5 April, 2016

Dear Dr. Toru Hirawake,
Editor of *Biogeosciences,*

MS No.: bg-2015-497
“Differential responses of seabirds to inter-annual environmental change in the continental shelf and oceanic habitats of southeastern Bering Sea” by Yamamoto et al.

We appreciate the critical comment and helpful suggestions on the previous version of this manuscript by the editor and referees. We have addressed all the comments made by the editor and referees, as indicated on the attached pages, and revised the manuscript following their very helpful comments. Specifically, we have destressed the discussion based on ‘cold’ and ‘warm’ years, just mentioning marine environmental differences over two years. We hope that our explanation and revisions are acceptable and that you now find the manuscript satisfactory for publication.

Sincerely yours,

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The comments by the referees highlighted with “**Q**” with the number, and our answers to comments highlighted with “**A**”. “P” and “L” indicate pages and lines in the marked-up manuscript.

Reply to the Editor

Q1. Two reviewers have reviewed your manuscript and they recognized that your paper is suitable for publication in the BG. There were several comments but no critical one. I hope that authors can answer appropriately to the comment on your extended conclusion based on the data from just two years.

A. We appreciate the editor for the favorable decision on the manuscript. We have revised the ms throughout to avoid discussing our results based on simply classifying ‘cold (2013)’ and ‘warm (2014)’ years. However, between the two study years, sea surface temperatures were relatively cooler with later sea ice retreat in 2013 compared to those in 2014. So, we focus on mentioning this point rather than applying to the “cold vs warm” story in the revised ms.

Reply to Referee #1

Q1. It would seem that in the poor, cold year, that RLKIs maintained their own condition and did not increase foraging effort, passing on the cost of poorer environmental conditions to their offspring. In contrast, TBMUs reduced their own condition and increased foraging effort, so that the adults experienced the cost of the poor conditions and did not pass those costs onto the chicks. Perhaps RLKIs are already at the limit and have no more scope to increase foraging effort?

A. We appreciate the reviewer’s comment. In the Pribilof islands, black-legged kittiwakes had switched their reliance upon Pollock during the 1970s and 1980s to myctophids by the 1990s. Myctophid is an important prey to red-legged kittiwakes, and there may have been an increase in competition between red-legged and black-legged kittiwakes for what was primarily a red-legged kittiwake prey item. Accordingly, red-legged kittiwakes are the species most threatened by population declines since the 1980s. Thus, there is a possibility that the foraging effort of red-legged kittiwakes is at the limit, as the indication of elevated CORT includes the increase in foraging effort. It may have resulted in the lower fledgling success of red-legged kittiwakes in 2013 (the year of relatively cooler SSTs with later sea ice retreat) compared to 2014 when the competition was considered to be higher. We have added this explanation in the revised ms (P18L390–P19L402 in the marked manuscript). We have also included the mean growth rate (g/day) of red-legged kittiwakes in the revised ms to support the prediction (i.e. increase in competition: P19L402–403).

Q2. The main drawback of the study is (1) the short duration and (2) the small sample sizes meaning low statistical power. With only two years' data, it is hard to make robust conclusions, and many of the purported explanations come across as 'just so' stories.

A. According to the reviewer's comment, we have avoided discussing seabird's responses to environmental variability by applying to the simple classification of 'cold' and 'warm' years (i.e. the inter-annual variability), and have focused more on how their foraging behaviour and physiological conditions changed against different marine environmental conditions over two years in the revised ms. Although our study was conducted only over two years with limited sample sizes, the results certainly indicate that there are possible interspecific differences in species' response to different environmental conditions in the Bering Sea, which probably reflect differences in ecosystem dynamics between oceanic and shelf habitats they use for foraging in the Bering Sea. Therefore, we believe that our study is still worthwhile and provides an insight into the effect of local climate variability on seabird demography in the region, which is essential information to predict the effect of possible future warming on them as well as ecosystems in this region (P21L454–458).

Q3. p17697 There is abundant information that devices can impact seabird behaviour, even if they are less than 5% of body mass. I am surprised the authors do not at least acknowledge this issue.

A. We have mentioned this issue in the revised ms as the following (P7L140–153);

The equipped birds were recaptured after 2-6 days since the deployment, and the loggers were recovered. We retrieved the loggers from 15 RLKI and 9 TBMU in 2013 and 10 RLKI and 11

TBMU in 2014. Some equipped birds were resighted, but we failed to recapture them as they nest at the cliff. Previous studies suggested that attachment of small and lightweight tags (usually <5% of body mass) do not appear to affect foraging and/or reproductive behaviour of individuals (e.g. Phillips et al., 2003; Carey, 2011), while other studies reported an adverse effect on their behaviour as well as physiological condition (e.g. Barron et al., 2010; Elliott et al., 2012). In this study, the total weight of the logger including the heat-shrink tubing and tape was 15-16 g, which corresponds to less than 5% of the mean body mass of equipped birds (the mean ± SD: RLKI 375 ± 29 g, TBMU 1024 ± 43 g). The recovery rate excluding some resighted individuals was relatively high (71-82%), and the attachment of tags was not resulted in, at least, the breeding abandon.

Q4. p17698 Ground speed during flight will be strongly impacted by wind speed. Given that you have GPS data and the availability of wind speed (e.g. from MoveBank or elsewhere), why not calculate airspeed, which would reduce the error associated with separating flight from non flight? i.e. some movement >3 m/s will be surface movement and some movement <3 m/s will be flight.

A. As the reviewer pointed out, ground speed of birds is supposed to be influenced by wind direction and speed (e.g. Garthe et al. 2007, Deep-Sea Res II, 54: 311–320). However, this issue is not such simple. For example, ocean current is also considered to influence moving speed when a tagged individual is on water (strong current may tide a bird fast) (e.g. Yoda et al. 2014, Prog Oceanogr, 122: 54–64), possibly classified as flight. In addition, we recorded fixes per min, so between fixes (an interval of one minute), we have no information on which directions and how they moved (i.e. straight flight or winding flight between fixes which should relate to wind they experienced in flight). So, although what the reviewer mentioned is definitely important and interesting issue to consider, we can only classify flight or on-water locations by the ground speed in thie study. In the future study, we would like to try this issue using high-resolution GPS data (probably 1 second recording interval) and fine-scale wind data.

Q5. p17703L27. Why are there no confidence intervals on fledging success? Are the values significantly different from one another? This difference in reproductive success should be mentioned in the Introduction to set up robust predictions.

A. We are sorry, but there is no information available on a confidence interval for the fledging success of both species. Instead, we have added the standard deviation in the fledging success in P16L348–352, as 8 plots are combined for red-legged kittiwakes (SD = 0.07 in 2013 and 0.02 in 2014) and 10 plots in 2013 and 12 plots in 2014 are combined for thick-billed murres. In the revised ms, we explain more for relationships between climate variables and breeding parameters of seabirds in the Introduction to set up the background of this study (P4L77–P5L108).

Q6. It would be worthwhile noting that the opposite trends (cold vs warm) are observed in seabirds farther north (Divoky, G. J., Lukacs, P. M., & Druckenmiller, M. L. 2015. Effects of recent decreases in arctic sea ice on an ice-associated marine bird. Progress in Oceanography).

A. We appreciate for the information. I have read it, and mention this issue (i.e. possible regional differences in seabirds' response to climate variability) (P21L454–460).

Q7. Fig. 5. Suggest deleting this figure as I don't see what it adds. OK, the d13C is different, but so what? Nothing is made of these data.

A. We have deleted Fig. 5 and text regarding δ^{13}C (P14L304–307, P16L339–347), as the reviewer suggested. However, we would like not to delete the information of δ^{15}N in the text (not in a figure, P14L302–304, P16L337–339) to examine the difference in prey between the years in addition to the result from diet observations.

