, <i>F</i> and <i>P</i>				<i>F</i> _{1,33} = 0.70	<i>F</i> _{1,33} = 1.62	<i>F</i> _{1,33} = 0.36	<i>F</i> _{1,157} = 0.02
values				<i>P</i> = 0.409	<i>P</i> = 0.212	<i>P</i> = 0.552	<i>P</i> = 0.892

Figure captions

Fig. 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 murre (COMU) and lower panels represent data for thick-billed murre (TBMU).

Fig. 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 murre (COMU) and right panels represent data for thick-billed murre (TBMU). Means \pm 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.

Fig. 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, D, E, F represent data for the daytime, and panels G, H, I, J represent data for the nighttime. Means \pm standard deviation (SD) are shown excepting for A and B, are calculated from individual bird data. Sample number of birds (N) and dives (n) are shown in C, D, G, H.

Fig. 4. Diet composition of (A) common murres (COMU) and (B) thick-billed murres (TBMU) based on direct observations of prey delivered to nests.

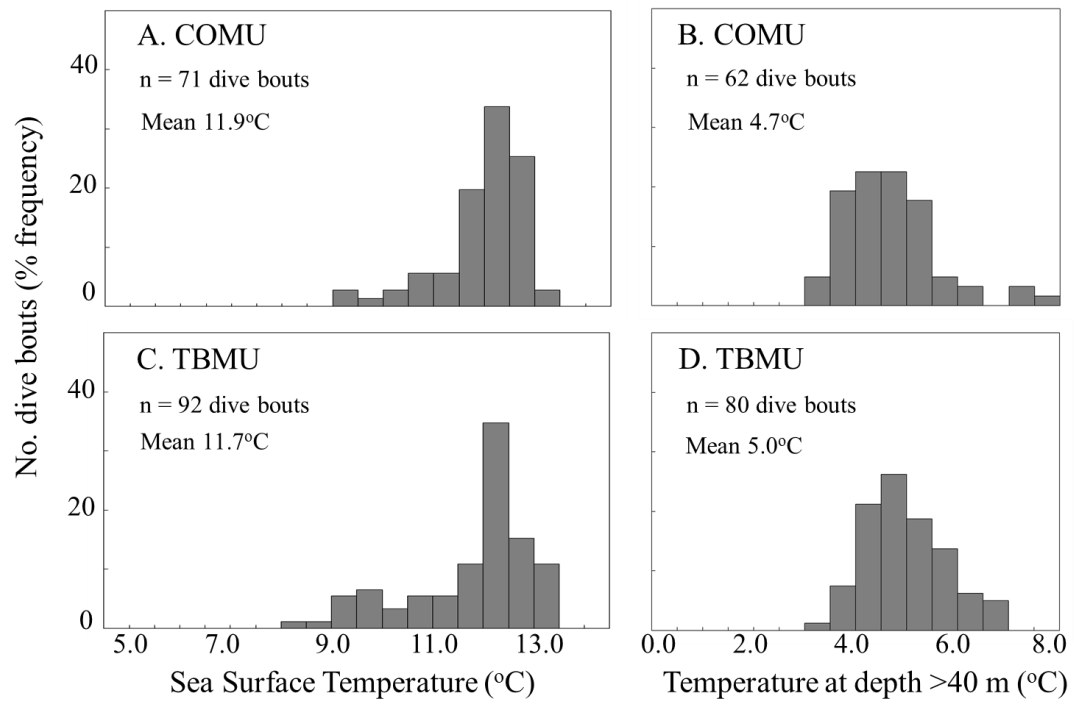
Fig. 5. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopic ratio values of common murres (COMU: open circles) and thick-billed murres (TBMU: closed circles) measured in red blood cells. Smaller circles show individual data, and larger circles with error bars show Means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

Fig. 6. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopic ratio values of potential food samples caught around the vicinity of the study colony. Different symbols represent

