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Breeding together, wintering an ocean apart: Foraging ecology of the northern Bering Sea thick-billed and common murres in years of contrasting sea-ice conditions

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ABSTRACT

Assessing impacts of environmental change on Arctic-breeding seabirds requires a better understanding of their year-round movement and foraging ecology. Here we examined the post-breeding movements and diving behavior of thick-billed (*Uria lomvia*) and common murres (*U. aalge*) breeding on St. Lawrence Island, northern Bering Sea, by using geolocators deployed in 2016 (n = 3, per species). During 2016–2019, we examined foraging niches and exposure to nutritional stress by using stable isotope signatures and corticosterone titers of blood and feather tissues (n = 60–96, per species). We found that thick-billed murres migrated to the Chukchi Sea in the fall and wintered in the western North Pacific, whereas common murres stayed in the eastern Bering Sea in the fall and wintered in the eastern North Pacific. Nutritional stress levels of breeding common murres were higher in 2017–2019, the period of historic low winter sea-ice extent, than in 2016. Higher nutritional stress levels of post-breeding thick-billed murres were associated with lower fall sea-ice extent in the Chukchi Sea. These results indicate that the loss of sea-ice might negatively affect murres breeding in the Pacific Arctic. Divergent migratory connectivity between the two murre species might also lead to different conservation threats both inside and outside the Arctic.

1. Introduction

Ongoing climate change and associated sea-ice decline are likely to transform marine ecosystems in the Pacific Arctic (Huntington et al., 2020). Seabirds are an important component of the Arctic marine ecosystem, and their ecology and population status are considered indicators of changing marine ecosystems (Provencher et al., 2012; Divoky et al., 2015; Vihtakari et al., 2018). As seabirds often face relatively high mortality during the non-breeding period compared to the breeding period, it is essential to characterize their winter foraging ecology to improve understanding of the potential effects of environmental changes and conservation threats to populations. In the Pacific Arctic, some seabird species remain in the ice-covered region throughout the year (Divoky et al., 2016). Still, the majority of Arctic-breeding seabirds migrate long distances and spend considerable time away from the

Arctic region during the non-breeding period. Such behavior may buffer the ecological responses of these species to environmental change occurring in the Arctic.

Recent tracking studies have suggested that closely-related and sympatrically-breeding seabird species show contrasting foraging ecology in winter (Thiebot et al., 2012; Fort et al., 2013; Cherel et al., 2016). These findings imply that sympatrically-breeding seabirds can be exposed to different environments and conservation threats, for example, if they spend the winter in different areas. Such 'migratory connectivity' (Webster et al., 2002) is increasingly recognized as important for effective conservation efforts of highly migratory and mobile marine animals such as seabirds (Dunn et al., 2019a), but is still poorly investigated.

Thick-billed (*Uria lomvia*) and common (*U. aalge*) murres are closely-related seabirds that often breed sympatrically in the Arctic and

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subarctic regions. Thick-billed murres tend to distribute in colder, higher latitude regions than common murres (Irons et al., 2008). In the North Atlantic, previous studies found that the two species tend to winter in different regions (Fort et al., 2013; McFarlane-Tranquilla et al., 2015), and multi-colony tracking of thick-billed murres allowed for the assessment of population-specific conservation threats during the non-breeding period (Frederiksen et al., 2016, 2019). However, in the Pacific sector, only two previous studies have reported the post-breeding foraging areas of thick-billed and common murres from the southern Chukchi Sea (Hatch et al., 2000a) and the wintering movements of thick-billed murres from the southeastern Bering Sea (Orben et al., 2015). These previous studies did not concurrently examine other aspects of foraging ecology, such as diving behavior (but see Fort et al., 2013; Young et al., 2017), trophic-levels, or nutritional state. Such information is useful for understanding the causes and consequences of species-specific migratory movements (Young et al., 2017; Orben et al., 2018; Will et al., 2018).

In the northern Bering Sea, sea-ice extent declined dramatically in recent years, as highlighted by a historic low extent observed in 2018, the lowest since satellite observation of sea-ice extent started in 1979 (Stabeno and Bell, 2019). Changes in sea-ice extent have been suggested to affect lower trophic level zooplankton and fish (Duffy-Anderson et al., 2019), and higher trophic level predators including seabirds (Divoky et al., 2015; Will et al., 2020a) breeding in the northern Bering Sea and the Chukchi Sea. However, it is not well known how recent dramatic changes in sea-ice conditions may affect the foraging and nutritional state of seabirds during the non-breeding period.

The goal of this study was to characterize the winter foraging ecology of thick-billed and common murres breeding in the northern Bering Sea, a region undergoing considerable changes in winter sea-ice conditions. Since a previous study suggested that environmental changes negatively affected the population trends of both species of murres (Irons et al., 2008), we hypothesized that ongoing declines in sea-ice extent affect murres breeding in the northern Bering Sea. We tested this hypothesis by documenting the inter-specific differences in migratory movements, diving behavior, and temporal dynamics of isotopic niches and nutritional stress. Based on these results, we also discuss the possible conservation threats to these two species during the non-breeding period.

2. Methods

2.1. Study site and geolocator deployments

Fieldwork was conducted from mid-July to late August in 2016–2019, and in late June 2019, on St. Lawrence Island, in the northern Bering Sea. The study sites were located at colonies near the village of Savoonga on the northern coast of the island: Myughi, Tuqaghuk, and Tanti (Fig. S1). Breeding thick-billed and common murres were captured with a noose pole at the cliff, where they form mixed colonies along the ledges. Upon capture, each bird was weighed, measured, and blood and feather samples were taken. These samples were obtained from both birds with and without geolocator deployments (see below). Mass mortality of adults and colony-wide reproductive failure was observed in the summer of 2018 (Will et al., 2020b); thus, our sample sizes were limited in 2018 (Table S1).

We deployed geolocators on 48 thick-billed (20 in 2016 and 28 in 2017) and 32 common murres (15 in 2016 and 17 in 2017) by attaching loggers to a plastic leg band. We used LAT2500 (8×36 mm, 3.6 g; Lotek Wireless Inc.) geolocators in 2016, and both LAT2500 and Mk3006 ($16 \times 16 \times 7$ mm, 2.5 g) geolocators in 2017 (15 LAT and 13 Mk for thick-billed, and 15 LAT and 2 Mk for common murres, respectively). The total mass of the deployed device, including the band, was 4.0–6.0 g, which represented 0.4–0.6% of the average body mass of tagged thick-billed and common murres (981 g and 979 g, respectively). We set out to recover geolocators in the summers of 2017, 2018, and 2019 and recovered 9 LAT2500 (all from Tuqaghuk) and no Mk3006 geolocators

(see subsection 3.1).

2.2. Geolocator data analysis

LAT2500 geolocators record sunrise and sunset times daily via on-board processing of light data and temperature every hour, which were used to reconstruct the bird's location twice daily using an iterative forward step selection framework through the R package ProbGLS (https://github.com/benjamin-merkel/probGLS; Merkel et al., 2016). In this package, location estimates were generated by calculating a cloud of possible locations (n = 1000) and weighting these according to daily median sea surface temperature recorded by the logger and NOAA optimally interpolated, high resolution SST data (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html; Reynolds et al., 2007). Based on these weightings, 100 likely movement paths were computed and the geographic median of each location cloud was selected. The resulting bird locations were used to calculate 50% kernel utilization distributions during fall and winter, using R package adehabitatHR (https://cran.r-project.org/package=adehabitatHR; Calenge, 2006), with the grid size of 1000 and the smoothing parameter 'href'. For each bird location, the seafloor depths were extracted from ETOPO1 bathymetry data using the R package xtractomatic (https://cran.r-project.org/package=xtractomatic).

LAT2500 geolocators were also set to record the depth and wet-dry state every 120 s throughout the recording period. The sampling interval of 120 s was not sufficient to identify individual dives but would enable us to infer daily diving effort and seasonal patterns of depth use (see Takahashi et al., 2018 for details). To examine diving activities, we calculated the following three parameters: 1) daily maximum dive depth, 2) frequency of inflection points in time-depth data, as a proxy for average dive depths, and 3) time spent diving (total time of >1 m depth per day), as an index of daily dive effort. We also calculated 4) time out of the water per day based on wet-dry state of the logger, as an index of daily flight or nest attendance activities. We analyzed the depth and wet-dry data using Ethographer (https://sites.google.com/site/ethographer/; Sakamoto et al., 2009) in Igor Pro (WaveMetrics, Inc. Lake Oswego, OR, USA).

