School of Aquatic and Fishery Sciences
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THEME SECTION

Seabird responses to a changing Bering Sea

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This Theme Section explores how seabirds inhabiting the southeastern Bering Sea region respond to oceanographic variability, including the timing of sea-ice retreat. It combines both colony-based and pelagic studies of seabirds, spanning a period of 100 years and an immense oceanographic region.

Photo: Chris Barger

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Contribution to the Theme Section 'Seabird responses to a changing Bering Sea'

INTRODUCTION

Seabird responses to a changing Bering Sea

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ABSTRACT: The eastern Bering Sea is well known for its spatial and temporal variability. Significant inter-annual changes in the abundance of zooplankton and forage fish are related to the timing of sea ice retreat. In this Theme Section, studies explore how different species and communities of seabirds inhabiting the region respond to contrasting patterns of spring sea-ice-retreat and summer temperatures. Data from the pelagic realm are used to explore climate-linked variability in the responses of seabird distributions to years with early and late sea-ice-retreat. Colony-based studies, relying on bird-borne data loggers and physiological parameters, examine how long-term changes in the foraging and migratory behaviors of individuals during cold and warm years may affect birds breeding on the Pribilof Islands (Alaska, USA). A unique aspect of this Theme Section is the availability of both colony-based and pelagic studies of seabirds that overlap in space and time. This body of work aims to provide an overview of seabird responses to oceanographic variability in the eastern Bering Sea, spanning a period of 100 yr and an immense oceanographic region.

KEY WORDS: Climate change · Ship surveys · Logger technology · Historical ecophysiology · Food-web stability · Nutritional stress

Introduction

The publication of this Theme Section comes as western Alaska is in the midst of its warmest winter and headed for the lowest winter sea-ice coverage in the recorded history of the Bering Sea (http://nsidc.org/data/seaice_index). Modeling studies forecast a reduction of winter sea-ice coverage in the Bering Sea in response to climate warming (Hermann et al. 2016). The major ecological challenge is to predict how such warming will affect Bering Sea ecosystems and the marine predators inhabiting the region. The potential impacts of future climate warming on marine ecosystems can be assessed by examining the effects of present-day and historical variations in climate. Understanding the effects of environmental change on seabirds requires the identification of region-specific responses and baselines that may act as reference conditions. Papers in this Theme Section focus on multi-decadal records of seabird responses to climate variability in the southeastern Bering Sea. The overarching goal is to explore how different species and communities of seabirds respond to contrasting patterns of spring sea-ice retreat and summer temperatures.

There are 2 broad themes covered in this Theme Section. The first, examined by Hunt et al. (2018), focuses on how the distribution and abundance of potential seabird prey are affected by climate variability via the timing of sea-ice retreat, and how these impacts on prey have affected the distributions of seabirds over the southeastern Bering Sea shelf since the mid-1970s. The second theme, addressed by colony-based studies relying on bird-borne data

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loggers (Kokubun et al. 2018, Orben et al. 2018), stable isotopic niche dynamics (Will & Kitaysky 2018) and physiological tools (Kokubun et al. 2018, Orben et al. 2018, Will et al. 2018), examines changes in the foraging behavior of individual seabirds and provides a mechanistic perspective on how and why environmental conditions in cold and warm years affect breeding and wintering birds. Reliance on long-term data series and the use of integrative approaches allows these colony-based studies to establish reference points and describe seabird responses to climate variability in a comprehensive way (e.g. spatial, temporal and in the context of seabird communities and individuals).

Seabird responses to environmental variability

Seabirds are sensitive to the spatial and temporal variability of their environment, especially the distribution and abundance of their prey. In the Bering Sea, particularly over the middle portion of the southeastern shelf, the recruitment of large, lipid-rich zooplankton varies with the timing of sea-ice retreat and the availability of ice algae in spring (Wang et al. 2015, Hunt et al. 2016, Sigler et al. 2016). The abundance of these zooplankton, in turn, affects the production and abundance of forage fish (e.g. Eisner & Yasumiichi 2017). Non-breeding seabirds are able to shift their foraging efforts to favorable locations within a region, or depart from that region altogether (e.g. Hunt & Harrison 1990, Coyle et al. 1992, Hunt et al. 1998, 2018, Nishizawa et al. 2017). However, seabird breeding colonies are fixed in place, and location-specific responses to climate (e.g. Gaston et al. 2005, Frederiksen et al. 2007) have the potential to complicate prediction of the effects of climate change (Brown et al. 2011), thereby preventing us from making generalizations (but see Satterthwaite et al. 2012). Papers in this Theme Section show that the ability of breeding seabirds to take advantage of changing food resources depends on a colony's location (Kokubun et al. 2018), the partitioning of food resources by members of the foraging guild and the heterogeneity of foraging habitat within reach of breeding seabirds (Will & Kitaysky 2018; also see Barger & Kitaysky 2012, Barger et al. 2016, and Kokubun et al. 2016), and the degree of foraging specialization of a particular species (Orben et al. 2018, Will et al. 2018).

Understanding the effects of climate variability on seabirds benefits from both long time-series and from an integrated research approach. Specifically, since climate change is likely to affect seabird food resources, it is essential that we are not only able to detect changes in food availability, but also to predict how those changes will affect breeding and wintering seabirds. In this regard, determination of the nutritional state of an individual and its effects on both reproduction and survival are needed. Physiological measurements, and in particular stress hormones (e.g. corticosterone) with known correlations with food supply and survival (e.g. Romero & Wikelski 2001, Brown et al. 2005, Blas et al. 2007, Kitaysky et al. 2007, 2010, Satterthwaite et al. 2010, Will et al. 2015), provide a practical method for assessing seabird responses to climate change in data-limited systems (Vincenzi & Mangel 2014). Three of 5 studies in this Theme Section use changes in corticosterone as a 'quantifier' of changes in food abundance on annual (Orben et al. 2018), decadal (Kokubun et al. 2018), and century scales (Will et al. 2018), which allowed them to interpret the effects of warm oceanographic conditions on seabirds at their breeding and wintering grounds.

In the continental shelf regions of the southeastern Bering Sea with seasonal ice cover, shifts between warm years with early sea-ice retreat and cold years with late sea-ice retreat result in foraging conditions that favor either piscivores (warm years) or planktivores (cold years). In recent years with early sea-ice retreat, age-0 walleye pollock *Gadus chalcogrammus* have been abundant in the near-surface waters of the southeastern Bering Sea (e.g. Renner et al. 2016, Hunt et al. 2018). This availability of prey improved foraging conditions for the piscivorous black-legged kittiwakes *Rissa tridactlya* and thick-billed murres *Uria lomvia* breeding on the Pribilof Islands (Alaska, USA; Satterthwaite et al. 2012, Kokubun et al. 2018). In contrast, in these warm years, the abundance of large, lipid-rich zooplankton over the middle shelf was reduced, leading to food stress in planktivores such as the least auklet *Aethia pusilla*, also nesting at the Pribilof Islands (Benowitz-Fredericks et al. 2008, Dorresteijn et al. 2012).

A similar situation occurs in the northern Sea of Okhotsk. There, contrasting patterns in food availability to sympatrically breeding planktivorous and piscivorous seabirds of Talan Island (Russia) have been reported since the mid-1980s, with warm oceanographic conditions being detrimental to planktivorous but beneficial to piscivorous seabirds (Kitaysky & Golubova 2000). Formerly, the Talan colony has been home to a thriving population of planktivorous crested auklets *Aethia cristatella*. As winter ice coverage dramatically decreased in the Sea of

Okhotsk, so did the crested auklet population of Talan Island (Andreev et al. 2010). Whether this might be a future scenario for planktivorous seabirds breeding in other regions of the North Pacific, including the southeastern Bering Sea, demands future focused investigation.