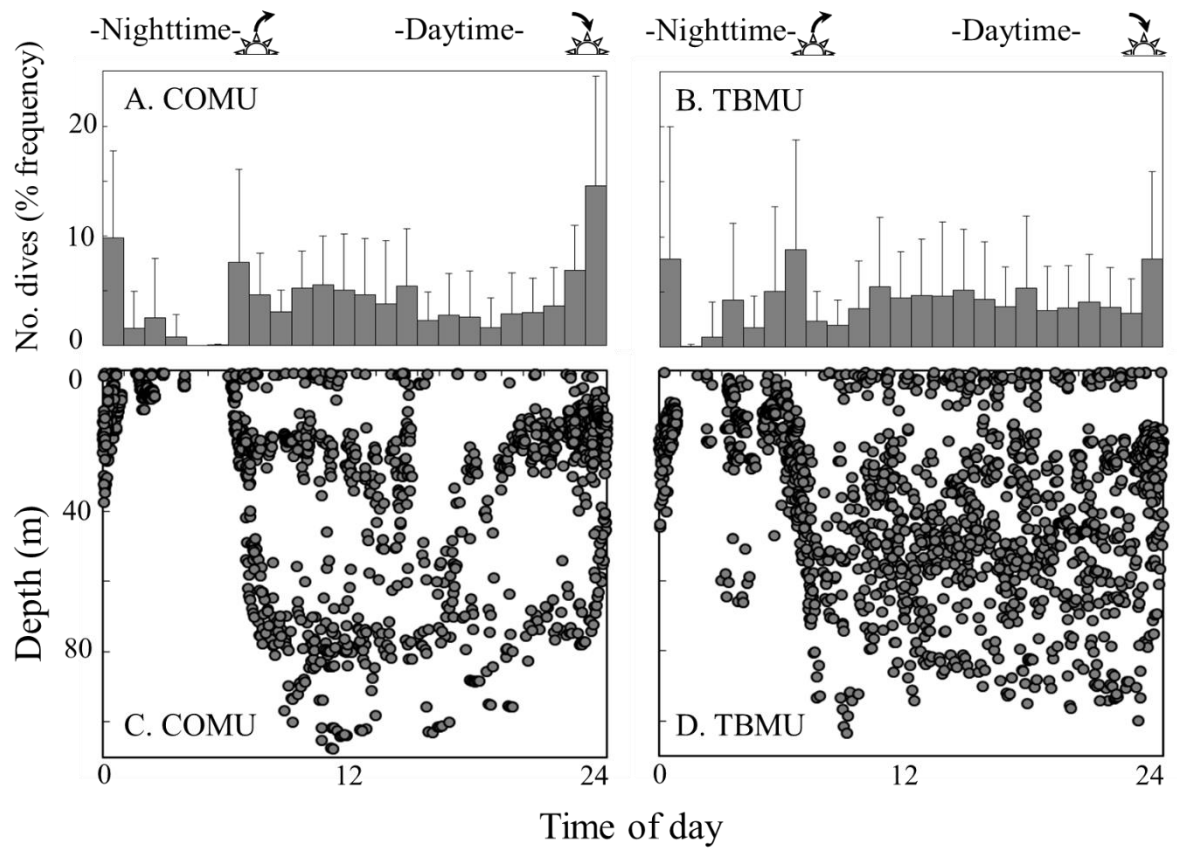
each potential food item. **The enrichment factors -0.19‰ for $\delta^{13}\text{C}$ and 2.25‰ for $\delta^{15}\text{N}$ were preliminarily applied to the bird data (open circles for common murre and closed circles for thick-billed murre). Note that the potential food samples were collected in 2009, as no data were available in 2014.

Fig. 7. Diet compositions of common (COMU: open boxes) and thick-billed murre (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 \pm 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.