2.3. Stable isotope analysis

To investigate interspecific differences in foraging niches characterized by carbon and nitrogen stable isotope values (i.e., isotopic niche, Hobson and Bond, 2012), we collected blood, primary (P1), and throat feather samples. These samples were collected from birds with geolocators upon deployments and retrieval, and also from birds without geolocators. We followed Will and Kitaysky (2018) for sampling and analysis procedures. Blood samples were collected using heparinized syringes, transferred to 1.5 mL vials, and stored cool until centrifugation. Whole blood samples were centrifuged for 5 min to separate plasma and red blood cells. The plasma and red blood cells were stored frozen until corticosterone and stable isotope laboratory analyses. Feather samples were prepared, washed and hormones extracted as described below (see subsection 2.4), primary feathers were pulverized prior to subsampling. A small portion of freeze-dried red blood cell samples, pulverized feather samples, or a single whole throat feather, (0.100–0.600 mg) was placed in a tin capsule, sealed and deposited in an EA autosampler. The stable isotope data were obtained using a continuous-flow isotope ratio mass spectrometer (CFIRMS). The instrumentation used was a Delta + XP interfaced with a Costech ESC 4010 elemental analyzer. Stable isotope ratios are reported in δ (Delta) notation as parts per thousand (‰) deviation from the international standards $\delta^{13}C$ PDB and $\delta^{15}N$ air according to $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N, R_{sample} and $R_{standard}$ are the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of samples and international standards. Replicate measurement of an internal laboratory standard (Peptone) indicated measurement errors to be ±0.16‰ for N and

±0.13‰ for C. Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility. Breeding season results of both species were also reported in Will et al., 2020a.

2.4. Corticosterone assay and molecular sexing

To examine levels of nutritional stress murres incurred during different periods of their annual cycle, we measured the concentration of corticosterone in blood plasma, primary feathers (P1), and throat feathers (Kitaysky et al., 2007; Kokubun et al., 2018; Will et al., 2019). Circulating levels of baseline corticosterone (CORT) in blood plasma (collected within 3 min of capture) indicate the level of nutritional stress during the summer breeding period. Corticosterone concentrations in feathers reflect the nutritional state of the birds during the feather molt (Will et al., 2019). Murres molt their primaries during a post-breeding molt in fall and throat feathers in a pre-breeding molt in late winter (Gaston and Hipfner, 2000). We followed the sampling and analysis procedures described in Will et al. (2018) and used the same blood and feather samples obtained for stable isotope analysis (see subsection 2.3). Primary feathers were subsampled, 20–30 mm of the inner vane was removed from the rachis 20 mm from the feather's tip, and five whole throat feathers, with the calamus removed, were measured to the nearest mm. All feathers were weighed to the nearest 0.1 mg. Feathers were briefly washed in 500 μl isopropanol (HPLC grade, Sigma-Aldrich), then extracted in 3 ml of HPLC grade methanol (Fisher Scientific), in a 50 °C sonicating water bath for an hour, then left overnight in a 50 °C water bath. Feathers were removed from the methanol post-extraction, recoveries were added, and samples were filtered via solid-phase extraction with a methanol wash and air-dried prior to adding phosphate-buffered saline with gelatin (PBSG) assay buffer. Blood plasma samples were frozen at −20 °C until analysis. 20 μl of plasma was extracted using 4.5 ml of HPLC grade dichloromethane (Fisher Scientific), and air-dried prior to adding PBSG assay buffer. Corticosterone concentrations were measured using radioimmunoassay (Wingfield and Farner, 1975). All samples were run in duplicate, with feather sample inter-assay CV: 4.2%, intra-assay CV: 0.93%, and corticosterone extraction efficiency with the organic solvent (recoveries): 92.78%. Plasma sample inter-assay CV: 1.94%, intra-assay CV: 1.16%, and recoveries: 91.3%. The final hormone concentrations were expressed as per plasma volume [ng/mL] or feather mass [ng/g] (Will et al., 2019). Breeding season results of both species were reported in Will et al., 2020a, and non-breeding season results of thick-billed murres were reported in Will et al., 2020b, in different contexts.

We used an additional dataset on primary feather corticosterone concentrations obtained from museum specimens (thick-billed murre: Will et al., 2020b; common murre: Kitaysky, A. S. unpublished data), for comparisons with inter-annual variation in the regional sea-ice extent (see subsection 2.5). These specimens were collected in the northern Bering Sea and the Chukchi Sea regions. Their primary feathers, subsampled in the same way as in live birds, were available for three years in thick-billed murres (1996, 1997, and 2003: n = 7, 11, and 4) and four years in common murres (1996, 1997, 1998, and 2001: n = 3, 4, 2, and 4). Samples were contributed by the University of Alaska's Museum of the North, the University of Washington's Burke Museum, and Alan Springer (see Table S4 for details).

We used DNA extracted from red blood cells to genetically sex our study birds (following Merkling et al., 2012).

2.5. Sea ice data

To assess the effects of changes in sea ice conditions on foraging niches and nutritional state of murres, we used monthly and daily regional sea ice extent data available at the National Sea Ice Data Center (https://nsidc.org/arcticseaicenews/sea-ice-tools/). February and October sea-ice extent values of the Bering Sea, the Chukchi Sea, and the Sea of Okhotsk were compared with the stable isotopic values and

nutritional stress levels of murres.

2.6. Statistical analysis

We used the R package SIBER (https://cran.r-project.org/package=SIBER) to calculate the standard ellipse area as a metric for species-specific foraging niche width characterized by carbon and nitrogen isotope values (i.e., isotopic niche width; Jackson et al., 2011). We reported Bayesian modes and 95% credible intervals for standard ellipse areas of each species for each year. We compared $\delta^{15}N$ and $\delta^{13}C$ values as well as CORT between the two murre species and among the four years using either one-way or two-way ANOVA (type III), using the R package car (https://cran.r-project.org/package=car). We also tested the effect of sex on $\delta^{15}N$ and $\delta^{13}C$ values in each species, accounting for possible between year effects, by using two-way ANOVA (type III). We examined the effect of the regional sea-ice extent on $\delta^{15}N$ and $\delta^{13}C$ values as well as CORT of each species, using linear mixed effect models with the R packages lme4 (https://cran.r-project.org/package=lme4) and multcomp (https://cran.r-project.org/package=multcomp), including study year as a random effect. For mixed effect models, we calculated the percentage of variance explained by the fixed effects (marginal R^2) and fixed and random effects (conditional R^2) (Nakagawa et al., 2017), with the R package MuMIn (https://cran.r-project.org/package=MuMIn).

3. Results

3.1. Logger and data recovery

We recovered geolocators from six thick-billed and three common murres (13% and 9% recovery rates, respectively) during 2017–2019. One of the geolocators was retrieved from a thick-billed murre by a local hunter during their subsistence hunting in the spring of 2018. We observed, but could not recapture, an additional seven thick-billed and six common murres with tags at the breeding colony. Of the recovered geolocators, two from thick-billed murres stopped after short recording periods (3 and 7 days), and one had corrupted geolocation data, due to unknown technological problems. Therefore, our final sample size for geolocator data was limited to three thick-billed (one male and two females) and three common murres (one male and two females), all deployed in 2016 and recorded continuously until the summer of 2017.