Reply to Referee #2 (Dr. Kozue Shiomi)

Q1. Comparisons of various parameters between two years looked robust and implied a potential link between seabirds' behaviours, physiological states and environmental conditions. However, I think it is difficult in principle to say that this study investigated "seabirds' responses to inter-annual differences of marine environments", because the data were obtained only from one cold year and one warm year. The interannual changes in seabirds' behaviours can happen independently from environmental changes. To examine the correlation, at least one more year of data would be required. For this reason, I would like to suggest changing the title and some relevant sentences (e.g. pp. 17703, L5-6; ...responses to the ocean variability differed...). I am not sure if it works, but one possible option to ease the issue described above may be to mention a prediction or hypothesis about seabirds' response to cold/warm years in Introduction (not in Discussion). For example, if some predictions from previous reports (like L7-10 in pp. 17706; Piscivorous birds breeding...) are put in Introduction, the present discussion may become convincing because of consistency with the predictions.

A. We appreciate the critical comment on the previous version of the ms by the reviewer. According to the reviewer's comment, we have avoided discussing seabird's responses to environmental variability by applying to the simple classification of 'cold' and 'warm' years (i.e. the inter-annual variability), and focused more on how their foraging behaviour and physiological conditions changed against different marine environmental conditions over two years in the revised ms (also see our replies to Q2 and Q5 of the reviewer #1). Also, we have added some predictions from previous studies in the Introduction (P4L77–P5L108), and changed the title as the following to avoid saying 'inter-annual' which may be confusing to readers: "Differential responses of seabirds to environmental variability over two years in the continental shelf and oceanic habitats of southeastern Bering Sea".

Q2. According to Results, GPS loggers failed to record some parts of a track in most trips. Is it possible to provide rough estimates of the proportion of the periods during which positional data were lost in each trip (e.g. [duration of data]/[duration between deployment and recovery])? This information should be essential to interpret distributions of foraging locations. If the proportion of the lost positions was substantial, the actual peak of the histograms in Fig. 2 could be different from the recorded one. Then, discussion on the peak values and bimodality may not be appropriate (e.g. pp. 17701, L10-11).

A. We recaptured the equipped birds not just after finishing a foraging trip, but sometimes after 2-6 days since the deployment (butteries ran out for some GPS loggers by that time). Therefore, the calculation that the reviewer suggested [(duration of data)/(duration between deployment and recovery)] may be not appropriate for this case, probably resulted in the overestimation of lost fix proportions. Instead, we have added the information on availability of location data during foraging trips in the Results as below (please also see Fig. 1 in Appendix A in the revised ms).

For RLKI, 12 trips in 2013 and eight trips in 2014 were recorded with GPS loggers. Two trips were recorded partially, and the other trips included complete tracks (*N* = 5) and tracks recorded until close to the beginning of or during the homing commute phase (*N* = 13, see Fig 1a. in Appendix A), having 59 ± 26% of available location fixes during the trips. (P12L262–P13L266)

For TBMU, 11 trips in 2013 and 22 trips in 2014 were recorded with GPS loggers, including two partial tracks, 29 complete tracks, and 2 incomplete tracks (recorded until close to the beginning of or during the homing commute phase) (Fig. 1b in Appendix A), having 68 ± 24% of available location fixes during the trips. (P13L274–278)

Most foraging trips by RLKI and TBMU were recorded until the homing commute phase (indicated as the continuous decrease in the distance from the colony: Weimerskirch 2007, see Fig. 1 in Appendix A), being able to record the foraging phase. In addition, more than half of fixes are available for these tracks, and, therefore, we believe that our results (the peak values and bimodality in the on-water location) can be representative.

Minor comments:

Q3. pp.17699, L24-25: Did these periods of data from geolocators and accelerometers correspond to those of GPS loggers? It would be good to show that the same periods were compared.

A. Yes. The geolocator and accelerometer data analyzed correspond to GPS data (P8L163–164, P11L221–223).

RLKI: (GPS data) 20 July–5 August, (geolocator data) 26 July-2 August
TBMU: (GPS data) 2–12 August, (accelerometer data) 31 July-12 August

Q4. How many birds were deployed with geolocators and accelerometers?

A. For the geolocator data (RLKI), we analyzed 22 trips from 4 birds in 2013 and 14 trips from 5 birds in 2014. For the accelerometer data (TBMU), we analyzed 9 trips from 9 birds in 2013 and 21 trips from 12 birds in 2014 (P11L221–223).

Q5. pp.17700, L25: Information on types of error distribution may be required.

A. Added (P12L253–254).

Q6. pp.17701, L8: How many on-water locations were obtained?

A. 2087 and 1765 on-water locations in 2013 and 2014 for RLKI and 4987 and 7650 on-water locations in 2013 and 2014 for TBMU were recorded, respectively. We are afraid, but we do not feel that this information is necessary; probably the proportion of on-water location in each marine habitat (P13L268–L270, P13L280–L282, Fig. 2) is important information here rather than the number of recorded on-water locations. However, if the editor feels that this information (the number of on-water location) should be included in the ms, we are happy to include it.

Q7. pp. 17705, L 8: A short note on CORT values reported in previous studies would be helpful for readers to understand the present results (what concentrations are considered to be high).

A. We apologize for the confusion. We meant that RLKI exhibited consistently high levels of CORT in both years "compared to TBMU". We have made our explanation clear in the revised ms (P18L390–L393). We could include CORT values of RLKI reported in previous studies, but these studies did not examine foraging behaviour in relation to environmental conditions in concert with the physiological condition. Therefore, we feel that the comparison of CORT with the previous studies is probably not straightforward and appropriate.

Q8. Fig. 1: It would be useful to indicate the position of the island in the maps.

A. Added (please see Fig. 1 in the revised ms).

Differential responses of seabirds to ~~inter-annual~~ environmental variability~~change~~ over two years in the continental shelf and oceanic habitats of southeastern Bering Sea

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Abstract

Seasonal sea-ice cover has been decreasing in the southeastern Bering Sea shelf, which might affect ecosystem dynamics and availability of food resources to marine top predators breeding in the region. In this study, we investigated the foraging responses of two seabird species, surface-foraging red-legged kittiwakes *Rissa brevirostris* (hereafter, RLKI) and pursuit-diving foraging thick-billed murres *Uria lomvia* (TBMU) to ~~the inter-annual change in~~ different marine environmental conditions over two years. At-sea distributions of RLKI and TBMU breeding on St. George Island, the largest seabird colony in the region, were recorded using GPS loggers, and blood samples were taken to examine their physiological condition and isotopic foraging niche in a given year. Between the study years, winter ice retreated earlier and summer water temperatures were warmer in 2014 compared to those in 2013. ~~At-sea distributions of RLKI and TBMU breeding on St. George Island, the largest seabird colony in the region, were recorded using GPS loggers, and blood samples were taken to examine their physiological condition and isotopic foraging niche in a given year.~~ RLKI foraging occurred mostly over the oceanic basin in both years. TBMU, however, foraged mostly over the shelf, but showed a relatively higher use of the shelf break and oceanic basin in~~ the colder year,~~ 2013. The foraging distances from the colony peaked at 250-300 km in 2013 and~~,~~ bimodally~~,~~ at 150-250 km and 300-350 km in 2014 for RLKI, and tended to be farther in 2013 compared to those in 2014 for TBMU. Plasma levels of corticosterone did not differ between years in RLKI, but differed in TBMU, showing higher levels of physiological stress

incurred by murres ~~during the colder year,~~in 2013, the year of relatively cooler sea surface temperatures with later sea ice retreat. δ^{13}N (a proxy of trophic level of prey) did not differ between the years in either RLKI or TBMU~~, while δ^{13}C (a proxy of prey origin) were lower in 2014 than in 2013 in both species, suggesting possible differences in influx of oceanic prey items into foraging areas~~. These results suggest that the response of ecosystem dynamics to climate variability in the southeast Bering Sea may differ between the ocean basin and continental shelf regions, which, in turn, may generate differential responses in seabirds relying on those habitats for foraging.