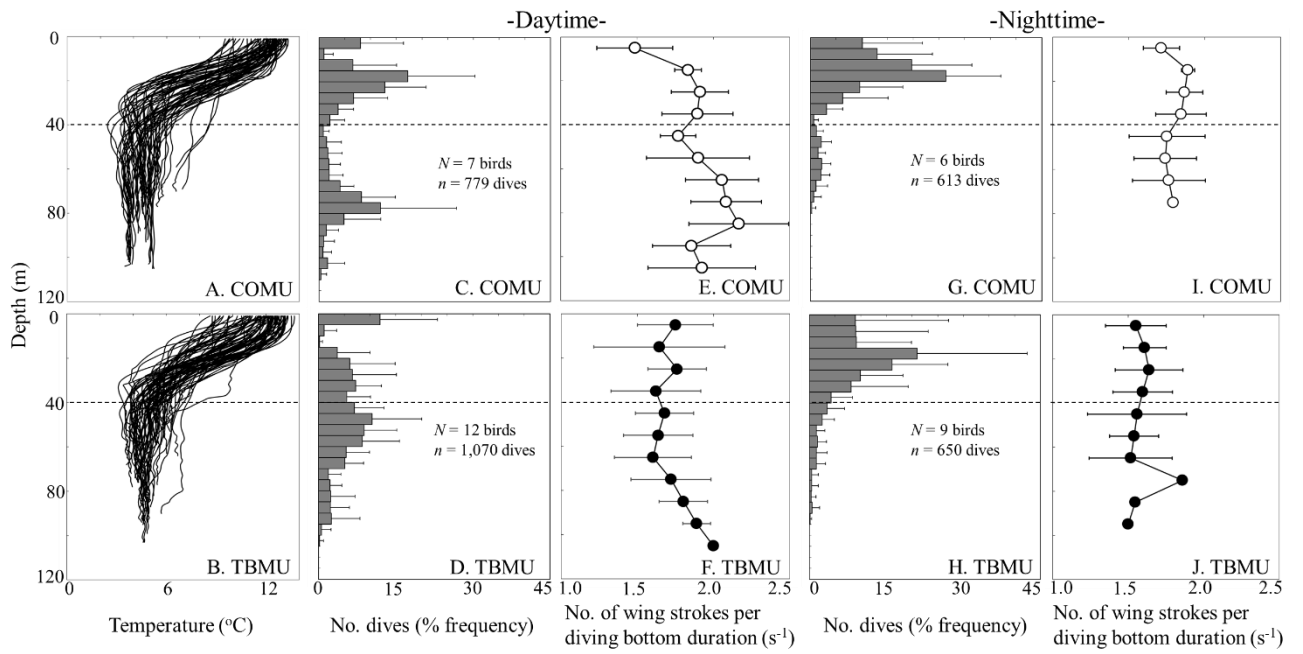
Figures



Kokubun et al. Fig. 1.

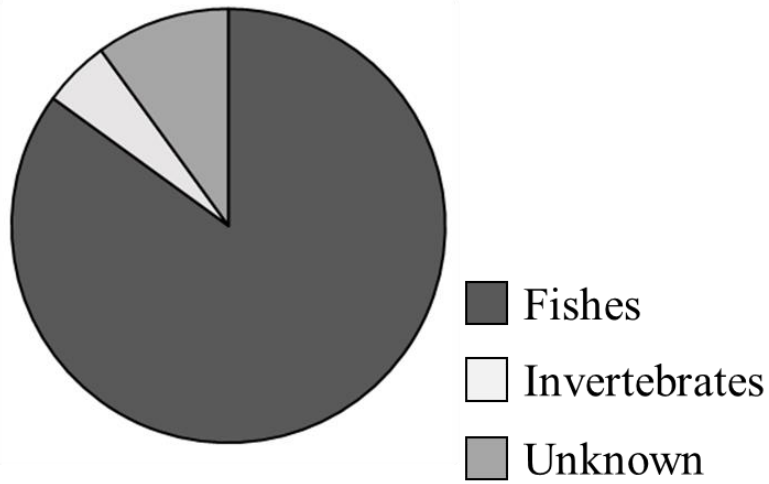


Kokubun et al. Fig. 2.