3.2. Migratory movements

Thick-billed and common murres showed markedly different migratory movement patterns after breeding. All three thick-billed murres moved north into the Chukchi Sea after breeding, while all three common murres stayed in the Bering Sea, south of St Lawrence Island, during September and October (Fig. 1A). In November and December, thick-billed murres moved southwest along the east coast of the Kamchatka Peninsula, while common murres remained in the eastern side of the Bering Sea (Fig. s2a and S2b). The three thick-billed murres left the Chukchi Sea on 28 Sep., 6 Nov., and 20 Nov. (based on the day the birds crossed 66°N heading south), and the latter two dates appeared to correspond to the timing of a rapid increase in sea-ice extent in the Chukchi Sea (Fig. 2). In February and March, two thick-billed murres stayed in the Sea of Okhotsk, and another thick-billed murre reached the southern part of the Japan Sea (Fig. 1B). All three common murres remained in the eastern Bering Sea, the Gulf of Alaska, or eastern North Pacific. Both species returned to the northern Bering Sea in early May (8–19 May and 1–11 May for thick-billed and common murres, respectively, based on the day the birds crossed 60°N heading north), as sea-ice started to retreat to the north, from the Bering Sea to the Chukchi Sea (Fig. 2). Distances from the colony (monthly basis) gradually increased seasonally and reached a maximum in the winter months (Jan.–Apr.) for both species (Fig. 3). The wintering destinations of thick-
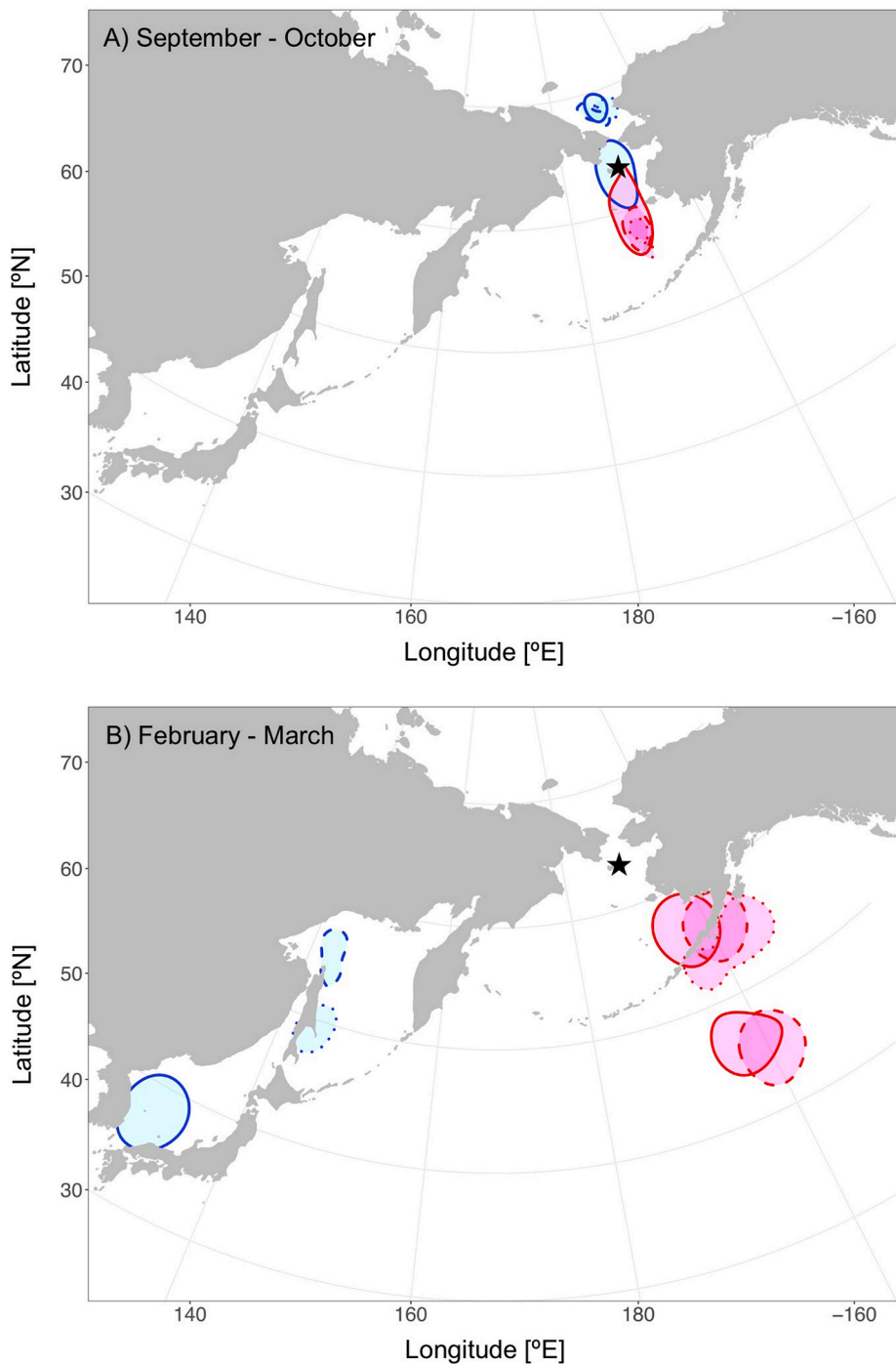
Fig. 1. Thick-billed and common murres breeding on St. Lawrence Island diverged in their post-breeding and wintering distributions. 50% kernel density distributions of thick-billed (blue) and common (red) murres during (A) fall (Sep–Oct) and (B) late winter (Feb–Mar) show divergent migratory movements between the two species. Data from individual birds (n = 3 birds for each species) are shown separately with solid, dashed, and dotted lines. Males shown as solid lines, and females shown as dashed or dotted lines, for both species, respectively. Location of breeding colony shown as a star.

billed murres were twice farther the distances from the colony than those of common murres (3972 ± 878 (SD) km and 1852 ± 486 (SD) km, respectively). Overall, wintering destinations of the two species were 4000–5000 km apart.

3.3. Diving activity

Seasonal changes in the maximum dive depths appeared to reflect the horizontal migratory movements in both thick-billed and common murres. In thick-billed murres, daily maximum dive depths were relatively constant (40–50 m depths) until early November (Fig. 4A), which matches the use of shallow shelf areas in the northern Bering Sea and the southern Chukchi Sea (Fig. 1, Fig. S3). During this period, thick-billed

murres dove close to seafloor depths, indicating feeding in benthic environments (Fig. 5A). After late November, when thick-billed murres left the Chukchi Sea and the northern Bering Sea, the daily maximum dive depths were more variable and reached to 134–145 m at the maximum (Fig. 4A), which matches with the use of deep ocean basins during migration and wintering (Fig. 1, Fig. S2). After May, thick-billed murres showed relatively constant maximum dive depths shallower than 50 m (Fig. 4A), reflecting constraints on maximum diving depth by the shallow seafloor in the vicinity of the breeding colony.

In common murres, daily maximum dive depths were more variable than those of thick-billed murres during fall (Fig. 4B). Common murres frequently dove to 30–40 m, well above the seafloor depths, indicating feeding in the middle of the water column (i.e., pelagic feeding) (Fig. 5B,
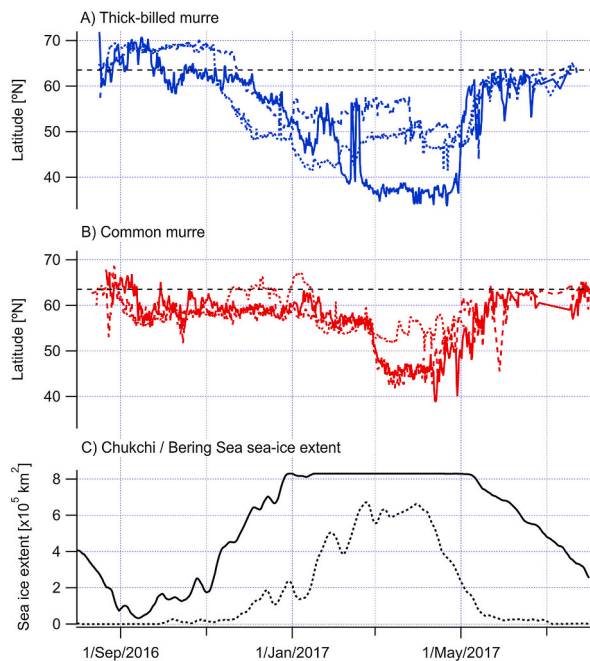
Fig. 2. Latitudinal movements of murres associated with seasonal advancement and retreat of sea-ice. Latitudinal positions of A) thick-billed and B) common murres. Note that fluctuations in latitudinal positions are due to errors associated with light- and temperature-based geolocation. Data from individual birds (n = 3 birds for each species) are shown separately with solid, dashed, and dotted lines. Horizontal dashed black lines indicate the latitude of the breeding colony. Males shown as solid lines, and females shown as dashed or dotted lines, for both species. C) Seasonal changes in sea-ice extent in Chukchi Sea and Bering Sea (solid and dotted lines, respectively).
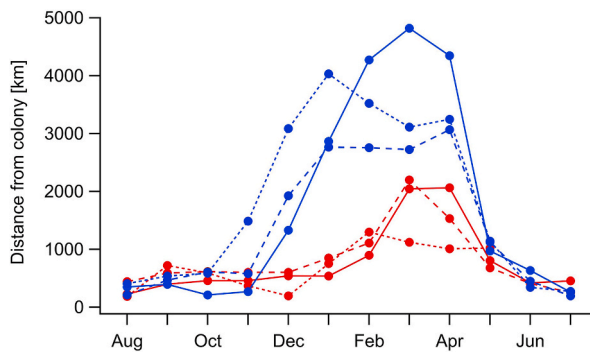

Fig. 3. Thick-billed murres migrated farther from the colony than common murres. Monthly-averaged distance from the colony for thick-billed (blue) and common murres (red). Data from individual birds (n = 3 birds for each species) are shown separately with solid, dashed, and dotted lines. Males shown as solid lines, and females shown as dashed or dotted lines, for both species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. S3B). During winter, common murres tended to perform deeper dives, 85–175 m deep at the maximum. After May, common murres also showed relatively constant maximum dive depths shallower than 50 m (Fig. 4B), reflecting constraints on maximum diving depth in shallow waters around the breeding colony, as in thick-billed murres.