1 Introduction

The Bering Sea is a productive marine ecosystem (Springer et al., 1996; Grebmeier, 2012) that supports immense populations of diverse marine fauna (Highsmith and Coyle, 1990; Piatt and Springer, 2003; Aydin and Mueter, 2007; Grebmeier, 2012). Sea-ice cover has been decreasing in duration and concentration over the southeastern Bering Sea shelf (Post et al., 2013), which influences the temperature of the water column in the region, including the extent of the “cold pool” (Stabeno and Overland, 2001; Overland and Stabeno, 2004; Sarmiento et al., 2004; Stabeno et al., 2007; Steele et al., 2008). Such shifts in the physical environment have been shown to affect the ecosystem, including the seasonality and biomass of primary production, metabolic rates, distribution, and abundance of consumers, and changes in pelagic–benthic coupling (Grebmeier et al., 2006; Mueter and Litzow, 2008; Hunt et al., 2011; Wassmann, 2011; Wassmann et al., 2011; Dorresteijn et al., 2012). The Bering Sea is a transition region between Arctic and sub-Arctic seas, and, hence, physical and biological changes in this region may also influence the extent of sea-ice cover and species abundance and composition in the adjacent Arctic Sea (i.e. the Chukchi Sea)~~,~~ (Shimada et al., 2006; Matsuno et al., 2012; Yamamoto et al., 2015).

Predicting the effects of climate change on marine top predators is a major challenge in ecology. Long-term monitoring of seabird demography has been conducted on the Pribilof Islands (Byrd et al., 2008a; Renner et al. 2012; Mudge et al., 2015), which host one of the largest concentrations of piscivorous seabirds in the North Pacific. Previous studies have demonstrated that historical fluctuations in ~~productivity (i.e. reproductive success) and~~ the diet of seabirds (Byrd et al., 2008a; Sinclair et al., 2008; Renner et al., 2012) might reflect broad-scale changes in climate (e.g. regime shift: Benson and Trites, 2002).~~,~~ ~~but the mechanistic response of seabirds to local climate variability has been elusive.~~ Although some studies found broad species- and regional-specific relationships between climate variables and breeding parameters~~seabird productivity~~ (Byrd et al., 2008b~~e.g. Sydeman et al., 2012~~), the mechanistic response of seabirds to local climate variability has been elusive and others suggested only weak relationships (~~Byrd et al., 2008b;~~ Satterthwaite et al., 2012; Renner et al., 2014). This~~ weak relationship~~ is probably due, in part, to reproductive failure that may occur at several stages of the breeding process (e.g. nest building, egg-laying, incubation, and chick-rearing). It may also be influenced by reproductive effort associated not only with foraging conditions in the current season, but also those during the previous breeding season (Harrison et al., 2011; Catry et al., 2013). Furthermore, seabirds can adapt their behaviour by increasing foraging range and effort in response to changes in the environment, potentially masking effects on some breeding parameters (Kitaysky et al., 2000; Pinaud et al., 2005; Harding et al., 2007). Meanwhile, changes in behaviour and prey availability relating to environmental conditions appear to affect their physiological condition (i.e. nutritional stress as reflected in secretion of corticosterone). For example, piscivorous birds breeding on the Pribilof Islands have been shown to experience greater food limitation on the continental shelf during cold years, attributed to higher levels of nutritional stress (Benowitz-Fredericks et al., 2008; Satterthwaite et al., 2012; Harding et al., 2013). To obtain more direct mechanistic insight into their responses to ecosystem dynamics in relation to climate variability, at-sea foraging behaviour of breeding seabirds should be examined in concert with the~~ir~~ physiological condition. ~~(i.e. nutritional stress as reflected in secretion of corticosterone), as elevated corticosterone levels indicate high reproductive effort and increased post-reproductive mortality (Kitaysky et al., 2010; Satterthwaite et al., 2010).~~ However, there is little information available for the comparative at-sea behaviour of seabirds in relation to ~~inter-annual climate variability~~different environmental conditions in this region (Kokubun et al., 2010; Paredes et al., 2014).

Ship-based observations can provide information on at-sea habitat utilization of species (Hunt et al., 2008; Hunt et al., 2014; Kuletz et al., 2014; Wong et al., 2014) together with oceanographic characteristics (Piatt and Springer, 2003; Gall et al., 2013). Although these studies are valuable to detect seasonal, annual, and decadal changes in species distributions (Gall et al., 2013; Hunt et al., 2014; Kuletz et al., 2014~~; Gall et al., 2013~~), spatial and temporal coverage as well as the context of reproductive processes studied at colonies are limited. The recent availability of animal-borne devices enhances our ability to examine habitat utilization of free-ranging individuals (review by Burger and Shaffer, 2008), and may provide more insight into population processes in relation to ocean variability (Weimerskirch et al., 2001; Paredes et al., 2014).

In this study, we examined the foraging behaviour of two seabird species that exhibit different habitat use: surface-foraging red-legged kittiwakes *Rissa brevirostris* (hereafter, RLKI) feeding in the oceanic habitat and pursuit-diving thick-billed murres *Uria lomvia* (TBMU) feeding mainly in the continental shelf habitats, and how they responded to changes in environmental conditions over two years. The effects of ocean variability on an ecosystem may differ between water masses, and, hence, seabird responses may show different patterns (Benowitz-Fredericks et al., 2008; Byrd et al., 2008b), which, in turn, could provide information on how ecosystem dynamics respond to fluctuations in marine environmental conditions (Frederiksen et al., 2007; Piatt et al., 2007).

2 Materials and methods

2.1 Study site

Fieldwork was conducted on St. George Island (56°34′ N, 169°37′ W) in the Pribilof Islands, Alaska, USA, over two years in July–August 2013 and 2014. Birds were captured from their nesting sites using a noose pole, and GPS loggers (GiPSy-2 with chip antenna or GiPSy-4 with patch antenna: TechnoSmart, Rome, Italy) were attached to the backs of 19 RLKI and 11 TBMU in 2013 and 14 RLKI and 14 TBMU in 2014 using Tesa® tape and cyanoacrylate glue (Loctite® 401). The loggers were housed in heat-shrink tubing for water-proofing, and were set to record five successive fixes every min for GiPSy-2 and one fix every min for GiPSy-4.~~,~~ The equipped birds were recaptured after 2-6 days since the deployment, and the loggers were recovered. We retrieved the loggers from 15 RLKI and 9 TBMU in 2013 and 10 RLKI and 11 TBMU in 2014. Some equipped birds were resighted, but we failed to recapture them as they nest at the cliff. Previous studies suggested that attachment of small and lightweight tags (usually <5% of body mass) do not appear to affect foraging and/or reproductive behaviour of individuals (e.g. Phillips et al., 2003; Carey, 2011), while other studies reported an adverse effect on their behaviour as well as physiological condition (e.g. Barron et al., 2010; Elliott et al., 2012). In this study, the total weight of the logger including the heat-shrink tubing and tape was 15-16 g, which corresponds to less than 5% of the mean body mass of equipped birds (the mean ± SD: RLKI 375 ± 29 g, TBMU 1024 ± 43 g). The recovery rate excluding some resighted individuals was relatively high (71-82%), and the attachment of tags was not resulted in, at least, the breeding abandon.~~The total weight of the logger including the heat-shrink tubing and tape was 15.1-16.3 g, which corresponds to less~~

~~than 5% of the mean body mass of equipped birds (the mean ± SD: RLKI 375.3 ± 29.0 g, TBMU 1024.0 ± 43.0 g). The loggers were set to record five fixes every min for GiPSy-2 and one fix every min for GiPSy-4.~~

~~The equipped birds were recaptured after 2-6 days since the deployment, and the loggers were recovered. We retrieved the loggers from 15 RLKI and 9 TBMU in 2013 and 10 RLKI and 11 TBMU in 2014, representing 71-82 % recovery rate.~~

Of the loggers retrieved, some failed to record locations. Hence, location data were available for 5 and 7 RLKI (20 July–5 August) and 5 and 10 TBMU (2–12 August) in 2013 and 2014, respectively. Data for RLKI in 2013 were reanalyzed from Kokubun et al. (2015). At the time of recapture, blood samples were taken from the brachial vein of each individual, and kept on ice until centrifugation to separate the plasma from the red blood cells, and both were kept frozen until assayed. Plasma was used for measurement of physiological stress exposure (corticosterone: CORT) and red blood cells for determining trophic level (stable isotopes: SI). CORT was measured only for samples that were taken within 3 min of capture, as it takes 3 min for levels of CORT to begin to rise in the blood in response to the acute stress of capture and restraint (Romero and Reed, 2005).