Distributions in cold and warm years

In this Theme Section, we take advantage of an unusual opportunity to compare and contrast shifts in seabird foraging distributions in warm and cold years, as seen from both at-sea observations and from the tracking of individuals from colonies. Data were available for 4 species of seabirds: red-legged kittiwake *Rissa brevirostris*, black-legged kittiwake, common murre *Uria aalge* and thick-billed murre.

Changes in the foraging distribution of red-legged kittiwakes during the breeding season were examined in 2 studies that used different approaches and time series, yet provided similar results. Hunt et al. (2018), working with a 4-decade-long pelagic data set (Fig. 1), found that red-legged kittiwakes made a fairly minor shift from deep basin waters to shallower waters in warm years. Will et al. (2018), using stable isotopes from a 100 yr data set based on museum specimens, found that breeding red-legged kittiwakes remained foraging in the ocean basin during warm years. These results provide evidence that red-legged kittiwakes do not usually adjust their foraging habits in response to a short-term climate variability and do not take advantage of the juvenile pollock subsidies available to them in the vicinity of the breeding colony during warm years. This relative inflexibility in foraging behavior might make them vulnerable to climate warming.

In Hunt et al. (2018), the at-sea distributions of both black-legged kittiwakes and common murres were centered on the inner shelf in cold years and shifted toward the middle shelf in warm years. These shifts may be comparable to those recorded for these 2 species by Will & Kitaysky (2018), who found in colony-based studies that these 2 species shift their foraging from basin waters to shelf waters in warm years. In warm years with early sea-ice retreat, middle and outer shelf waters have abundant age-0 walleye pollock in near-surface waters (Hunt et al. 2018), and this source of prey was likely attractive to the 2 piscivorous bird species. Likewise, 3 contributions to this Theme Section found that the off-shelf-foraging thick-billed murres shifted their foraging to shelf

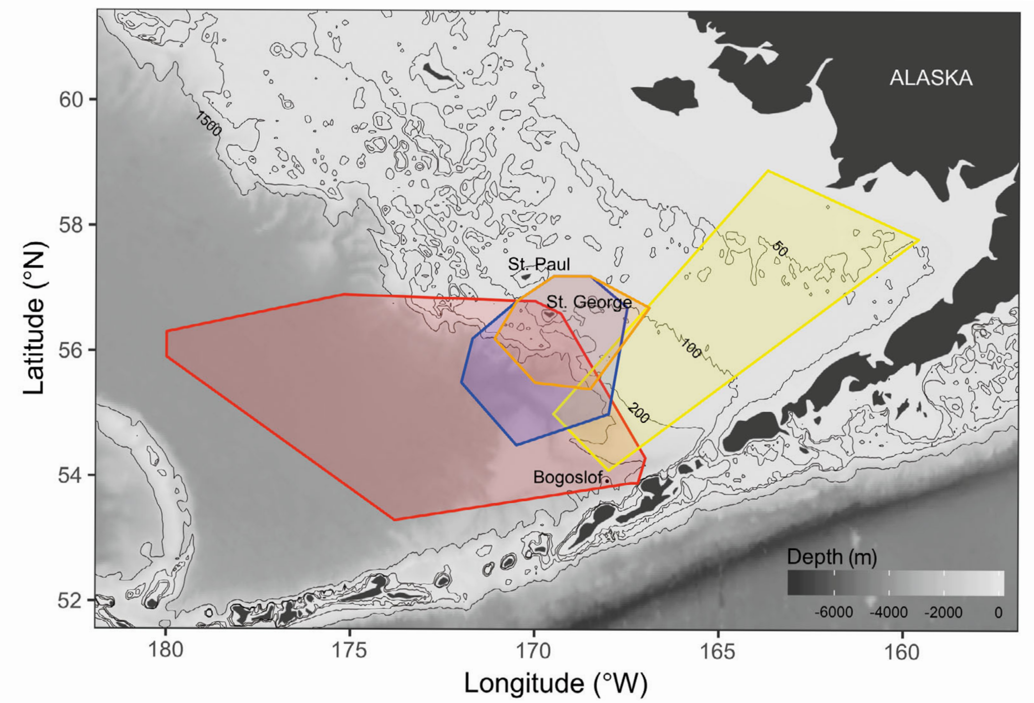

Fig. 1. Southeastern Bering Sea showing Bogoslof Island and the Pribilof Islands (St. Paul and St. George Islands). The yellow polygon approximates the area from which Hunt et al. (2018) obtained data on the pelagic distribution of seabirds. The other polygons approximate the foraging areas used by seabirds nesting on St. George Island as determined from GPS tracks: orange, thick-billed murre (Kokubun et al. 2018); blue, black-legged kittiwake (Paredes et al. 2014); red, red-legged kittiwake (Yamamoto et al. 2016; R. Orben, unpubl. data). Map courtesy of Rachael Orben

waters in warm years (Hunt et al. 2018, Kokubun et al. 2018, Will & Kitaysky 2018), again possibly because of the availability of age-0 walleye pollock there.

These apparent similarities among different studies indicate that shifts in foraging distributions of seabirds are a widespread phenomenon in the southeastern Bering Sea. The shift into the shelf regions was associated with an improvement of foraging conditions for thick-billed murres and black-legged kittiwakes breeding on the Pribilof Islands, as reflected in the improvement of their nutritional state (Satterthwaite et al. 2012, Kokubun et al. 2018). However, warm conditions have not been uniformly beneficial to piscivorous seabirds in all southeastern Bering Sea colonies. Studies of seabirds on Bogoslof Island, a large breeding colony located in the basin off the continental shelf (Fig. 1), have shown that black-legged kittiwakes and both species of murres experienced higher nutritional stress during warm years (Barger & Kitaysky 2012, Satterthwaite et al. 2012). Seabirds nesting on Bogoslof Island tend to forage close to the island, often over deep basin waters, or along the coasts of the nearby Aleutian Islands (e.g. Paredes et al. 2012, Harding et al. 2013). These areas support a different suite of forage fish than the continental shelf (Paredes et al. 2012) with its high abundance of walleye pollock, and warm upper-ocean conditions over the basin may not be favorable for the fish found there (see also Hunt et al. 2018). Thus, the shift in distribution of surface-foraging species from basin waters to the shelf edge or farther on-shelf, documented by Hunt et al. (2018), might be associated with worsening foraging conditions over the basin in warm years, at least for some species of breeding seabirds.

This Theme Section adds considerably to our understanding of the pelagic ecology of the red-legged kittiwake, an IUCN listed ‘Vulnerable’ species (BirdLife International 2017) endemic to the Bering Sea. Red-legged kittiwakes remain specialized foragers on oceanic prey during reproduction (Kokubun et al. 2015, Yamamoto et al. 2016) and associate with deep ocean-basin water areas during wintering (Orben et al. 2018). The paper by Will et al. (2018) shows that during 1913 to 2015, warmer oceanographic conditions during the late breeding and wintering seasons have been beneficial to red-legged kittiwakes breeding on St. George Island (Pribilof Islands; Fig.1). Stress and stable isotopic signatures reflect foraging conditions that red-legged kittiwakes experience during 2 specific periods: the end of reproduction (~August to September) and prior to the spring migration back to the breeding colony (~February) (Orben et al. 2018). Will et al. (2018) report that foraging conditions between these 2 seasons are highly auto-correlated, suggesting that oceanographic processes affecting food supplies of breeding red-legged kittiwakes may carry over from the late summer to the following winter. At the same time, there seems to be no connection between the late winter and the following summer (Will et al. 2018). Since birds experience less stress during warm winters and during the period of population growth (Will et al. 2018), one might expect that warm oceanographic conditions during the winter would also be associated with a high performance of red-legged kittiwakes during the subsequent breeding season. However, this is not the case, as multidecadal observations of reproductive performances in the St. George Island colonies show that the reproductive failure of red-legged kittiwakes is usually associated with the failure of birds to lay eggs during warm years with early ice retreat (Byrd et al. 2008).