Seasonal changes in diving effort showed different patterns between the sexes. After breeding, males of both species (n = 1 for each species) spent more extended time diving per day for 2–3 months (Fig. S4). After October in thick-billed murres and November for common murres, there were no apparent differences in diving effort between sexes. Thick-billed
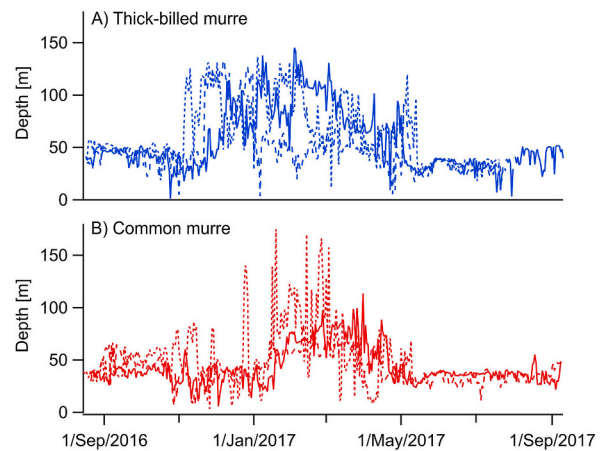

Fig. 4. Daily maximum dive depths fluctuated seasonally. A) Thick-billed and B) common murres. Data from individual birds (n = 3 birds for each species) are shown separately with solid, dashed, and dotted lines. Males shown as solid lines, and females shown as dashed or dotted lines, for both species, respectively.

murres showed the highest diving effort in May (Fig. S4A), whereas common murres showed the highest diving effort in March to April (Fig. S4B).

Seasonal changes in daily dry time showed that both thick-billed and common murres had relatively short daily dry time around September and October (Fig. S5). The short dry time in the fall suggests that they reduced flying activity during primary feather molt, when they were in the Chukchi Sea or the northern Bering Sea (Fig. 1A). Both species showed extensive daily dry time in June–August, mirroring the colony attendance activities during the breeding season.

3.4. Isotopic niche

Nitrogen and carbon stable isotope (δ^{15}N and δ^{13}C) values differed significantly between the two species for primary (fall) and throat (late winter) feathers, with varying degrees of between-year effects (Fig. 6, Table S1). δ^{15}N values in red blood cells (summer) tended to be higher in common murres than in thick-billed murres, with significant interaction effects of year and species (Fig. 6, Table S1). Common murres showed higher δ^{15}N values than thick-billed murres in both primary and throat feathers (Table S1). For thick-billed murres, δ^{15}N values were relatively high in primary feathers, but subsequently declined to relatively low levels in throat feathers (Fig. 6), which might reflect the bird's shift in spatial distributions (Fig. 1B) or dietary changes that included lower trophic-level prey in late winter. Mean isotopic distances between the two species were largest in throat feathers (Table S1), compared to primary feathers and red blood cells, suggesting that the highest degree of spatial/dietary differences occurred between the two species in late winter. The δ^{15}N and δ^{13}C values of two female thick-billed murres with geolocators were relatively far apart (Fig. 6C). However, both birds wintered in the Sea of Okhotsk (Fig. 1B), suggesting that relatively small-scale spatial differences or dietary differences might affect isotopic signatures. Sex differences were only found in δ^{13}C in red blood cells and throat feathers for thick-billed murres, and in δ^{15}N in primary feathers for common murres (Fig. S6).

Isotopic niche width, estimated as the standard ellipse area, of thick-billed and common murres varied between years and seasons (summer, fall, and late winter) (Table S2). Both species had relatively smaller isotopic niche widths in fall (primary feathers) than in late winter (throat feathers), possibly reflecting relatively restricted spatial movements in fall than in late winter (Fig. 1). The two species had similar isotopic niche widths based on the overlap of 95% credible intervals in all years and seasons, except in their red blood cells (summer) in 2016
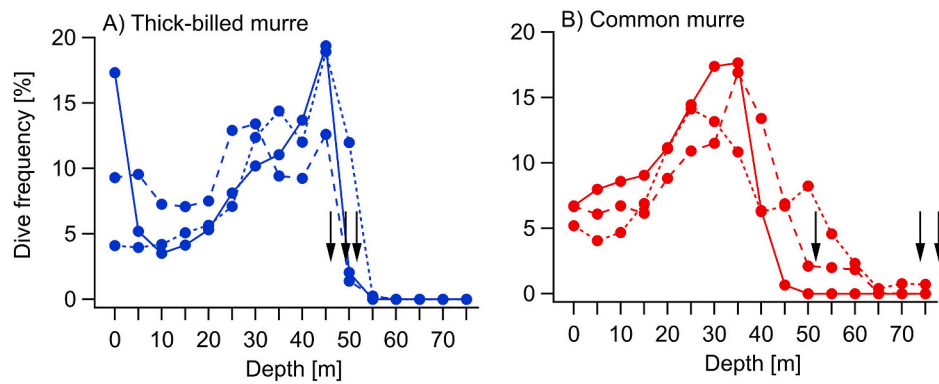
Fig. 5. Depth distribution of dives in relation to bathymetry in fall. Frequency of dives to different depths for A) thick-billed and B) common murres, during fall (until Oct 31, 2016). Arrows indicate median sea floor depths estimated from bird location and bathymetry. Data from individual birds (n = 3 birds for each species) are shown separately with solid, dashed, and dotted lines. Males shown as solid lines, and females shown as dashed or dotted lines, for both species, respectively.
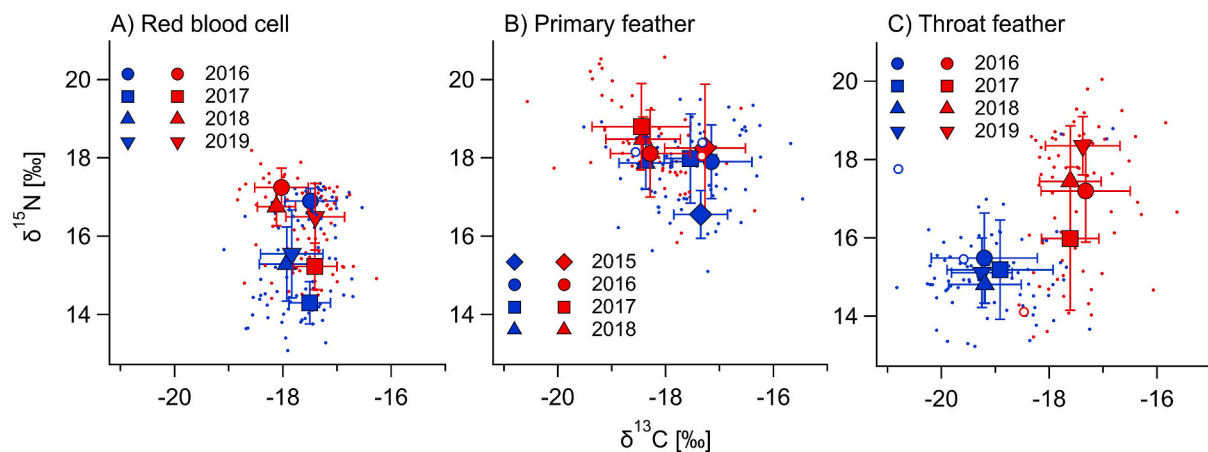

Fig. 6. Thick-billed and common murres diverged in their throat feather stable isotopic signatures. $\delta^{15}N$ and $\delta^{13}C$ values (mean ± SD) of (A) red blood cell (summer: Jul–Aug), (B) primary feathers (fall: Sep–Oct), and (C) throat feathers (late winter: Feb–Mar), in thick-billed (blue) and common (red) murres, across four years (2015–2018 for primary feathers, and 2016–2019 for red blood cells and throat feathers; for (B) and (C), year indicates the year when birds molted the feather). Colored dots indicate data points from individual birds, with open circles indicate those from geolocator birds (feathers only, two female thick-billed and one female common murre). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

when thick-billed murres had a smaller isotopic niche width than common murres (Table S2).