During the study period, we opportunistically obtained adult diets of RLKI by regurgitation at the time of logger deployment and/or retrieval. Prey species of RLKI samples were identified visually or using otoliths (*N* = 22 in 2013 and *N* =15 in 2014) (also see Kokubun et al., 2015). TBMU chick diet was recorded from direct observation of adult birds (both with and without data loggers) carrying prey items back to their nests in their bill. Prey items were visually identified during observation or later from photographs (*N* = 13 in 2013 and *N* = 39 in 2014).

2.2 Data analysis

GPS locations were re-sampled every 1 min by averaging fixes recorded within each min for GiPSy-2. We used a forward-backward speed filter (McConnell et al., 1992), and positions that exceeded 20 m s^{-1} were considered erroneous and removed (Paredes et al., 2012; Evans et al., 2013). We defined foraging trips as any time period when the birds beyond a 500 m buffer around the colony for more than 30 min. We determined locations of resting on water (as a proxy for foraging) during foraging trips based on flight speed (Zavalaga et al., 2011; Kokubun et al., 2015). Flight speed less than 3 m s^{-1} for RLKI (Paredes et al., 2012) and 5 m s^{-1} for TBMU (Evans et al., 2013) were considered "resting on water." The straight-line distances between the colony and on-water locations were measured, as were the bottom depths where the birds were resting on the water. The marine habitats were categorized into three regions based on bathymetry as follows; on-shelf (0-200 m bottom depth), shelf break (200-1000 m bottom depth), and oceanic basin (>1000 m bottom depth, Paredes et al., 2012).

To examine the differences in marine environment between the two study years (2013 *vs*. 2014), satellite remote-sensed monthly mean sea surface temperatures in August (SST: NOAA POES AVHRR, GAC, 0.1° degree) within 350 km around the colony (within the foraging ranges of RLKI and TBMU; see Results) and the timing of sea ice retreat in the southeastern Bering Sea (a Bering Sea Ice Retreat Index: IRI) were obtained from the National Oceanic and Atmospheric Administration (NOAA): available at http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp for SST and http://access.afsc.noaa.gov/reem/ecoweb/dataWindow.php?Data=IRI for IRI. IRI represents the number of days after March 15 in which areal sea ice concentration was greater than 10% in a 2º × 1º box (bounded by 56.5°-57.5°N and 163°-165°W). Locations and environmental data were analyzed and mapped using the ESRI® ArcGIS.

In addition to the GPS tracking, we also analyzed behavioral data of birds obtained by geolocators (2.5 g, Mk19; Biotrack Ltd., UK) and accelerometers (12 mm diameter × 45 mm length, 10 g, ORI-380 D3GT; Little Leonardo, Japan). As the location records did not cover a complete foraging trip in several GPS tracks (see Results, Fig. 1 in Appendix A), we used these data to confirm the foraging trip durations in each year supplementarily. For the geolocator-carrying birds, the foraging trip duration was defined as the time between the first and last landing on water (i.e. immersion) before and after a long dry event, which is likely an underestimation, though comparable between the years (see Fig.1 in Appendix B~~A~~). For the accelerometer-carrying birds, the start and end of a foraging trip was identified from changes in bird posture as well as outward/inward flight activity recorded as cyclic fluctuations of acceleration (see details for Takahashi et al., 2008).

Data were analyzed for 22 trips from 4 birds in 2013 and 14 trips from 5 birds in 2014 for RLKI (26 July-2 August) and 9 trips from 9 birds in 2013 and 21 trips from 12 birds in 2014 for TBMU (31 July-12 August).

CORT concentrations were measured for 8 RLKI and 20 TBMU in 2013 and 7 RLKI and 21 TBMU in 2014. CORT concentrations (ng ml^{-1}) were measured using a radioimmunoassay (for details see Kitaysky et al., 1999). Briefly, each sample was equilibrated with 2000 cpm of tritiated CORT prior to extraction with 4 ml re-distilled dichloromethane. After extraction, percent tritiated hormone recovered from each individual sample (average hormone recovery was, mean ± SD, 94.68% ± 2.86) was used to correct final CORT concentrations. Samples were reconstituted in phosphate-buffered saline gelatin buffer and combined with antibody and radiolabel in a radioimmunoassay. Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. All samples were analyzed in 2 different assays; CV = 7% for inter-assay and <2% for intra-assay).

Stable isotopes (δ^{15}N~~ and δ^{13}C~~) were measured for 8 RLKI and 20 TBMU in 2013 and 7 RLKI and 15 TBMU in 2014 following Hobson (1993) and Barger and Kitaysky (2012). 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: $\delta^{15}N$~~ or $\delta^{13}C$~~ = $[(R_{sample}/R_{standard}) - 1] \times 1000‰$, where $R_{sample/standard}$ is the corresponding ratio~~ $^{13}C/^{12}C$ or~~ $^{14}N/^{15}N$. 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.

2.3 Statistical analysis

Statistical analyses were carried out in R software (version 2.15.3, R Development Core Team 2008). Differences in foraging parameters (bathymetry and distance from the colony in on-water locations and trip duration) between the years were examined with generalized linear mixed models (GLMM) using Poisson (for the bathymetry and trip duration) or Gaussian (for the distance) distributions, including bird identity as a random factor. We tested the inter-annual differences in CORT (log-transformed) and SI by conducting one-way ANOVA. Statistical significance was assumed at $P < 0.05$. Values reported are means ± standard errors (SE) or standard deviations (SD).

3 Results

3.1. Foraging behaviour

For RLKI, 12 trips in 2013 and eight trips in 2014 were recorded with GPS loggers.~~, including four and one round-trip, respectively.~~ Two trips were recorded partially, and the other trips included complete tracks (*N* = 5) and tracks recorded until close to the beginning of or during the homing commute phase (*N* = 13, see Fig 1a. in Appendix A), having 59 ± 26% of available location fixes during the trips. In both years, RLKI travelled predominantly towards the south from the colony and to a lesser extent towards the north and west (Fig. 1a, b). On-water locations (a proxy for foraging) occurred mostly over the oceanic basin in both years (>87% of the locations: Fig. 2) (GLMM, $Z = -0.28$, $P = 0.78$). Foraging distances from the colony peaked at 250-300 km in 2013 and bimodally at 150-250 km and 300-350 km in 2014 (Fig. 3), though mean distance did not differ significantly between the years (GLMM, $t = 0.92$, $P = 0.36$).

For TBMU, 11 trips in 2013 and 22 trips in 2014 were recorded with GPS loggers, including ~~five and 17 round trips, respectively~~ two partial tracks, 29 complete tracks, and 2 incomplete tracks (recorded until close to the beginning of or during the homing commute phase) (Fig. 1b in Appendix A), having 68 ± 24% of available location fixes during the trips. TBMU traveled to the southeast and west of the colony in 2013 (Fig. 1c), while birds traveled mostly towards the north and east in 2014 (Fig. 1d). In both years, TBMU foraged mostly over the shelf (GLMM, $Z = 0.23$, $P = 0.82$), but showed a relatively higher use of the shelf break and oceanic basin in 2013 (Fig. 2). The foraging distances from the colony tended to be farther in 2013 compared to these in 2014, though not significantly so (GLMM, $t = -1.30$, $P = 0.19$) (Fig. 3).