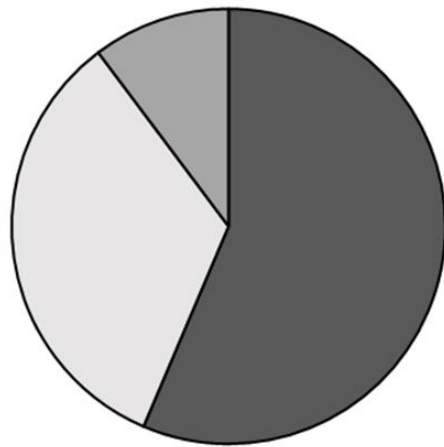


Kokubun et al. Fig. 3.

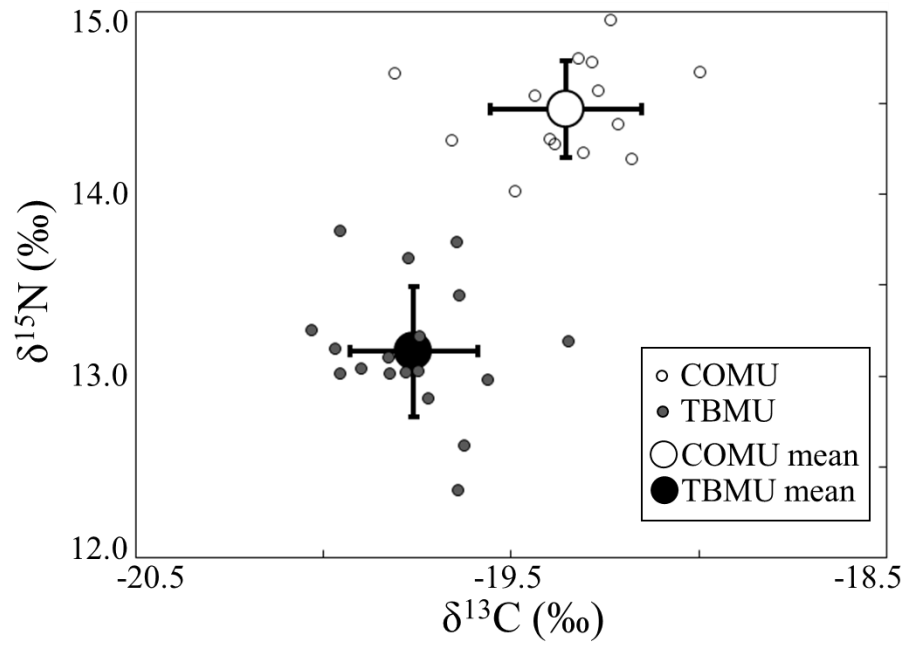
A. COMU $n = 20$ observations



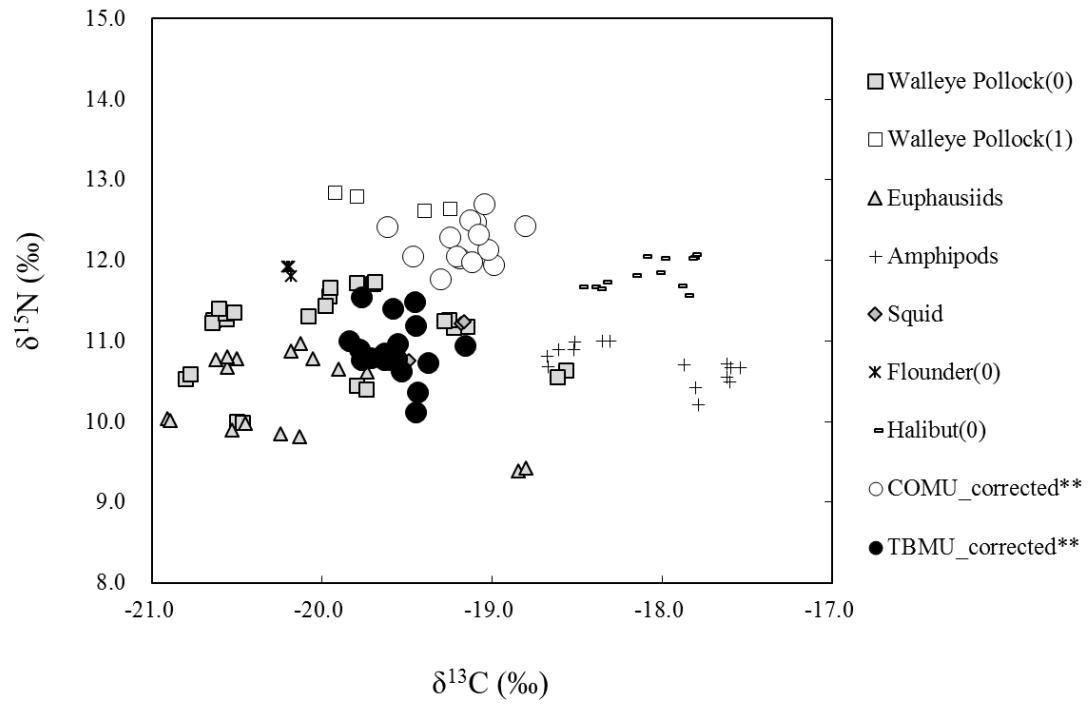