Thick-billed murres had higher $\delta^{13}C$ values in summer, and lower $\delta^{15}N$ values in fall, in years of more extensive sea-ice extent (Figs. 7 and 8: linear mixed-effect models: slope coefficient of sea-ice extent = 0.18 ± 0.05 (SE) and −0.80 ± 0.16 (SE), with marginal R^2 = 0.11 and 0.25, and conditional R^2 = 0.11 and 0.25, P < 0.001 and < 0.001, for summer $\delta^{13}C$ and fall $\delta^{15}N$ values, respectively). Common murres had higher $\delta^{13}C$ values in fall, in years of more extensive sea-ice extent (Fig. 8: linear mixed-effect models: slope coefficient of sea-ice extent = 0.65 ± 0.20 (SE), with marginal and conditional R^2 = 0.15 and 0.15, P < 0.001). Regional sea-ice extent did not show significant relationships with $\delta^{15}N$ and $\delta^{13}C$ values in late winter (Fig. S7: linear mixed-effect models: P > 0.17), nor with the mode of standard ellipse area for either species and in any season (Spearman's rank correlations, rho = −0.8 – 0.8, P > 0.33).

3.5. Nutritional stress

Corticosterone concentrations (CORT) in blood plasma (summer), primary (fall), and throat (late winter) feathers differed significantly between species (Table S3). Common murres had higher CORT than thick-billed murres, with the most pronounced differences found in primary feathers (Table S3). No significant sex differences were found in

plasma, primary, and throat CORT values, in either thick-billed or common murres (p > 0.31 in all cases).

CORT values in blood and feathers did not associate with variations in $\delta^{15}N$ or $\delta^{13}C$ values at the level of individual birds in either species or in any season (p > 0.16), except for the following two cases. Summer CORT (plasma) negatively correlated with $\delta^{15}N$, and fall CORT (primary feather) negatively correlated with $\delta^{13}C$ in thick-billed murres (Fig. S8: linear mixed-effect models: slope coefficient of $\delta^{15}N$ = −0.06 ± 0.02 (SE), with marginal and conditional R^2 = 0.09 and 0.09, P < 0.05; slope coefficient of $\delta^{13}C$ = −0.07 ± 0.03 (SE), with marginal and conditional R^2 = 0.08 and 0.11, P < 0.05). Late winter CORT (throat feathers) positively correlated with fall CORT (primary feathers) in common murres (Fig. S8D: slope coefficient of fall CORT = 0.43 ± 0.10 (SE), with marginal and conditional R^2 = 0.22 and 0.25, P < 0.001), but not in thick-billed murres (Fig. S8C: slope coefficient of fall CORT = −0.06 ± 0.11 (SE), with marginal and conditional R^2 = 0.03 and 0.17, P = 0.88).

Summer (blood plasma) CORT values were significantly higher in 2017–2019, the period of historic low winter sea-ice extent, than in 2016, the year of relatively high pre-breeding sea-ice extent in the Bering Sea in common murres, but not in thick-billed murres, when each species was analyzed separately (Fig. 9, Table S3; one-way ANOVA with Tukey HSD test, common murres: p < 0.05; thick-billed murres: p = 0.23). However, the February regional sea-ice extent in the Bering Sea did not show linear effects on summer CORT values for either species
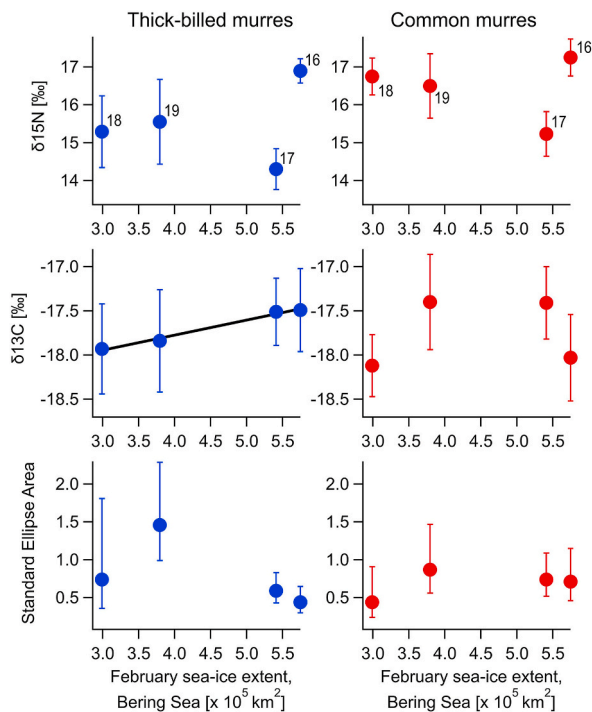
Fig. 7. Summer isotopic niche and regional sea-ice extent of Bering Sea in 2016–2019. δ^{15}N, δ^{13}C values and Bayesian estimated Standard Ellipse Area (isotopic niche width) of red blood cells collected during summer breeding periods from thick-billed (left panels) and common murres (right panels), in relation to pre-breeding (February) monthly-averaged sea-ice extent of Bering Sea during 2016–2019. Mean and SD are shown for δ^{15}N and δ^{13}C values. Mode and 95% upper and lower credible intervals are shown for Standard Ellipse Area. Black regression line is shown to indicate a statistically significant relationship, resulting from linear mixed effect models including year as a random effect. The numbers near the data points are shown to indicate the year (the last two numerals of each year).

(Fig. 9: linear mixed-effect models, P > 0.14). Fall CORT values of thick-billed murres were significantly higher in years of lower fall sea-ice extent in the Chukchi Sea, when an additional three years of data from museum specimens were included (Fig. 9: linear mixed-effect models, slope coefficient of sea-ice extent = −0.06 ± 0.02 (SE), with marginal and conditional R^2 = 0.07 and 0.07, P < 0.01). Fall and late winter CORT values of common murres and late winter CORT values of thick-billed murres did not show significant relationships with the regional sea-ice extent (Fig. 9: linear mixed-effect models, P > 0.20).