Summary and future directions

This Theme Section summarizes much of our current knowledge and establishes reference points for the effects of climate on several species of seabirds breeding on the Pribilof Islands and those foraging in the southeastern Bering Sea. Warm oceanographic conditions have been beneficial to piscivorous seabirds (e.g. thick-billed murres and black-legged kittiwakes) breeding in the Pribilof colonies during the 2 recent decades and have negatively affected planktivorous seabirds (e.g. least auklets) breeding there. The large, lipid-rich copepods, that the auklets feed on, form the base of the regional food web, and if these zooplankton become scarce, the food web of the continental shelf regions of the Bering Sea may become vulnerable to collapse. Such a collapse would have dire consequences for both the seabirds and the fish stocks in the region.

To date, research in the Bering Sea has been dominated by observations from the southeastern Bering Sea shelf. The ecosystems of the shelf-slope, southwestern and ocean basin regions have been largely neglected. More information is needed from these areas. There is also a need for a compilation of existing time series in different regions of the Bering Sea shelf for a comprehensive review of the effects of climate warming on food web structure and productivity, including not only commercially valuable fish stocks, but also upper-trophic-level predators such as seabirds and marine mammals. We need to understand the proximate and ultimate mechanisms by which seabirds are adapting to warming conditions if we are to interpret the signals from seabirds and to relate these signals to the responses of zooplankton and fish stocks.

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Contribution to the Theme Section 'Seabird responses to a changing Bering Sea'

Inter-annual climate variability affects foraging behavior and nutritional state of thick-billed murres breeding in the southeastern Bering Sea

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ABSTRACT: Warm oceanographic conditions of the continental shelf regions in the southeastern Bering Sea are associated with drastic increases in the abundance of juvenile walleye pollock *Gadus chalcogrammus* at shallow depths. We hypothesized that thick-billed murres *Uria lomvia* would benefit from these warm conditions by taking advantage of such an abundant prey resource available near their breeding colonies. We compiled a large dataset on the foraging behavior and nutritional state of murres breeding on St. George Island between 2003 and 2015. Murres foraged mostly on the continental shelf in warm years, but foraged in both on-shelf and off-shelf habitats in cold years. Shifts in foraging locations were associated with changes in diving depths. Nighttime foraging and daily diving effort increased during cold years, suggesting murres had to work more to obtain food under cold compared to warm conditions. Chick diets shifted from squid and benthic fishes in cold years to juvenile pollock in warm years. Foraging trip duration and reproductive success of birds were not affected by shifting oceanographic conditions, suggesting that murres behaviorally mediated the effects of inter-annual climate variability on their reproduction. However, this 'behavioral buffering' had associated costs, reflected in higher corticosterone concentrations in the blood of murres in cold compared to warm years, indicating that breeding birds incurred higher levels of nutritional stress under cold conditions. Our multiyear integrative study provides support that warmer conditions on the continental shelf might benefit piscivorous seabirds due to an increase in the availability of juvenile walleye pollock in the southeastern Bering Sea.

KEY WORDS: Seabirds · Behavioral plasticity · Diving · GPS tracking · Nutritional stress · Corticosterone

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INTRODUCTION

Climate impacts on seabirds have been documented worldwide (reviewed in Sydeman et al. 2012, Jenouvrier 2013). The effect of climate change on seabirds can be positive, negative, or neutral, and responses may be non-linear, often involving complex species- and/or region- specific ecological processes (Sydeman et al. 2012). Seabird foraging behavior is considered to be the most sensitive parameter to changes in food availability, and seabirds may buffer the effects of environmental changes by changing diet and at-sea foraging behavior (e.g. Cairns 1987, Piatt et al. 2007, Grémillet et al. 2012). Long-term variability in seabird foraging behavior could provide vital information on the ecological processes affecting them under changing ocean conditions. However, only a few studies have reported foraging responses of seabirds in relation to long-term inter-annual changes in ocean climate conditions (Weimerskirch et al. 2012, Bost et al. 2015).

The southeastern Bering Sea is one of the most productive regions in the world (Aydin & Mueter 2007), providing important foraging habitat for a variety of marine predators, including seabirds. In recent decades, this region has experienced a series of cold and warm regimes which have affected the biomass and distribution of plankton and nekton communities (Coyle et al. 2011, Hunt et al. 2011, Eisner et al. 2014). One of the dominant environmental features that has a profound influence on the ecological conditions of the continental shelf of the southeastern Bering Sea is the bottom temperature during summer (Wyllie-Echeverria & Wooster 1998). Extensive winter sea-ice cover usually contributes to the formation and extension of cold bottom water, the 'cold pool' (temperature < 2°C), over the continental shelf in the following summer (Stabeno et al. 2012). In cold summers, the distribution of fish species that are associated with cold bottom temperatures such as capelin *Mallotus villosus* or Arctic cod *Boreogadus saida* shift southward (Brodeur et al. 1999, Mueter & Litzow 2008, Hollowed et al. 2012). On the other hand, in warm summers, the distribution of warm-water fishes such as age-0 walleye pollock *Gadus chalcogrammus* shifts northward over the continental shelf (Wyllie-Echeverria & Wooster 1998, Brodeur et al. 1999, Siddon et al. 2013). Walleye pollock are an important prey for higher trophic level predators in the Bering Sea (Sinclair et al. 2008). Recent studies have shown that age-0 pollock have 51 times higher near-surface densities when sea ice retreats early (typically warm) compared to years when sea ice retreats late (typically cold years) (Renner et al. 2016, Hunt et al. 2018, this Theme Section). Shifting temperature regimes also affect the quality of prey available to seabirds, as age-0 pollock are 33% higher in energy density during cold years than in warm years (Heintz et al. 2013). Whether such a high abundance of lower quality age-0 pollock available on the shelf in warm years offers favorable foraging conditions for piscivorous seabirds breeding in the region is not well known (but see Satterthwaite et al. 2012).

Thick-billed murres *Uria lomvia* (hereafter referred to as 'murres') are pursuit diving seabirds abundant in the Bering Sea, with a large breeding colony located at St. George Island, Pribilof Islands. Murres might be sensitive to changes in the availability of forage fish near their breeding colonies due to high energetic costs of flight (Elliott et al. 2013). Changes in prey species delivered by parent murres to feed their chicks reflect changes in the abundance of forage fish and invertebrates near the breeding colonies (Gaston et al. 2003). On the Pribilof Islands, pollock and squid have been recorded as the major prey species in chick diets, though the relationship between diet composition and environmental parameters is unclear (Renner et al. 2012). Previous studies on foraging locations showed that during cold years, murres fed in both the nearby on-shelf and distant off-shelf (located >30 km away from St. George Island) habitats, and squid appeared to dominate their diet (Harding et al. 2013, Paredes et al. 2015). It is currently unknown if during warm years, murres would concentrate their foraging efforts on the abundant age-0 pollock in the continental shelf region near the breeding colony. Alternatively, since age-0 pollock are relatively low in energy content in warm years (Heintz et al. 2013), murres may continue feeding on higher quality prey at the distant off-shelf habitats as they do during cold years (Harding et al. 2013, Paredes et al. 2015). Therefore, a study on inter-annual changes in foraging locations, diet, and associated changes in diving behavior is needed to examine how murres respond to oscillating warm and cold oceanographic conditions in the southeastern Bering Sea.