B. TBMU $n = 39$ observations



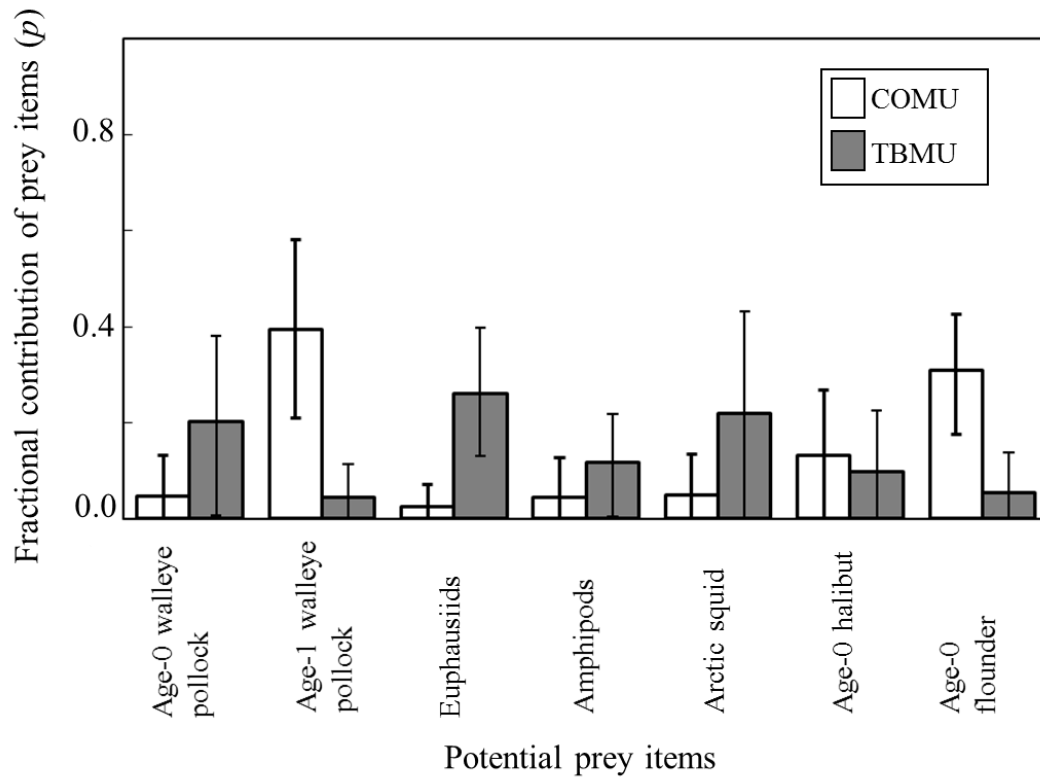
Kokubun et al. Fig. 4.



Kokubun et al. Fig. 5.



Kokubun et al. Fig. 6.



Kokubun et al. Fig. 7.