4. Discussion

4.1. Migratory movements and diving behavior

The recovery rates of geolocators were relatively low in this study (13% and 9% for thick-billed and common murres, respectively), compared to previous studies on the same species in other regions (thick-billed murres: 65–68%, Orben et al., 2015, McFarlane-Tranquilla et al., 2015, Frederiksen et al., 2016; common murres: 49%, McFarlane-Tranquilla et al., 2015). The low recovery rate could be related to the high sensitivity of murres to human presence at St. Lawrence Island (personal observations), possibly associated with subsistence harvest of murre eggs in and near the study colony (Naves, 2018). Also, mass mortality events and colony-wide reproductive failures of thick-billed murres occurred in May–July 2018 (Will et al., 2020b; see below), which prevented the effort to recover the geolocators in the breeding season of 2018. The resulting sample size for geolocators was small, though three birds from each species showed similar movement patterns
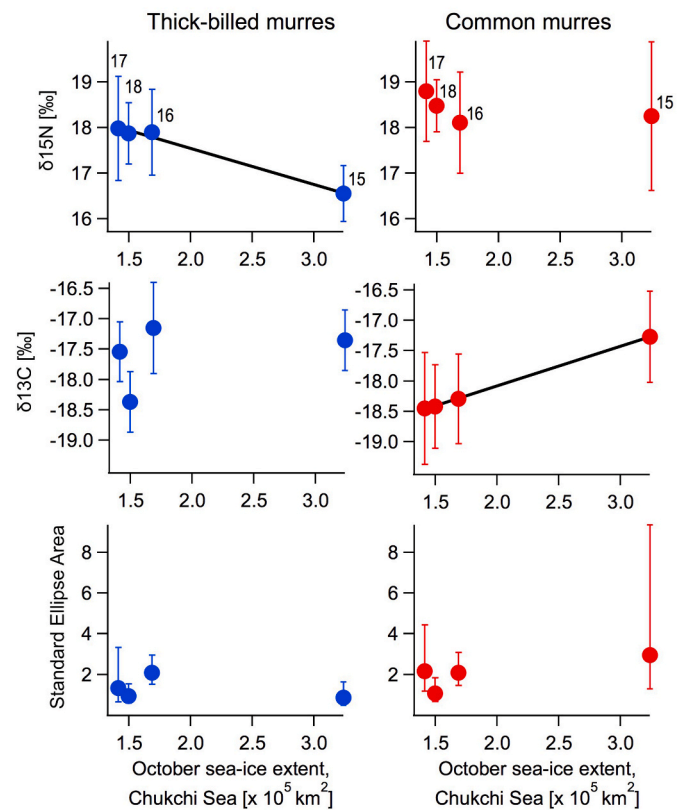
Fig. 8. Fall isotopic niche and regional sea-ice extent of Chukchi Sea in 2015–2018. δ^{15}N, δ^{13}C values and Bayesian estimated Standard Ellipse Area (isotopic niche width) of primary feathers that molt in fall, obtained from thick-billed (left panels) and common murres (right panels), in relation to fall (October) monthly-averaged sea-ice extent of Chukchi Sea during 2015–2018. Mean and SD are shown for δ^{15}N and δ^{13}C values. Mode and 95% upper and lower credible intervals are shown for Standard Ellipse Area. Black regression lines are shown to indicate statistically significant relationships, resulting from linear mixed effect models including year as a random effect. The numbers near the data points indicate the year when birds molted the feather (the last two numerals of each year).

and diving activities.

Our geolocator results indicate that thick-billed and common murres from St Lawrence Island have contrasting migratory movements and diving behaviors. Although our sample size for geolocators is limited, stable isotope signatures of the larger number of untracked birds supported divergent movements and foraging ecology between thick-billed and common murres (see subsection 4.2). In fall, thick-billed murres migrated into the Chukchi Sea and showed benthic diving behavior. The benthic habitat of the Chukchi Sea is known for its high biological productivity because of strong pelagic-benthic coupling in this shallow shelf sea (Grebmeier et al., 2018). Thick-billed murres are known to feed on benthic fish species, such as sculpins, pricklebacks, or flatfish near the seafloor, depending on the prey available (Gaston and Hipfner, 2000; Kokubun et al., 2018). The high benthic productivity might especially be important in fall when thick-billed murres molt their primary feathers and become flightless for 4–6 weeks (Elliott and Gaston, 2014). In contrast, common murres stayed in the Bering Sea southeast of St. Lawrence Island and performed pelagic diving behavior. The shelf areas between St. Lawrence Island and the Pribilof Islands are known to have concentrations of pelagic forage fish such as capelin and Pacific herring (Smith et al., 2017), and common murres might forage on these pelagic fish.

The wintering areas of thick-billed murres from St. Lawrence Island appeared to differ drastically from those breeding in the Chukchi Sea and the southeastern Bering Sea. Thick-billed murres from St. Lawrence
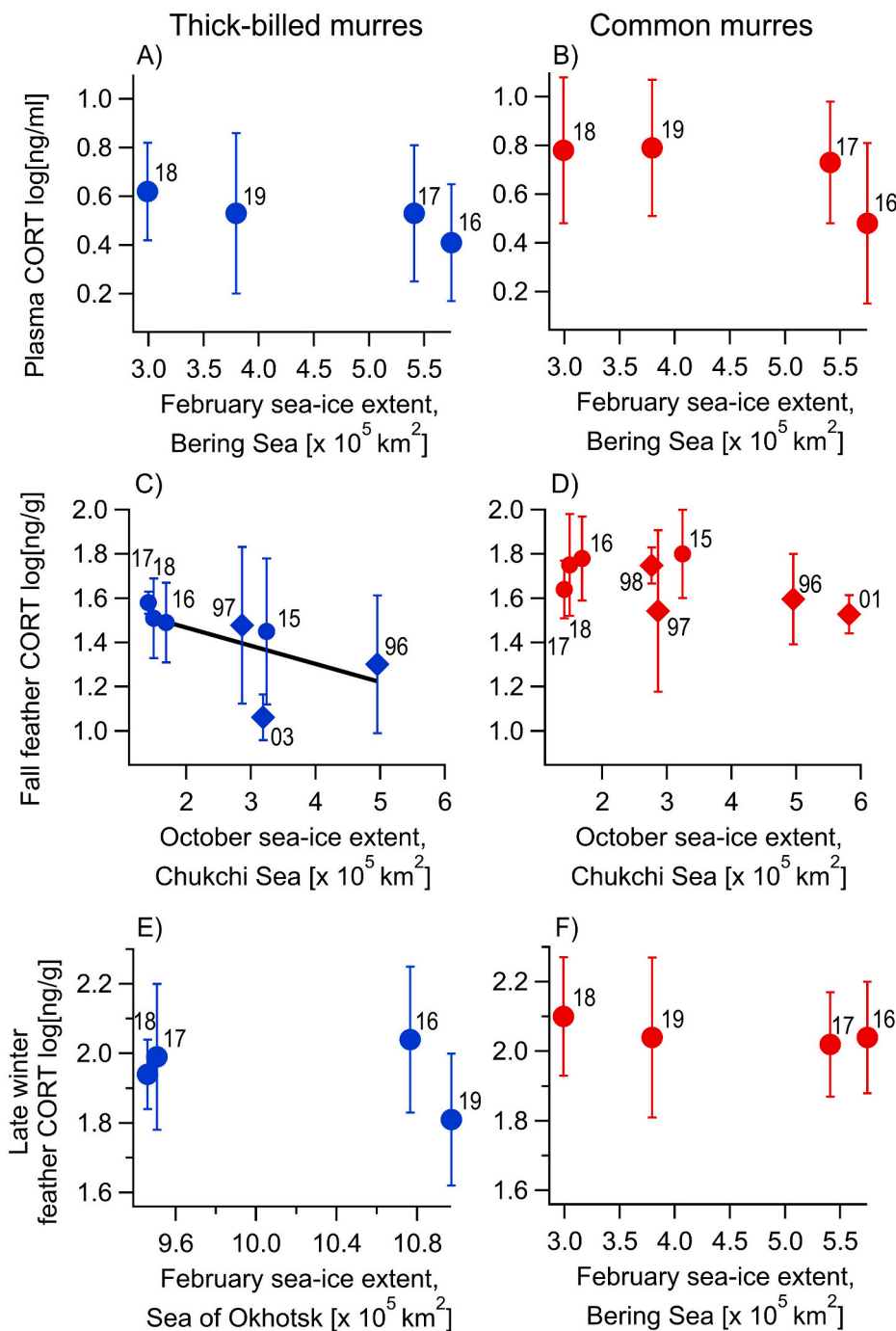
Fig. 9. Temporal dynamics of nutritional stress in relation to changes in regional sea-ice extent. Corticosterone concentrations in plasma (summer: A and B), primary feathers (fall: C and D), and throat feathers (late winter: E and F) of thick-billed (left panels) and common murres (right panels) in relation to regional sea-ice extent. Summer CORT values (n = 4 years, 2016–2019) were compared with pre-breeding February sea-ice extent in the Bering Sea for both species. Fall CORT values in thick-billed murres (n = 7 years, 2015–2018, shown as circles, and three additional years, 1996, 1997, and 2003, from museum specimen data shown as diamonds) negatively correlated with October sea-ice extent in the Chukchi Sea. Fall CORT values in common murres (n = 8 years, 2015–2018, shown as circles, and four additional years, 1996–1998, and 2001, from museum specimen data, shown as diamonds) showed no correlation with October sea-ice extent in the Chukchi Sea. Late winter CORT values (n = 4 years, 2016–2019) of thick-billed and common murres were compared with February sea-ice extent of the Sea of Okhotsk and the Bering Sea, respectively, to reflect the differences of wintering areas between species. For C) – F), 'year' indicates the year when birds molted the feather. Mean and SD are shown. The numbers near the data points indicate the year (the last two numerals of each year).