Changes in foraging behavior and diet may result in changes in energy expenditures (Kitaysky et al. 2000, Welcker et al. 2015), which in turn may affect the homeostasis, reproductive success or survival of parent birds. In seabirds, concentrations of the adrenocortical hormone corticosterone in blood plasma have been shown to increase with a decline in food availability (Kitaysky et al. 1999, Riechert et al. 2014, Barrett et al. 2015, reviewed in Sorenson et al. 2017) and are negatively correlated with reproductive performance (Kitaysky et al. 2007, 2010, Satterthwaite et al. 2012) and adult survival (Kitaysky et al. 2007, 2010, Satterthwaite et al. 2010). We used this measure to determine whether changes in foraging behavior are coming at a cost to adult seabirds, and examined whether warm or cold ocean conditions impose different levels of nutritional stress on thick-billed murres. Previous long-term studies have suggested that warming conditions might be beneficial (reflected in low levels of nutritional stress as measured by baseline corticosterone) for black-legged kittiwakes *Rissa tridactyla*, surface-feeding piscivorous seabirds that also breed on the Pribilof Islands (Satterthwaite et al. 2012). Whether this pattern might also apply to thick-billed murres (Benowitz-Fredericks et al. 2008, Yamamoto et al. 2016), which have access to prey at depth, has not yet been examined in the context of long-term inter-annual variability in oceanographic conditions.

In this study, we examined the foraging and physiological responses of thick-billed murres to ocean climate conditions in the southeastern Bering Sea. We hypothesized that (1) if pollock is abundant on the continental shelf during warm years, murres will concentrate their foraging efforts on this region, and their diet and diving behavior will reflect associated changes compared to cold years, and (2) if warming conditions are beneficial for murres, lower nutritional stress will be expected given the favorable conditions both in abundance and proximity of pollock to the breeding colony. We tested these hypotheses by compiling data on at-sea foraging behavior and chick diet collected across 9 yr and baseline corticosterone across 10 yr (2003 to 2015), and by examining their relationships to inter-annual variability in summer bottom temperature.

MATERIALS AND METHODS

Study site

The field study was conducted on St. George Island, Pribilof Islands, a part of the Alaska Maritime National Wildlife Refuge, during late July to early August 2003 to 2015. The study sites on the island varied between years: we studied on both the northern (Village Cove: 56° 36′ N, 169° 33′ W) and southern (Zapadni Bay: 56° 35′ N, 169° 41′ W and Red Bluffs: 56° 33′ N, 169° 40′ W) coasts of the island in 2008, 2009, and 2010, and only on the northern coast (High Bluffs: 56° 36′ N, 169° 39′ W) in other years.

Data availability

The type of available data on behavioral and physiological parameters varied between years (detailed in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m593p195_supp.pdf). We obtained data on foraging locations with GPS data loggers for 6 yr during 2008 to 2015, diving behavior with time–depth recorders (TDRs) or accelerometers for 9 yr during 2004 to 2015, and chick diet for 9 yr during 2004 to 2015 (detailed in Table S3). We obtained blood samples and measured baseline corticosterone levels of chick-rearing birds for 10 yr during 2003 to 2015 (from birds with and without data loggers; see Table S4). Our dataset included previously reported data on foraging locations (Paredes et al. 2015, Yamamoto et al. 2016), diving behavior and chick diet (Takahashi et al. 2008, Ito et al. 2010, Kokubun et al. 2010b, 2016, Paredes et al. 2015, Young et al. 2015), and baseline corticosterone (Benowitz-Fredericks et al. 2008, Paredes et al. 2015, Yamamoto et al. 2016, Young et al. 2016).

Data logger deployment and recovery

We captured birds attending their chicks with a 5 to 8 m noose pole. We deployed data loggers on the back (in case of GPS and some accelerometers), on the belly (most accelerometers and TDRs), or on the leg with a plastic ring (TDRs with GPS loggers). The loggers that were attached to the back or belly feathers were secured with strips of Tesa® tape and cyanoacrylate glue (Loctite® 401). Birds were handled for less than 20 min. The birds were recaptured between 1 to 6 d after the logger deployment (overall recovery rate: 73.5%; Table S2); the loggers were then removed and the data downloaded to a computer. We sampled blood to determine sex (following Griffiths et al. 1998) and measure baseline plasma corticosterone levels (see below).

Foraging location and distance

We used several types of GPS loggers to obtain data on foraging locations: GiPSy2, GiPSy4 (TechnoSmart), or CatTraQ (Catnip Technologies; Table S2). The loggers were set to record locations every 1 to 2 s, 1 min (for 2008 to 2010), or at the rate of 0.5 to 5 fixes min^{-1} (for 2013 to 2015). GPS positions were resampled every 1 min if the data were obtained more frequently, and the last location just prior to a dive was used as the location of the dive. The GPS loggers sometimes failed positioning continuously. In these cases, the locations of dives were interpolated linearly using nearest neighbor locations associated with the times when the dives occurred (Kokubun et al. 2010a). If GPS loggers failed positioning continuously for more than 4 h, we regarded the dive locations as unknown during these periods. We calculated the maximum distance from the colony (straight line distance between the nest site and most distant trip location) for each trip. We also recorded the latitude of the most distant GPS locations from the colony ('trip latitude'), and examined annual differences in trip latitude.

Foraging trip duration

We calculated foraging trip durations of birds carrying accelerometers, TDRs, or GPS loggers. For accelerometer birds, acceleration data were filtered to visualize the body angle and body movement, and then were used to determine the periods of colony attendance and foraging trips (see Takahashi et al. 2008). For TDR birds, temperature records were used to determine departure from and arrival to the colony (Ito et al. 2010). For GPS birds, the start of a foraging trip was defined when a bird was 500 m from the nest, and was often supported by temperature readings from the concurrently attached TDRs. We categorized foraging trips that crossed local midnight as overnight foraging trips, and all other trips that did not cross local midnight as day foraging trips (Harding et al. 2013, Paredes et al. 2015).

Diving behavior

We used several types of accelerometers and TDRs to obtain data on diving behavior: UME-D2GT, ORI-D3GT (Little Leonardo), Axy-Depth (TechnoSmart), Cefas-G5 (CEFAS Technology), and LAT1500, LAT2500 (Lotek Wireless) (Table S2). The sampling interval and depth threshold to start recording varied among study years (Table S2). For the entire dataset, we considered dives only when depth readings reached deeper than 5 m. First, this reduces noise due to bird's activities at the sea surface, such as bathing or avoiding waves. Second, only diving depths deeper than 5 m were recorded for 12 birds in 2008 and 2009 (Table S2). The statistical results, and thus our conclusion, remained the same when we removed these 12 birds and used the depth readings deeper than 1 m.

We categorized dives into day or night dives based on local sunset (23:00 to 23:40 h) and sunrise times (07:10 to 07:50 h) calculated for each day of the study period, available from the Hydrographic and Oceanographic Department of Japan Coast Guard (www1.kaiho.mlit.go.jp/KOHO/automail/sun_form3.html). We then calculated the proportion of night dives to total number of dives for each bird. We also calculated mean dive depth during nighttime and during the midday period (defined as a 6 h period spanning local midday), and total dive time (sum of dive durations) per day during the deployment periods.