As some of the GPS data were incomplete (i.e. ended before reaching to the colony, Fig. 1 in Appendix A)~~partial~~, the analysis of behavioral data obtained using geolocators and accelerometers was also conducted. These results showed similar foraging trip durations (minimum estimate as an index: see Fig 1. in Appendix B~~A~~) between both years for RLKIs (12.7 ± 3.0 h in 2013 and 12.3 ± 5.1 h in 2014; GLMM, t = -0.32, P = 0.75) and relatively longer foraging trip durations in 2013 (mean ± SD: 15.9 ± 6.9 h) compared to 2014 (10.4 ± 7.1 h) for TBMUs (GLMM, t = -1.94, P = 0.06).

3.2. Stress hormone

Log-transformed baseline CORT concentrations in RLKI were 0.72 ± 0.09 ng ml^{-1} and 0.72 ± 0.05 ng ml^{-1} in 2013 and 2014, respectively (Fig. 4). CORT levels did not differ between years in RLKIs (ANOVA, $F_{1,13}$ = 0.01, P = 0.94). On the other hand, CORT concentrations in TBMUs were significantly ($F_{1,39}$ = 24.97, P < 0.001) higher in 2013 (0.78 ± 0.05 ng ml^{-1}) than in 2014 (0.38 ± 0.06 ng ml^{-1}, Fig. 4).

3.3. Diet

δ^{13}N did not differ between the years in either RLKI (13.52 ± 0.27‰ in 2013 and 13.65 ± 0.17‰ in 2014: $F_{1,13}$ = 1.30, P = 0.28) or TBMU (13.15 ± 0.42‰ in 2013 and 13.11 ± 0.42‰ in 2014: $F_{1,33}$ = 0.09, P = 0.77~~; Fig. 5~~). ~~Whereas, δ^{13}C significantly differed in both RLKI (-19.81 ± 0.15‰ in 2013 and -20.09 ± 0.16‰ in 2014: $F_{1,13}$ = 12.37, P < 0.01) and TBMU (-19.13 ± 0.18‰ in 2013 and -19.77 ± 0.17‰ in 2014: $F_{1,33}$ = 109.91, P < 0.001; Fig. 5).~~ Based on the diet sampling and observations, regurgitated prey for RLKI mostly consisted of myctophids (the percent of occurrence; 100% in 2013 and 93.3% in 2014) but also included amphipods (27.3% in 2013 and 6.7% in 2014), shrimp (9.1% in 2013 and 13.3% in 2014), euphausiids (4.6% in 2013 and 6.7% in 2014), and squid (13.6% in 2013). For TBMU, observed prey was mostly fish including age-0 and age-1walleye pollock (53.9% in 2013 and 56.4% in 2014) and to a lesser extent included squid and meso-zooplankton (46.2% in 2013 and 33.3% in 2014) as well as unidentified prey (10.3% in 2014).

3.4. Annual differences in marine environment

SSTs within the foraging range (<350 km from the colony; Fig. 3) were relatively warmer in 2014 (mean ± SD: on-shelf 12.3 ± 0.8 ºC, shelf break 11.6 ± 0.9 ºC, oceanic basin 11.7 ± 0.8 ºC) compared to 2013 (on-shelf 9.8 ± 1.0 ºC, shelf break 10.3 ± 1.2 ºC, oceanic basin 10.2 ± 1.0 ºC). IRI was 36.7 in 2013 and 0.02 in 2014, representing later sea ice retreat in 2013.

4 Discussion

Surface-feeding RLKI and pursuit-diving TBMU showed differences in habitat use. RLKI foraged extensively over the deep oceanic basin, while TBMU foraged mostly on the shelf. The behavioral and physiological responses to the ocean variability over two years differed between the species. Between the two study years, SST~~s~~ around the colony was~~ere~~ relatively cooler in 2013 than in 2014, probably reflecting the later sea ice retreat in 2013 as winter sea ice conditions strongly influence water temperatures during the following summer (Khen, 1999; Overland et al., 1999; Kokubun et al., 2010; Stabeno et al., 2012).

RLKI showed a consistent use of the oceanic habitat with similar levels of CORT in both years, though they reached to relatively farther areas in 2013 than 2014. In comparison, TBMU used the oceanic basin to the south of the colony more frequently in ~~the relatively colder year of~~ 2013, exhibiting relatively farther travel distances and higher levels of CORT. Based on the δ^{15}N values (an indicator for trophic level: Hobson et al., 2002) and diet sampling/observation, both RLKI and TBMU probably had similar prey composition between the years. ~~δ^{13}C signatures normally decline along the continental shelf-ocean basin gradient (Hobson et al., 1994; Young et al., 2015), however δ^{13}C values (also an indicator for origin of prey) were lower when birds were foraging extensively on the shelf, particularly in TBMU. This is possibly due to differences in the influx of oceanic water into the shelf region (Dorresteijn et al., 2012) that might be affected by the strength of oceanic circulation along the Bering Sea basin, for example the Aleutian North Slope Current (ANSC) that flows east along the northern edge of the Aleutian Islands (Ladd, 2014; also see Fig. 1 in Appendix B).~~

During the study period, the fledgling success (the mean ± SD) of RLKI and TBMU on St. George Island differed between the ~~cold (2013) and warm (2014)~~ years;~~:~~ dramatically for RLKI, 0.57 ± 0.07 in 2013 and 0.92 ± 0.02 in 2014~~ for RLKI,~~ and~~,~~ less so for TBMU, 0.95 ± 0.02 in 2013 and 0.89 ± 0.02 in 2014 (Mudge et al., 2015). Fledgling success may be related to behaviour prior to breeding (i.e. the timing of breeding: Renner et al., 2014), but the hatching date (the mean ± SD) appeared not to differ between the years for either RLKI (6 July ± 7.0 days in 2013 and 4 July ± 4.8 days in 2014) or TBMU (27 July ± 6.6 days in 2013 and 28 July ± 7.4 days in 2014) (Mudge et al., 2015). Therefore, the fledgling success during the study period may be related to food resource conditions during the breeding season in the given years, suggesting better conditions in ~~the warm year, ~~2014 (relatively warmer SSTs with earlier sea ice retreat) than 2013 (relatively cooler SSTs with later sea ice retreat)~~, than during the cold year, 2013~~.

RLKI mainly feed on myctophids over deep oceanic regions (Sinclair et al., 2008; Kokubun et al., 2015). As RLKIs are a surface-feeding seabird, they are considered to feed on vertically migrating myctophids (Hunt et al., 1981). The water column in the deep ocean may show less inter-annual variation in water temperature compared to that of the shallower shelf region (see Results in this study) where the deep cold pool (temperature remains below <2 ºC) forms in relation to the timing of sea ice retreat (Stabeno et al., 2012). Previous studies suggested that the availability of prey for seabirds in shelf habitats may be less stable (Einoder et al., 2011) and less predictable over long-time scales compared to basin habitats (Weimerskirch, 2007). Furthermore, myctophids are supposed to be still available when prey availability over the shelf is low (Sinclair et al., 2008; Paredes et al., 2014). Nonetheless, RLKI showed a slight difference in foraging locations over the oceanic basin between the years, which may be affected by other factors besides SST and IRI (Sinclair et al., 2008). Recently, Paredes et al. (2014) hypothesized that the existence of meso-scale eddies, that typically develop in the Aleutian Basin (Mizobata et al., 2002), may affect the vertical distribution of myctophids for kittiwakes (Godø et al., 2012). The sympatric and closely ~~-~~related black-legged kittiwakes (*Rissa tridactyla*) foraged at locations near the perimeter of anticyclonic eddies (upwelling) and inside or near cyclonic eddies (downwelling), and experienced higher levels of nutritional stress when eddies were weak possibly due to low availability of prey (Paredes et al., 2014). Similarly, RLKI in this study may have altered their foraging locations in relation to the existence of these eddies (Fig. 1 in Appendix C~~B~~). However, it has been~~is~~ not certain how distribution and abundance of myctophids are actually related to the strength of eddies, and no correlations were found between eddy kinetic energy and fledging success of black-legged kittiwakes (Paredes et al., 2014).~~ Elevated CORT indicates that birds are consuming less food, lower-quality food, or working harder (Kitaysky et al., 2010), and lower productivity has been reported during cold years in adults of black-legged kittiwakes (Satterthwaite et al., 2012) which appears to coincide with our results (lower fledgling success during a relatively cooler year).~~ ~~However~~Compared to TBMU, RLKI exhibited consistently high levels of CORT in both years with different fledgling success~~ compared to TBMU~~. This may reflect potential competition with black-legged kittiwakes that also feed on myctophids in the ocean basin (Sinclair et al., 2008; Renner et al., 2012).~~,~~ In the Pribilof islands, black-legged kittiwakes had switched their reliance upon Pollock during the 1970s and 1980s to myctophids by the 1990s (Sinclair et al., 2008). Accordingly, red-legged kittiwakes are the species most threatened by population declines since the 1980s. Hence, there is a possibility that the foraging effort of RLKI is at the limit, as the indication of elevated CORT includes the increase in foraging effort (Kitaysky et al., 2010). Such the inter-specific competition appears to be relatively higher during cold years (Satterthwaite et al., 2012; Paredes et al., 2014), possibly resulted in the lower fledgling success in 2013, the year of relatively cooler SSTs with later sea ice retreat. In fact, the mean (± SD) growth rate (g/day) of RLKI was better in 2014 (14.9 ± 3.7 g) than 2013 (11.7 ± 3.6 g) (Mudge et al., 2015).~~especially during cold years (Paredes et al., 2014). This inter-species competition may contribute to the relatively lower fledgling success of RLKI in the cold year, 2013.~~