Island moved southwest to the Sea of Okhotsk and the Japan Sea after leaving the Chukchi Sea in late fall (Fig. 1 and S2). In contrast, Hatch et al. (2000a), Hatch et al., 2000b reported that two post-breeding thick-billed murres from the southern Chukchi Sea (internally-implanted transmitters were deployed in August 1995 on one bird from Cape Lisburne, which was tracked until April, and on one bird from Cape Thompson tracked until January) remained in the eastern Bering Sea and did not go farther south than the Pribilof Islands in winter. Orben et al. (2015) reported that Pribilof Island thick-billed murres stayed in the basin of the southeastern Bering Sea or south of the Aleutian Islands throughout the fall and the winter, based on three years of geolocator tracking. The Pribilof Island birds (29 birds from St. Paul Island, and 14 birds from St. George Island) appeared to use the southeastern Bering Sea consistently across the three study years. These

results indicate that suitable wintering habitats in the regions of the Bering Sea basin and south of the Aleutian Islands are not used by St. Lawrence Island thick-billed murres. Since these winter tracking studies were conducted during different periods (1995–1996: Hatch et al., 2000a, 2008–2011: Orben et al., 2015, 2016–2017: this study), the colony-specific differences in migratory movements need to be confirmed with a larger sample size from the northern Bering Sea and the southern Chukchi Sea.

It is unclear why St. Lawrence Island thick-billed murres migrate much longer distances to the western North Pacific, while Chukchi Sea and Pribilof Island birds stay in the eastern Bering Sea. St. Lawrence Island birds may be avoiding intraspecific competition in the wintering areas, as large populations of thick-billed murres breed in the southeastern Bering Sea (Smith et al., 2017). The southwestern Japan Sea is

an important winter foraging ground for both piscivorous and planktivorous alcids (rhinoceros auklets *Cerorhinca monocerata*: Takahashi et al., 2015; ancient murrelets *Synthliboramphus antiquus*: Gaston et al., 2017). One tracked thick-billed murre wintered in the southwestern Japan Sea, suggesting this region might also provide favorable foraging habitat for thick-billed murres.

Colony-specific differences in non-breeding distributions may lead to differences in population genetic structure (Friesen et al., 2007). A recent study reported no genetic differences between western and eastern North Pacific colonies but some genetic differentiations between thick-billed murres breeding in the Chukchi Sea and those breeding on the Pribilof Islands and the Kamchatka Peninsula (Tigano et al., 2015). It is currently unknown if the St. Lawrence Island thick-billed murres are genetically distinct from these groups, which deserves a further focused investigation.

Information on colony-specific migratory movements might have important implications for population monitoring. For example, different migratory routes may lead to differences in exposure to various pathogens carried by migratory birds (Ramey et al., 2010). Recent studies suggest that an *en masse* die-off of thick-billed but not common murres was recorded in 2018 on St. Lawrence Island (Romano et al., 2020; Will et al., 2020b). This species-specific die-off could be related to an exposure of the St. Lawrence Island thick-billed murres to Eurasian strains of avian influenza during wintering in the Asian regions (see Will et al., 2020b for detailed discussion). This single die-off event was associated with a subsequent decline in numbers of thick-billed murres breeding on St. Lawrence Island (Will et al., 2020b) pointing at a potential importance of the inter-specific differences in migratory connectivity.

Common murres from St. Lawrence Island moved to the eastern Bering Sea regions, the Gulf of Alaska, and eastern North Pacific, with their wintering grounds being much closer to the colony than those of thick-billed murres (Fig. 3). These wintering grounds appear to be similar to those of common murres tracked from Cape Thompson and Cape Lisburne in the Chukchi Sea in 1995 and 1996 (Hatch et al., 2000a). The relative short migratory distances of common murres compared to thick-billed murres are consistent with previous studies in the North Atlantic (Fort et al., 2013; McFarlane-Tranquilla et al., 2015). Thick-billed murres, which tend to distribute at higher latitudes than common murres, may necessarily possess a higher migratory capacity as an adaptation to the highly seasonal Arctic environment.

Some aspects of diving behavior were similar between thick-billed and common murres. Although the sample size is limited, males showed higher daily diving effort than females in fall in both species (Fig. S4), which is likely associated with male-only post-fledging care (Elliott and Gaston, 2014; Dunn et al., 2019b). Both species showed the highest diving effort in winter and spring, which might be associated with high energy expenditure during the winter period, and corresponds with the building up of energy reserves for the upcoming breeding season (Fort et al., 2013; Burke and Montevecchi, 2018).

4.2. Isotopic niche and nutritional stress

Thick-billed and common murres appeared to have different foraging niches based on nitrogen and carbon stable isotope values. Common murres showed higher $\delta^{15}N$ values than thick-billed murres, in red blood cells, primary feathers, and throat feathers. This is consistent with previous reports on the interspecific differences in isotopic signatures in the southeastern Bering Sea during the breeding season (Barger and Kitaysky, 2012; Barger et al., 2016; Kokubun et al., 2016). Stomach content analysis of fishery by-catch birds indicated that both species of murres feed on fish, euphausiid, and amphipods in different proportions between regions in the western North Pacific (Ogi and Tsujita, 1977; Ogi, 1980; Ogi et al., 1985). On St. Lawrence Island, chick-diet observations in 2016 and 2017 showed that both thick-billed and common murres fed mainly on benthic fish, but common murres tended to have more pelagic

schooling fish in the diet during the breeding season (Tsukamoto, 2019). In the North Atlantic, during winter, some studies reported the occurrence of crustaceans in the stomach contents of thick-billed murres (Erikstad, 1990; Gaston and Hipfner, 2000), but other isotopic studies reported no significant differences in $\delta^{15}N$ values between the two species (Linnebjerg et al., 2013). Some previous studies reported that starvation (i.e., higher nutritional stress) could cause enrichment of $\delta^{15}N$ (e.g., Williams et al., 2007), but this does not apply to this study, as we found no or negative relationships between corticosterone levels and $\delta^{15}N$ values at the level of individual birds (Fig. S8A). Our data support the conclusion that common murres tended to consistently feed on higher trophic level fish species throughout the non-breeding period, and thick-billed murres might feed on lower trophic level prey such as zooplankton, especially in winter. However, due to large spatial movements of both thick-billed and common murres during the non-breeding period, it is difficult to separate the effects of dietary changes from spatial differences in baseline isotope values (Schell et al., 1998; Gorbatenko et al., 2014; Magozzi et al., 2017).

Inter-specific differences in corticosterone concentrations may reflect differences in ecology, physiology, and stress-exposures, between the two murre species. We found that corticosterone concentrations in primary and throat feathers were generally higher in common murres than in thick-billed murres (Table S3). In fact, common murres tended to have higher corticosterone concentrations in primary feathers than thick-billed murres when compared over time (n = 25 and 22 years, for thick-billed and common murres from the northern Bering Sea, respectively; Kitaysky, A. S. and Will, A. P. unpublished data). Corticosterone concentrations in feathers are considered as indicators of stress-exposure during the feather molt (Bortolotti et al., 2008; Will et al., 2019), which occurs in fall (September–October) for primary and in late winter (February–March) for throat feathers in murres (Gaston and Hipfner, 2000). One possible explanation is that common murres have relatively higher daily energy expenditure (up to 7 x basal metabolic rates, Burke and Montevecchi, 2018; Dunn et al., 2020) than thick-billed murres (Fort et al., 2013), which results in higher nutritional stress exposure. Another explanation would be related to the inter-specific dietary differences. Our isotopic niche data indicate that common murres consume relatively high trophic level prey, which is generally considered as high quality for seabirds (Kowalczyk et al., 2014). High $\delta^{15}N$ values were associated with lower CORT values in summer in thick-billed murres (Fig. S8A), but no such relationship was found in common murres or in other seasons for thick-billed murres. In the winter, these relatively high-quality prey might be hard to find at shallow depths in pelagic waters due to deeper vertical distribution as surface waters become cold (Burke and Montevecchi, 2018). These changes in prey availability may be mirrored in the relatively high daily diving effort and deeper diving depths of common murres in winter (Fig. 4 and S4B). Relatively high energy expenditures and difficulties in finding prey fish might put common murres in a negative energy balance in winter, as reflected in relatively high corticosterone secretion.