Chick diet

Chick diet was recorded each year from the visual observations of prey items carried by adults to their chicks. Visual observations were made colony-wide, not only for adults with data loggers. Prey items were visually identified to the lowest taxonomic level possible during the observation or later from photographs. We calculated the frequency of occurrence for each taxon of the observed prey items.

Blood sampling and corticosterone assay

To assess the physiological condition of the birds, blood samples were collected and baseline corticosterone (CORT) levels were measured from birds with and without data loggers (see Table S4). Attachment of data loggers did not affect baseline corticosterone levels in a previous study (Takahashi et al. 2008). In cases where we had CORT data for both initial capture and recapture from the same bird, we used the average CORT value. Blood collection and handling procedures followed those described in Kitaysky et al. (1999) and Benowitz-Fredericks et al. (2008). In brief, all samples for baseline CORT were collected within 3 min of capture. Plasma samples were frozen at −20°C and transported to the University of Alaska Fairbanks for analysis. Plasma CORT levels were measured in duplicate for each sample after extraction with redistilled dichloromethane using radioimmunoassay (for detailed methods see Kitaysky et al. 1999). Before extraction, tritiated CORT (2000 counts per minute [cpm]) was added to each plasma sample to control for loss of CORT during extraction. Recovery values ranged from 80 to 99% and were used to adjust assayed concentrations of CORT. Coefficient of variation (CV) for inter- and intra-assay were less than 4 and 2%, respectively.

Environmental data and GIS analyses

The bathymetry where the dives occurred was investigated using ArcGIS® v.10.3 (ESRI) with digital bathymetric data (Etopo 1, provided by NOAA National Centers for Environmental Information). Areas with bottom depth shallower than 200 m were defined as on-shelf (Paredes et al. 2015), and other areas (bottom depth > 200 m) were defined as off-shelf. We categorized each dive into on- or off-shelf dives based on the bathymetry of the dive location. We categorized foraging trips into on- or off-shelf trips based on the location of the dive that was most distant from the colony in the focal foraging trip.

Bottom temperature data from the Eastern Bering Sea Continental Shelf Survey of NOAA Alaska Fisheries Science Center (www.afsc.noaa.gov/RACE/groundfish/survey_data/ebswater.htm) were used to assess the summer oceanographic conditions around Pribilof Islands for each year. The average summer bottom temperature within a 150 km radius of the Pribilof Islands trawl survey was calculated for each year. We also examined the southern extent of the cold pool (where bottom temperature <2°C), by spatially interpolating the bottom temperature data by the kriging function of ArcGIS®. Based on bottom temperature (see Table S1), we considered 2003 to 2005 and 2014 to 2015 as warm years, 2006 as an intermediate year, and 2007 to 2013 as cold years — which are in accordance with warm versus cold classifications based on the timing of winter ice retreat (Ice Retreat Index in Zador 2015), or a combination of several oceanographic parameters (Will & Kitaysky 2018, this Theme Section).

Statistics

We examined the effect of summer bottom temperature on foraging parameters and nutritional stress levels with linear mixed models (LMM). For the models of foraging trip parameters, where multiple values were obtained per bird, we set annual mean summer bottom temperature as a continuous fixed factor, sex and trip type (overnight or day trips) as categorical fixed factors, and year and bird ID as random factors. For the models of dive depth, where multiple values were obtained per bird, we set annual mean summer bottom temperature as a continuous fixed factor, sex as a categorical fixed factor, and year and bird ID as random factors. For the models of daily total dive time, proportion of night dives, and baseline corticosterone levels, where a single value was obtained for each individual, we set annual mean summer bottom temperature as a continuous fixed factor, sex as a categorical fixed factor, and year as a random factor. We used the 'lme4' and 'multcomp' packages in R v.23.1.1 software (R Core Team 2014). We examined the effect of summer bottom temperature on the frequency of occurrence of prey items in chick diet by calculating Pearson correlation coefficients. Data are presented as mean values ± SD, unless stated otherwise.

RESULTS

Foraging location and distance

Data on foraging locations were available for a total of 67 trips from 54 birds deployed with GPS over 4 cold (2008, 2009, 2010, 2013) and 2 warm (2014, 2015) years. Murres foraged on the continental shelf regions near the breeding colony during day foraging trips in both cold and warm years (Fig. 1A,B). In contrast, murres tended to forage to the south of the colony, in both on-shelf and off-shelf habitats, during overnight foraging trips in cold years (Fig. 1C, Table S1). Murres tended to forage to the north of the colony, in on-shelf regions, during overnight foraging trips in warm years (Fig. 1D, Table S1). Murres appeared to 'avoid' the cold bottom water (cold pool) located to the north of the colony in cold years, because a relatively low proportion of dives occurred in the regions of bottom temperature <2°C (Fig. 1A,C, Table S1).

The latitudinal positions of the foraging trips (at the most distant location from the colony) were positively related to summer bottom temperature for overnight foraging trips (Fig. 2A, Table 1). Day foraging trips had smaller foraging ranges (20.5 ± 11.2 km, n = 16 trips) than overnight foraging trips (67.3 ± 44.6 km, n = 41 trips). Foraging range did not relate to summer bottom temperature, after controlling for the effects of sex and trip types. (Table 1, Fig. 2B).

Foraging trip duration

Data on foraging trip durations were available for a total of 434 trips from 156 birds deployed with accelerometers, TDRs, or GPS over 9 yr. Foraging trip durations did not differ significantly among the type of devices where data on 2 types of devices were available (TDR vs. accelerometers in 2006 to 2007 and GPS vs. accelerometers in 2013 to 2015; LMM: effect of device type, estimate = 2.17 ± 2.57 and 0.26

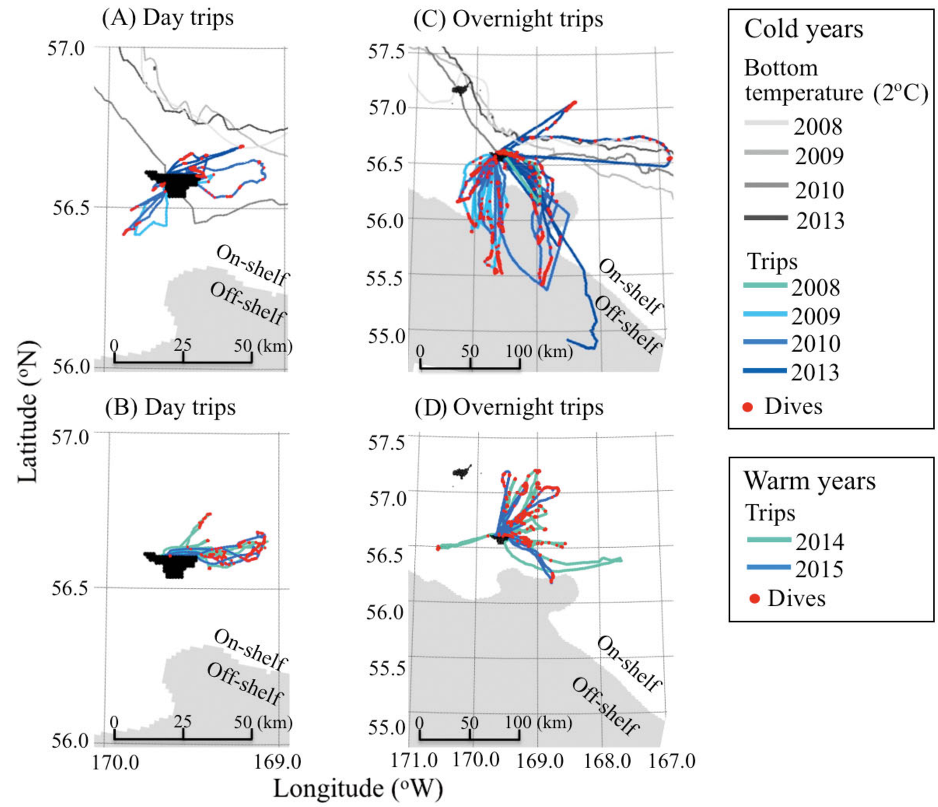

Fig. 1. Foraging tracks of thick-billed murres from St. George Island during (A,B) day trips and (C,D) overnight trips in (A,C) cold and (B,D) warm years. Tracks from different years are shown in different colors. For cold years, the southernmost extent of the cold pool (where bottom temperature = 2°C) is also shown for each year