Compared to RLKI, TBMU exhibited fluctuating physiological condition and flexible behavioral changes in parallel to the ocean variability between the years, yet without a difference in fledgling success. Late sea ~~-~~ice retreat is associated with an early, cold-water phytoplankton bloom, relatively low biomass of small shelf copepods, and poor survival of larval and juvenile forage fish, including their main prey (juvenile walleye pollock: Hunt et al., 1996; Sinclair et al., 2008; Renner et al. 2012). On the other hand, early sea-ice retreat is associated with a later, warm-water plankton bloom, a large biomass of small shelf copepods later in the season, and high abundance of larval and juvenile forage fish (Hunt et al., 2002). Moreover, forage fish species including juvenile walleye pollock are less abundant on the continental shelf during cold years because they either disperse or travel deeper to avoid cold waters (Hollowed et al., 2012), as juvenile pollock are associated with warm bottom temperatures (Brodeur et al., 1998). A northern location of the ice edge during spring may be linked to higher SST and water temperature at depth (Kokubun et al., 2010; Stabeno et al., 2012). The cold pool acts as a cross-shelf migration barrier for subarctic fish species (e.g. walleye pollock and Pacific cod), forcing these fish to remain on the outer shelf and separating them from food sources in the middle shelf and coastal domain. Thus, a warmer shelf would provide them with a larger area of suitable habitat (Ciannelli and Bailey, 2005; Kotwicki et al., 2005~~; Ciannelli and Bailey, 2005~~). In addition, distribution and availability of euphausiids and copepods, the prey species for juvenile walleye pollock (Schabetsberger et al., 2000; Ciannelli et al., 2002), likely change in relation to inter-annual differences in water temperatures in the shelf region (Smith, 1991; Ohashi et al., 2013; Yamamoto et al., 2015). Hence, we assume that the abundance/availability of pollock on the shelf was probably relatively higher in 2014 (the year of warmer SSTs and earlier sea ice retreat) compared to 2013 (the year of cooler SSTs and later sea ice retreat)~~, the warmer year~~. ~~Piscivorous birds breeding on the Pribilof Islands have been shown to experience greater food limitation on the continental shelf during cold years, attributed to higher levels of nutritional stress (Benowitz-Fredericks et al., 2008; Satterthwaite et al., 2012; Harding et al., 2013).~~ The closer proximity of St. George to the continental shelf-break may be considered to be an important buffer in years when food supply on the shelf is poor (Byrd et al., 2008b; Renner et al., 2014). Previous studies showed that TBMU breeding on St. George Island traveled longer distances to forage at the shelf break and the ocean basin in a cold year (Harding et al., 2013). Seabirds are known to increase foraging ranges in response to reductions in prey availability (Suryan et al. 2000~~, Bertrand et al. 2012~~; Pinaud et al., 2005; Harding et al., 2007; Bertrand et al. 2012), but longer and farther foraging trips likely cause higher levels of nutritional stress (2013 in this study), especially for TBMU whose flight cost is presumed to be high (Houston et al., 1996).

In this study, chick-rearing RLKI did not change their foraging locations largely in relation to marine environmental changes probably due to their reliance on myctophids, which live in the deep waters of the pelagic zone (Sinclair and Stabeno, 2002), for feeding young (Kokubun et al., 2015). However, their foraging effort might also be affected by the position and strength of local eddies, which are reflected by atmospheric control (the North Pacific Index and Multivariate ENSO Index: Ladd et al., 2012; Ladd, 2014). TBMU showed fluctuations in physiological condition and flexible foraging behavior, which probably corresponded to ocean variability (exhibited longer and farther trips in the relatively cooler year of 2013~~ a cold year~~). Hence, although we compared foraging behaviour of seabirds in different environmental conditions only over two years with limited sample sizes, our study has suggested that there is possible interspecific differences in species' response to warming, which may reflect differences in ecosystem dynamics between habitats they use for foraging, as the decrease in sea-ice extent showed negative effects on foraging behaviour for other species in a different Arctic region (e.g. black guillemots *Cepphus grylle mandtii*: Divokey et al., 2015).~~there might be interspecific differences in these species' response to warming in the Bering Sea, which may reflect differences in ecosystem dynamics between oceanic and shelf habitats they~~

~~use for foraging. Furthermore,~~ E~~e~~levated stress levels may have a cascading effect on subsequent life stages, such as migration, post-breeding survival, breeding propensity, and timing of breeding (Verhulst and Nilsson, 2008; Schoech et al., 2009; Goutte et al., 2010; Kitaysky et al., 2010;~~ Verhulst and Nilsson, 2008; Goutte et al., 2010;~~ Harrison et al., 2011) and, as a result, overall productivity (Kitaysky et al., 2007, 2010; Renner et al., 2014). We suggest that year-round monitoring of foraging distribution and stress incurred by birds, including those during the post-breeding migration, should be conducted to understand further how these species are affected by changing climate (~~e.g.~~Kitaysky et al., 2010; Satterthwaite et al., 2010; Schultner et al., 2014).

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Figure legends

Figure 1. Foraging trip trajectories of red-legged kittiwakes: RLKI (a, b) and thick-billed murres: TBMU (c, d) in 2013 and 2014, respectively. Black dots represent location fixes and blue or red circles represent on-water (i.e. foraging) locations. The star indicates the breeding colony, St. George Island. The background shows the bathymetry: white: on-shelf (0-200 m bottom depth), light grey: shelf break (200-1000 m) and grey: oceanic basin (>1000 m).

Figure 2. The marine habitats of on-water locations during the foraging trips in red-legged kittiwakes (RLKI), and thick-billed murres (TBMU); on-shelf (0-200 m bottom depth), shelf break (200-1000 m bottom depth), and oceanic basin (>1000 m bottom depth). Red bars represent 2013 and blue bars in 2014 (the mean and standard error).

Figure 3. The straight-line distances between the colony and on-water locations of red-legged kittiwakes (RLKI), and thick-billed murres (TBMU) in 2013 (blue bars)

and 2014 (red bars). The mean and standard error are presented.

Figure 4. The mean and standard errors in plasma corticosterone concentrations of red-legged kittiwakes (RLKI), and thick-billed murres (TBMU) in 2013 (blue symbol) and 2014 (red symbol).