Inter-specific differences in migratory patterns appeared to be reflected in the patterns of correlation in nutritional stress levels between fall and late winter. CORT values were correlated between fall and late winter at the individual level in common but not in thick-billed murres (Figs. S8C and D). Common murres might experience ecologically similar conditions between the fall and late winter periods, which appeared to match their tendency to reside in the eastern North Pacific regions (Fig. 1). In contrast, thick-billed murres might experience very different ecological conditions between fall and late winter, which matches their migratory movements over ecologically disconnected regions, from the southern Chukchi Sea to the southwestern North Pacific (Fig. 1).

4.3. Effects of changing sea-ice conditions

The migratory timing of thick-billed and common murres appeared

to be influenced by the seasonal advancement and retreat of sea-ice extent, but in slightly different ways between species. Seasonal advancement of sea-ice extent in the fall may affect the timing of southward migration from the Chukchi Sea in thick-billed murres, but not in common murres who stayed in the northern Bering Sea (Fig. 2). The seasonal sea-ice retreat may also affect the timing of return to the northern Bering Sea (mid-May) in both species, which is roughly 1.5 months before the median laying date (1 July and 29 June, for thick-billed and common murres, respectively; Piatt et al., 1988). In the North Atlantic, a recent study reported the long-term advancement of arrival dates to the colony both in thick-billed and common murres (Merkel et al., 2019). A multi-year geolocator study with large sample size is needed to examine how changes in the timing of sea-ice advancement and retreat might affect the migratory phenology of murres in the Pacific Arctic.

Trophic ecology of thick-billed and common murres appeared to have responded to annual variations in sea-ice conditions. Our isotopic niche and nutritional stress data covered four relatively warm years (except for primary feather stress data having an additional 3–4 years of data from museum specimens), and included a year of historic low winter sea-ice extent (2018) in the Bering Sea (Stabeno and Bell, 2019; Duffy-Anderson et al., 2019). Annual variations in sea-ice conditions have been shown to affect the abundance and distribution of lower trophic level zooplankton and forage fish (Renner et al., 2016; Duffy-Anderson et al., 2019). Changes in $\delta^{15}N$ and $\delta^{13}C$ values in thick-billed and common murres associated with regional sea-ice extent (Figs. 7 and 8) might reflect changes in prey resources. For example, higher $\delta^{13}C$ values with greater regional sea-ice extent may be related to a higher proportion of benthic fish species in the diet, as pelagic and benthic fish species tend to have low and high $\delta^{13}C$ values, respectively, in the northern Bering Sea (Will et al., 2020a).

Changes in foraging ecology presumably mediated the effect of sea-ice conditions on the nutritional state of both species of murres. Common murres, but not thick-billed murres, had higher summer CORT in 2017–2019, the period of anomalously warm conditions, than in 2016, the year of relatively high winter (February) sea-ice extent (Fig. 9, Table S3). Using the same summer CORT dataset, Will et al., 2020a reported that nutritional stress levels of both thick-billed and common murres increased with decreasing 15th February sea-ice concentration (calculated over the area of 61–67°N, −180 to −165°W) during 2016–2019, indicating a possible link between winter sea ice concentration and nutritional stress during the breeding period. In the present analysis, monthly-averaged February sea-ice extent in the Bering Sea did not show significant linear effects on murre's nutritional stress, possibly because the index covered a much larger area than the area analyzed in Will et al., 2020a. Fall feather CORT in thick-billed murres was higher in years of lower fall sea-ice extent in the Chukchi Sea (Fig. 9), suggesting a negative effect of sea-ice loss on the nutritional state of molting thick-billed murres in the fall. These results partially support the hypothesis that the ongoing loss of sea-ice might negatively affect both species of murres, especially post-breeding thick-billed murres, in the Pacific Arctic. However, the highest nutritional stress levels observed in this study for thick-billed murres (in fall 2017) is not unprecedented, as Will et al., 2020b indicated, thick-billed murres were exposed to similar levels of food stress in the fall (primary feathers) during 1975–1977, before the era of satellite sea-ice observations. We, therefore, still need to improve our knowledge on how different levels of nutritional stress affect the breeding success and survival rates of adult birds (e.g., Kitaysky et al., 2007), to fully understand the effects of changing sea-ice conditions on the population performance of murres.

4.4. Potential conservation threats

We suggest that thick-billed and common murres from St Lawrence Island are potentially exposed to different conservation threats during the non-breeding period. Thick-billed murres may be affected by

possible changes in the benthic foraging habitat of the Chukchi Sea, which they exploit for an extended period in the fall. In that season, murres molt their primary feathers and become flightless, which makes them more susceptible to changes in prey availability (Davoren et al., 2002). A recent study showed that nutritional stress levels in primary feathers were higher in the thick-billed murres that were found dead than murres caught alive at the breeding colony in the following summer (Will et al., 2020b). This result indicates the possible importance of nutritional stress levels incurred in the fall to birds' subsequent survival.

The benthic ecosystems of the northern Bering Sea and the Chukchi Sea have experienced spatial shifts, gains and losses in biomass, and changes in community structure, associated with recent sea-ice declines (Grebmeier et al., 2018; Huntington et al., 2020). If these changes reduce the abundance of prey species that thick-billed murres feed on in the fall (but see Will et al., 2020a), further sea-ice declines may negatively impact thick-billed murres, as indicated by the negative relationship between fall CORT and regional sea-ice extent (Fig. 9). A ship-based seabird study reported that seabird community composition shifted from fish-feeding species to plankton-feeding species in the Chukchi Sea, based on comparisons between recent (2007–2012) and historical (1975–1981) at-sea observation records (Gall et al., 2017). Gall et al. (2017) also showed the decline in the density of thick-billed murres, which may indicate the negative impact of long-term sea-ice decline on this species.

Thick-billed murres may also be susceptible to anthropogenic activities during the course of migration. As ongoing sea-ice loss opens Northern sea-routes, an increase in ship traffic (Huntington et al., 2020) and potential development of oil and gas platforms in the Chukchi Sea may pose threats to thick-billed murres in the fall. In the winter, thick-billed murres distribute to the Sea of Okhotsk and the Japan Sea, where their spatial distribution partially overlaps with areas of oil and gas platform development, such as off the northeastern coast of Sakhalin Island. Oil spill events could be a potential threat to seabirds visiting this region and have been observed previously in February and March 2006 (Ohshima and Simizu, 2008).

Common murres may be sensitive to the changes in the pelagic foraging habitat in the southeastern Bering Sea, the Gulf of Alaska, and eastern North Pacific. Our results showed that common murres had higher corticosterone secretion than thick-billed murres throughout the non-breeding period (Table S3) and were possibly exposed more frequently to food limitations in winter. Large-scale winter mass mortality of common murres was reported in 2014–2016, along the eastern North Pacific coast from California to Alaska, associated with the occurrence of a marine heat wave (Piatt et al., 2020). The regions of high mortality partially overlapped with the wintering areas of common murres determined in this study, suggesting that St. Lawrence Island common murres could have been affected by this mass mortality event and may be susceptible to future oceanographic perturbations in the North Pacific.

5. Conclusions

Our results indicate that the closely-related and sympatrically-breeding thick-billed and common murres from the northern Bering Sea have divergent migratory connectivity between species both inside and outside the Pacific Arctic. They also showed differences in various aspects of foraging ecology, including spatial distribution, pelagic and benthic habitat use, trophic ecology, and stress hormone levels. Both species appeared to show foraging flexibility to annual changes in regional sea-ice extent, at least during the four relatively warm study years with low winter sea-ice extent in the Bering Sea. Nevertheless, common murres showed relatively high nutritional stress levels during the breeding season in years of relatively low (2017–2019), compared to relatively high (2016), winter sea ice extent. Thick-billed murres also showed higher nutritional stress levels in the fall, in years of lower fall sea-ice extent in the Chukchi Sea. These results suggest that the ongoing

loss of sea-ice might negatively affect both species of murres, especially post-breeding thick-billed murres, in the Pacific Arctic. Thick-billed and common murres are susceptible to different threats during the non-breeding period, which has important implications for population monitoring and conservation of these seabirds in the rapidly changing Pacific Arctic.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.polar.2020.100552.

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