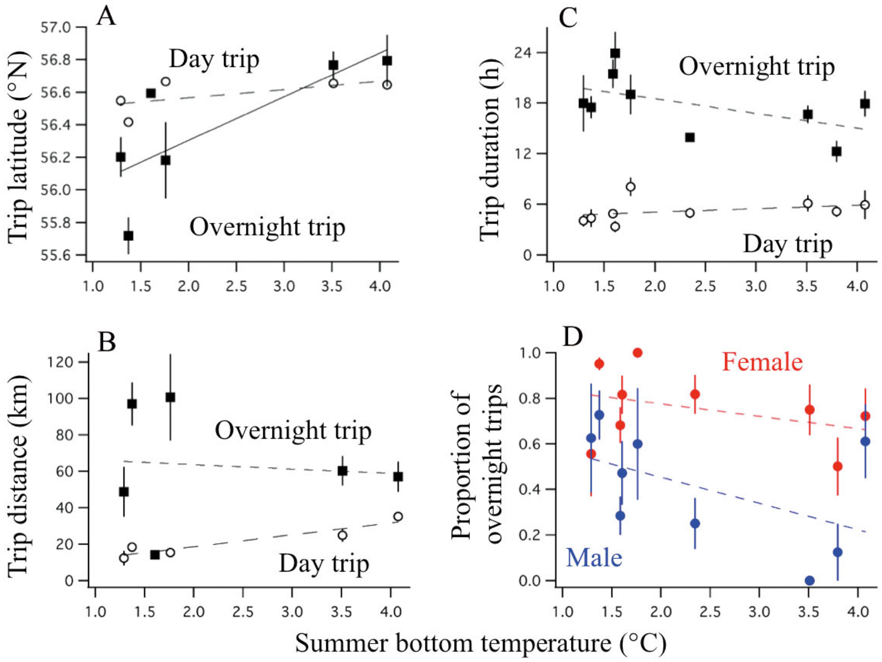

Fig. 2. Relationships between foraging trip parameters of thick-billed murres and summer bottom temperature. (A) Latitude of the most distant location from the colony, (B) maximum distance reached from the colony, and (C) foraging trip durations. Day and overnight foraging trips (trips ended before and after local midnight, respectively) are shown separately (open circles and closed squares). (D) Proportion of overnight trips of all trips in males (blue) and females (red). Annual mean and SE values are shown with a simple regression line. Solid lines: statistically significant relationships; dashed lines: non-significant relationships. Statistical analyses were conducted with linear mixed effect models (see Table 1)

± 1.88, p = 0.49 and 0.99, respectively, with year and bird ID included as random factors). Therefore, we pooled the data on trip durations from accelerometers, TDRs, and GPS birds. Foraging trip durations were consistently shorter during the day than overnight foraging trips (Fig. 2C), and were shorter for females than males (Table 1). Trip duration did not relate to the summer bottom temperature, after controlling for the effects of sex and trip types (Table 1, Fig. 2C). Proportion of overnight foraging

Table 1. Effect of bottom temperature on foraging trip parameters of thick-billed murres. Statistical significance: $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Linear mixed models	Intercept	Slope coefficient	SE of slope coefficient	Sex effects (on males)	SE of sex effects	Effect of trip type (on overnight trips)	SE of trip type effects	p-value		
								Slope coefficient	Sex effects	Trip type effects
Trip latitude ~ BottomTemp + Sex + TripType + (1|BirdID) + (1|Year)	56.21	0.21	0.06	−0.14	0.13	−0.26	0.12	0.002**	0.676	0.087
Trip distance ~ BottomTemp + Sex + TripType + (1|BirdID) + (1|Year)	35.08	−2.82	9.06	−16.96	12.93	42.82	12.59	0.992	0.499	0.002**
Foraging trip duration ~ BottomTemp + Sex + TripType + (1|BirdID) + (1|Year)	3.24	−0.62	1.17	3.97	1.08	15.37	0.93	0.949	<0.001***	<0.001***
Proportion of overnight foraging trip ~ BottomTemp + Sex + (1|Year)	0.89	−0.06	0.05	−0.30	0.06	–	–	0.51	<0.001***	–

trips in all trips were higher for females than males (Table 1), but did not relate to summer bottom temperature (Table 1, Fig. 2D).

Diving behavior

Data on diving behavior were available for a total of 156 birds deployed with accelerometer, GPS-TDRs or TDRs over the 9 yr (Table S1). Maximum dive depths showed clear diel patterns in all years, being shallower at night and deeper during the day as previously shown (Takahashi et al. 2008, Paredes et al. 2015, Young et al. 2015). During nighttime (time between sunset and sunrise), maximum dive depths were deeper in years of higher summer bottom temperature (Table 2, Fig. 3A). During the middle of the day (6 h period spanning local midday), maximum dive depths were shallower in years when higher proportions of pollock occurred in chick diets (Table 2, Fig. 3B; see below for chick diet results), and were not related to summer bottom temperatures (Table 2). Total time spent diving (≥5 m depth) per day was higher in years of lower summer bottom temperature, suggesting that total diving effort of murres increased in cold years (Table 2, Fig. 3C). The proportion of nighttime dives differed between males and females, and was lower in years of higher summer bottom temperature for males, but did not change for females (Table 2, Fig. 3D).

Chick diet

A total of 621 chick meals delivered by parents were observed over the 9 yr. Juvenile walleye pollock, Pacific sandlance, benthic fishes (including prickleback, sculpin, flatfish, and others listed in Table S3), and cephalopods were the major prey items during 2004 to 2015 (Table S3). Frequency of occurrence of cephalopods and benthic fishes in chick meals correlated negatively with summer bottom temperature (Pearson's $r = -0.849$, $p = 0.004$, and $r = -0.843$, $p = 0.004$, respectively, $n = 9$ yr), whereas that of walleye pollock correlated positively with summer bottom temperature ($r = 0.759$, $p = 0.018$; Fig. 4).