~~**Figure 5.** Stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) of red-legged kittiwakes (RLKI), and thick-billed murres (TBMU) red-blood cells in 2013 (blue open circles) and 2014 (red open circles). The filled circles represent the mean and standard error.~~

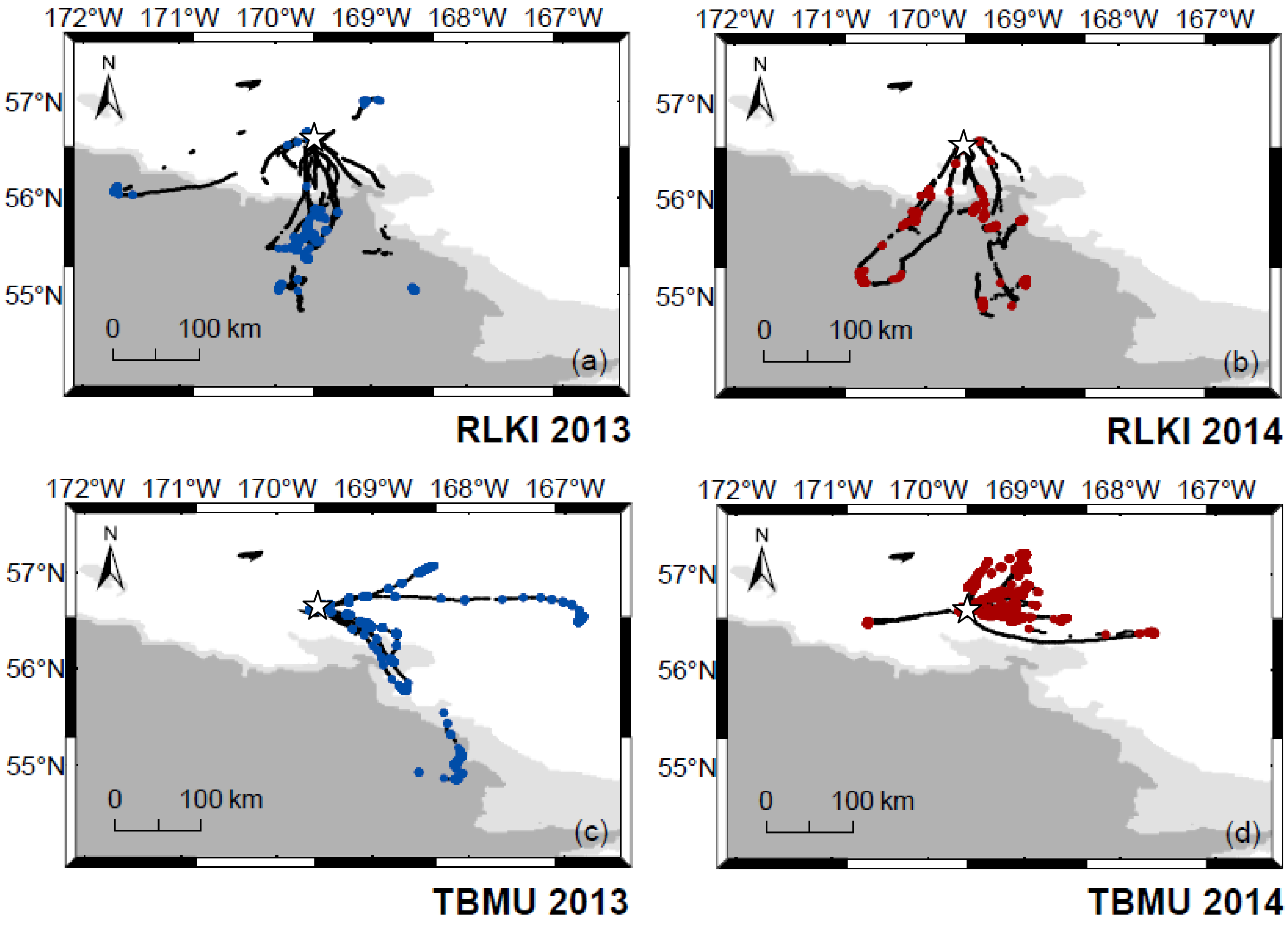
172°W 171°W 170°W 169°W 168°W 167°W
57°N
56°N
55°N
N
0 100 km
(a)
RLKI 2013
(b)
RLKI 2014
(c)
TBMU 2013
(d)
TBMU 2014

Figure 1

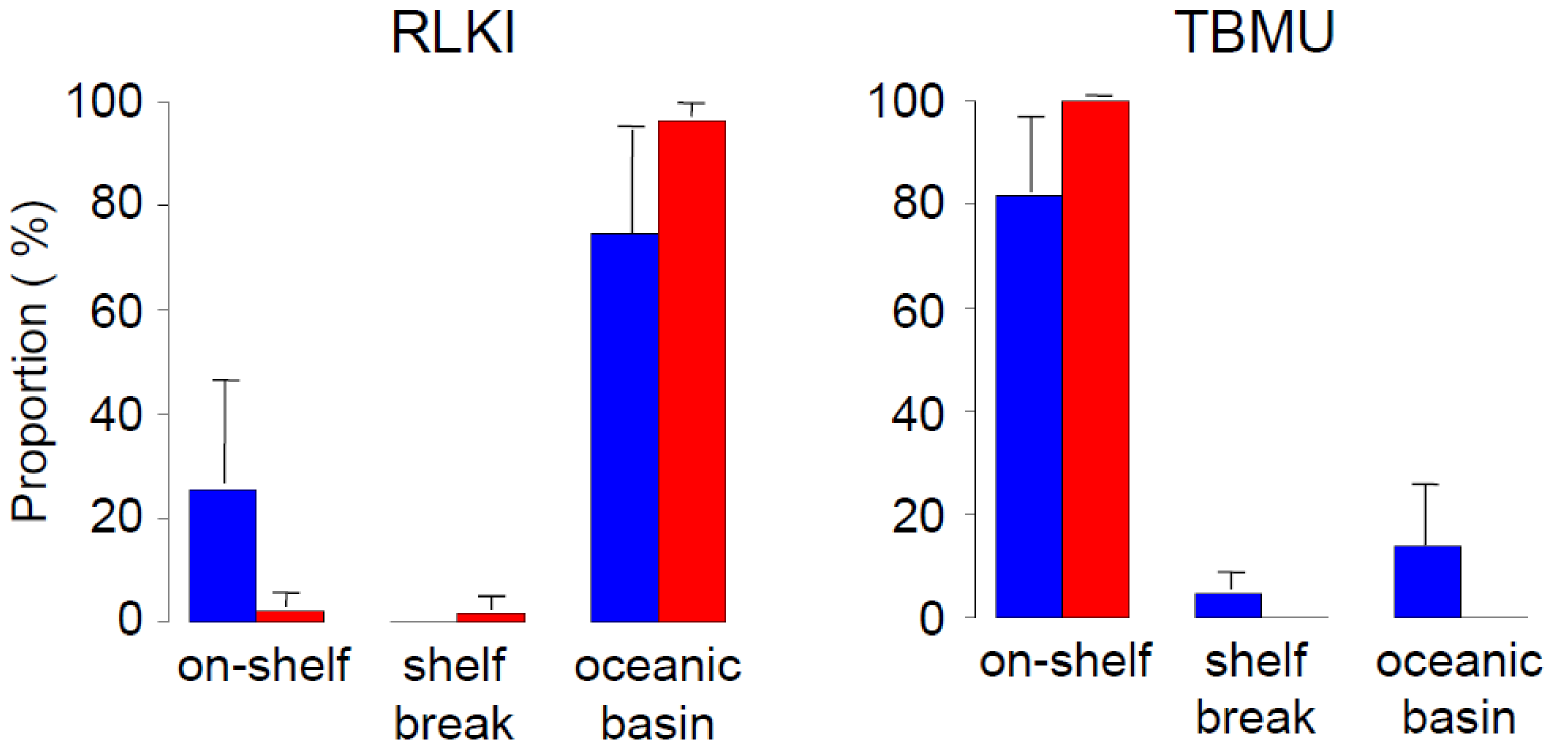
RLKI
TBMU
Proportion (%)
100
80
60
40
20
0
on-shelf
shelf break
oceanic basin