Baseline corticosterone

Data on baseline corticosterone samples were available for a total of 509 birds for 10 yr during 2003

Table 2. Effect of bottom temperature and diet on diving behaviors of thick-billed murres. Statistical significance: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$

Linear mixed models	Intercept	Slope coefficient	SE of slope coefficient	Sex effects (on males)	SE of sex effects	p-value Slope coefficient	p-value Sex effects	Interaction term
Nighttime Depth ~ BottomTemp + Sex + (1|BirdID) + (1|Year)	12.74	4.24	0.96	−1.91	1.67	<0.001***	0.489	Not significant
Midday Depth ~ BottomTemp + Sex + (1|BirdID) + (1|Year)	61.11	−4.63	3.08	−4.30	3.31	0.285	0.397	Not significant
Midday Depth ~ Proportion of Pollock in diet + Sex + (1|BirdID) + (1|Year)	57.58	−35.95	14.68	−3.87	3.31	0.039*	0.509	Not significant
Daily dive time ~ BottomTemp + Sex + (1|Year)	3.19	−0.30	0.12	−0.11	0.17	0.037*	0.815	Not significant
Proportion of night dives ~ BottomTemp + Sex + (1|Year)	0.65	−0.07	0.035	−0.19	0.04	0.095	<0.001***	Marginally non-significant (p = 0.077)
Proportion of night dives~ BottomTemp + (1|Year) (for male only)	0.57	−0.12	0.047	–	–	0.012*	–	
Proportion of night dives ~ Bottom Temp + (1|Year) (for female only)	0.60	−0.04	0.033	–	–	0.266	–	

to 2015 (Table S4). Baseline corticosterone concentrations were lower in years of higher summer bottom temperature (Table 3, Fig. 5A). Data on both baseline corticosterone and diving behavior were available for 53 females and 34 males from 7 yr (Table S4). The proportion of nighttime diving increased in birds with higher baseline corticosterone levels (Table 3, Fig. 5B), with a statistically significant increase in males ($p < 0.001$) and a marginal increase in females ($p = 0.0581$).

DISCUSSION

We examined foraging and physiological responses of breeding thick-billed murres to inter-annual climate variability in the continental shelf of the Bering Sea between 2003 and 2015. The southeastern Bering Sea shelf region experienced a prolonged 'warm' regime between 2000 and 2005, then a prolonged 'cold' regime between 2007 and 2013, and has returned to a 'warm' regime since

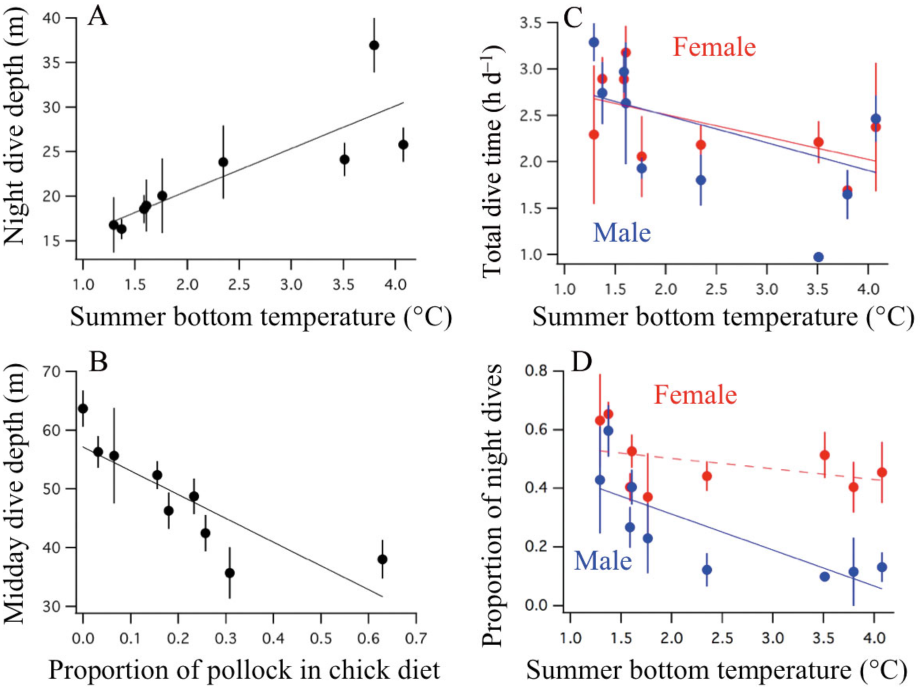

Fig. 3. Responses of diving parameters of thick-billed murres to (A,C,D) summer bottom temperature or to (B) annual proportion of pollock in chick diet. Male and female values are shown separately for (C) total dive time and (D) proportion of night dives. Grand mean and SE for the mean values of individual birds are shown with a simple regression line. Solid lines: statistically significant relationships; dashed lines: non-significant relationships. Statistical analyses were conducted with linear mixed effect models (see Table 2)

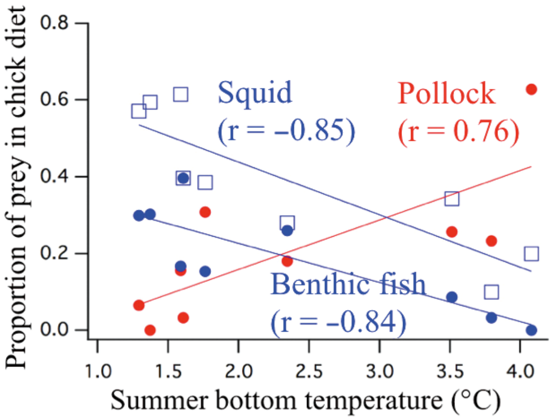

Fig. 4. Proportion of prey (frequency of occurrence) in thick-billed murre chick diets in relation to annual mean summer bottom temperature of the southeastern Bering Sea. Pearson correlation coefficient values are shown for each prey category. Statistical significance of regression lines as in Fig. 3

2014 (Zador 2015). Therefore, our dataset covered a wide range of oceanographic conditions. Our results were consistent with the hypothesis that warmer conditions increase the availability of juvenile walleye pollock on the shelf and have been beneficial for piscivorous seabirds breeding in the continental shelf regions of the southeastern Bering Sea.

Foraging responses in warm and cold years

In warm years, parent murres concentrated their foraging on the continental shelf during both day and overnight foraging trips, and delivered juvenile walleye pollock to their chicks more frequently (Figs. 1 & 4). In warm years, which were usually associated with early ice retreat, age-0 pollock were distributed over the continental shelf and had 51 times higher near-surface density than in cold years (Renner et al. 2016, Hunt et al. 2017). We did not have information on the age of pollock delivered to chicks, but the pollock size was estimated in 2006 and 2007 relative to adult bill size (Ito 2011). The size of pollock ranged from 80 to 130 mm, with the length of 100 to 110 mm observed most frequently (Ito 2011), which overlaps with the common sizes of age-0 fish (Brodeur & Wilson 1996). Parent murres appeared to prey on

Table 3. Effect of bottom temperature on baseline corticosterone values, and on the effect of baseline corticosterone on proportion of nighttime dives in thick-billed murres. Statistical significance: $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Linear mixed models	Intercept	Slope coefficient	SE of slope coefficient	Sex effects (on males)	SE of sex effects	p-value		Interaction term
						Slope coefficient	Sex effects	
LogCORT ~ BottomTemp + (1|Year)	0.85	−0.09	0.03	–	–	0.010*	–	
Proportion of night dives ~ logCORT+ Sex+ (1|Year)	0.24	0.41	0.08	−0.16	0.05	<0.001***	0.002**	Marginally non-significant (p = 0.074)
Proportion of night dives ~ logCORT+ (1|Year) (for male only)	−0.03	0.59	0.10	–	–	<0.001***	–	
Proportion of night dives ~ logCORT+ (1|Year) (for female only)	0.38	0.23	0.11	–	–	0.058	–	