Figure 2

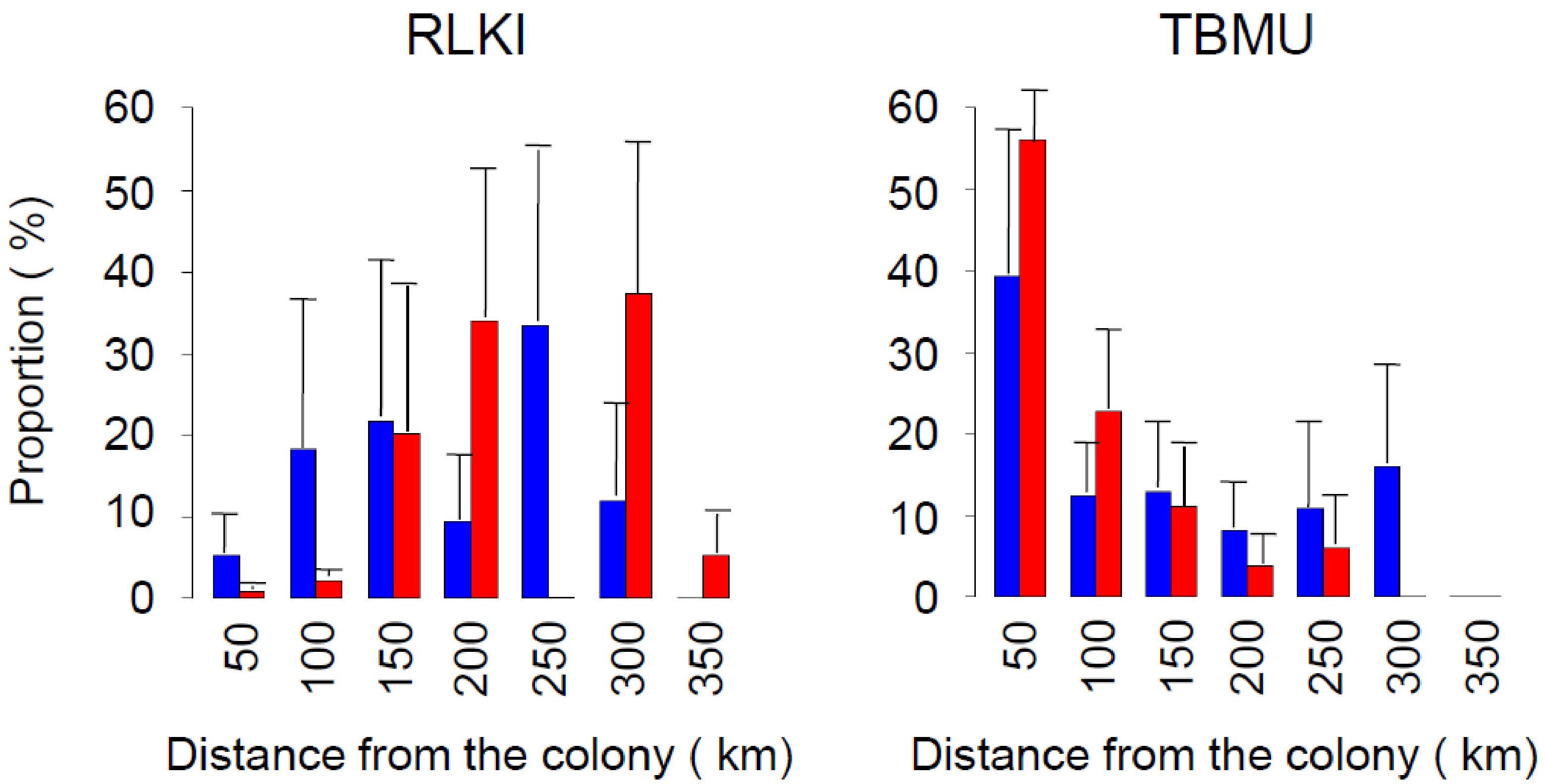
RLKI
TBMU
Proportion (%)
0
10
20
30
40
50
60
50
100
150
200
250
300
350
Distance from the colony (km)
Distance from the colony (km)

Figure 3

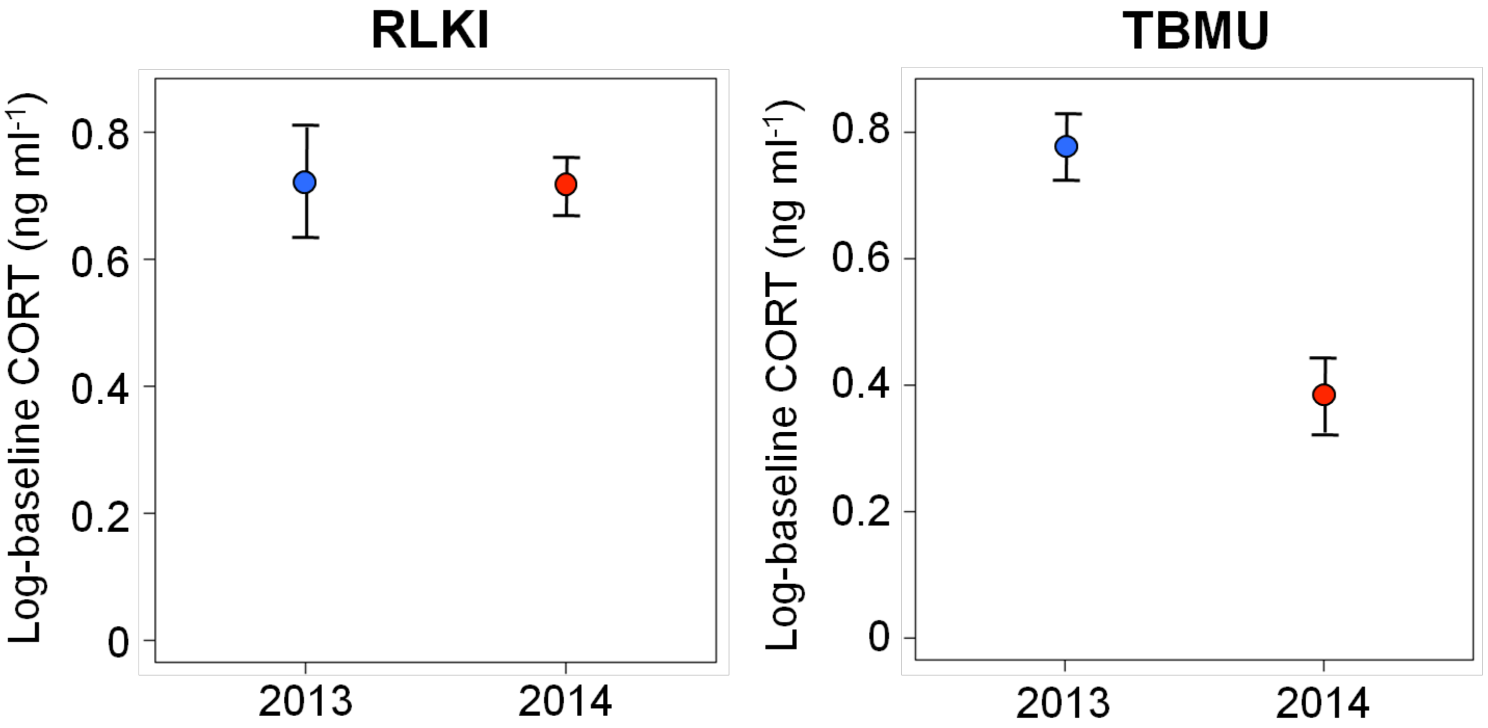

Figure 4

~~**Figure 5**~~