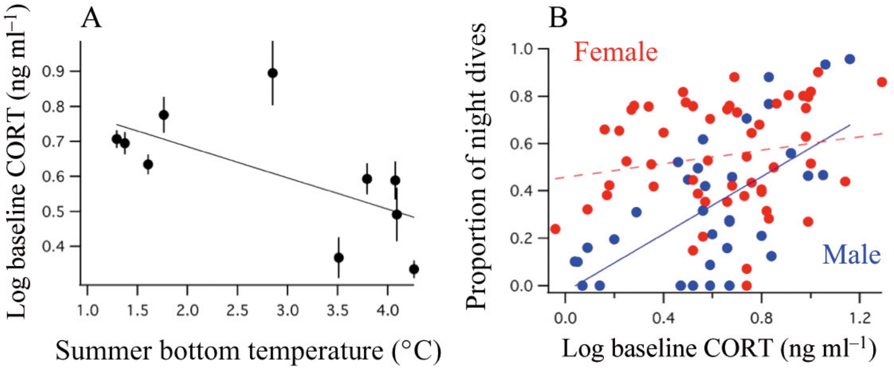

Fig. 5. (A) Relationship between thick-billed murre baseline corticosterone (CORT) levels and summer bottom temperature over 10 yr during 2003 to 2015. Annual mean and SE values are shown with a simple regression line. (B) Relationship between proportion of night dives and baseline CORT in males (blue: n = 34 birds) and females (red: n = 53 birds). Data points indicate individual birds. See Table 3 for linear mixed model statistics. Statistical significance of regression lines as in Fig. 3

juvenile pollock, not only for chick provisioning but also for self-feeding during warm years. Video records from bird-borne cameras showed that murres frequently fed on juvenile pollock in 2014, a warm year (Sato et al. 2015). Otoliths of juvenile pollock were also found in samples of stomach lavage (Ito 2011, Paredes et al. 2015). In 2004, another warm year, murres concentrated their dives at depths just below the thermocline (20 to 40 m depths; Takahashi et al. 2008), where schools of juvenile pollock have been observed (Brodeur 1998). We found that murres dove shallower during midday in years with a high proportion of juvenile pollock in chick diets, suggesting they relied on this abundant prey aggregated at shallow depths over the continental shelf in warm years. Also, because murres spent less time diving per day (Fig. 3C) and showed lower baseline corticosterone concentrations in warm years (Fig. 5A), we suggest that feeding on nearby juvenile pollock in warm years is beneficial for parent murres. Although age-0 pollock were reported to have lower energy density in warm years than cold years (Heintz et al. 2013), we presume that the benefit of higher abundance and accessibility of age-0 pollock outweighed the disadvantage of lower prey quality for parent murres in warm years.

In cold years, during overnight trips, murres tended to target off-shelf regions south of St. George Island, and dove in both on-shelf and off-shelf habitats (Fig. 1). In on-shelf habitats, they made relatively fewer dives in the area of the cold pool (bottom temperature <2°C) (Fig. 1C). Male murres increased the proportion of night dives, and nighttime dives were shallower for both sexes in cold years (Table 1, Fig. 3A,D). In cold years, the biomass of euphausiids was elevated in shelf break regions (175 to 200 m water depth; Hunt et al. 2017). Euphausiids were not found in chick diets, but were found in the stomach contents of adults (Ito 2011, Paredes et al. 2015). Our results show that squid dominated chick diets in cold years (Fig. 4), and a previous study reported that squid beaks occurred in >60% of stomach contents of adult birds from St. George Island in cold years (Paredes et al. 2015). These results suggest that murres feed on prey such as euphausiids or squids which might be more readily available in shelf break and off-shelf regions at night due to their diel vertical migration behavior and/or advection to ocean surface by upwelling (Schabetsberger et al. 2000, Nishikawa et al. 2001). In contrast to overnight trips, murres remained in the on-shelf habitat during day trips (Fig. 1). They tended to dive deeper during the day in cold years, and delivered a higher proportion of benthic fish and squid to their offspring. Harding et al. (2013) and Paredes et al. (2015) suggested that prey species available in the off-shelf ocean basin habitat might be of higher quality than those available on the shelf in cold years, and proximity to off-shelf habitat might buffer against food shortages on the continental shelf (Paredes et al. 2012). Our nutritional stress results suggest that on-shelf foraging on juvenile pollock in warm years was more beneficial than combined on-shelf and off-shelf foraging for other prey in cold years.

Constraints on foraging responses

Central place foraging from a breeding colony might constrain the ability of parent murres to change the duration and distance of their foraging trips. This appears to be the case for day trips, as murres kept foraging on the shelf and had similar foraging trip durations in warm and cold years, presumably to maintain chick-provisioning rates. However, in cold years, benthic fishes made up a greater proportion of chick diets (Fig. 4), which were presumably obtained during deep daytime dives reaching to or near the sea floor. Paredes et al. (2015) reported that flatfish were offered by parents, but often chicks were not able to swallow these prey. Thus, murres might need to rely on suboptimal prey for chick-provisioning in cold years, due to a restricted foraging range of day trips (20 km from breeding colony, on average). Sex differences in reproductive duties might also constrain the foraging of male murres. For murres breeding at a relatively low-latitudes like St. George Island, chick fledging occurs at night and male parents accompany their fledglings. Therefore, males usually attend nests at night and forage during the day (Paredes et al. 2008, but see also Elliott et al. 2010). This appeared to be the case in our study, based on the lower proportion of overnight foraging trips and night dives by males compared to females (Figs. 2D & 3D). In cold years, however, males increased nighttime foraging, presumably because they experienced difficult self-feeding conditions (as suggested by elevated corticosterone levels) during the daytime (Fig. 5B). A strong positive relationship between corticosterone levels and the proportion of nighttime diving supports this argument. We suggest that sexual differences in reproductive duties might affect an individual's response to inter-annual changes in foraging conditions.

Possible confounding factors

We need to consider potential confounding factors when interpreting our results. First, the type and size of data loggers used were different among study years. Nevertheless, we used accelerometers and TDRs during 2006 and 2007, and accelerometers and GPS loggers from 2013 to 2015, and found that foraging trip durations did not differ among device types (see 'Results'). We thus were able to pool the foraging trip durations from 2 types of devices. Second, the attachment of data loggers might influence the behavior of the birds. Ito (2011) and Paredes et al. (2015) compared the foraging trip durations and chick feeding rates of 'loggered' birds with those of control birds from 2006 to 2009. Foraging trip durations and chick feeding rates of birds carrying loggers were longer and lower than those of control birds in 1 of 4 years (in 2006 for trip duration and in 2009 for chick feeding rates). Although we cannot dismiss the effect of data logger attachment, we believe that the behavior of the birds was not radically modified and our between-year comparisons of foraging behavior of birds with data loggers were reasonably representative. Third, our deployment sites on the island were not always the same between different years, which might confound annual changes in the foraging locations (e.g. Soanes et al. 2014). We used study sites at the northern side of the island in most years, but also used sites on the southern side of the colony in 2009, one of the cold years. However, our results on the shift of foraging locations toward off-shelf regions in cold years were consistent, even if we restricted our dataset to foraging tracks from only the northern side of the island (see Fig. S1 in the Supplement).

Implications

Our results on the shifts of foraging locations of murres toward the continental shelf in warm years and toward shelf break and off-shelf habitats in cold years are consistent with the results of other studies comparing the distribution and diet of seabirds in the southeastern Bering Sea. Renner et al. (2016) and Hunt et al. (2017) reported that thick-billed murres were observed in shallower waters in early-ice-retreat (typically warm) compared to late-ice-retreat (typically cold) years. Stable isotope analysis of blood tissues suggested that thick-billed murres relied more on shelf-based prey in warm years than in cold years (Will & Kitaysky 2017). Thus, our results on the foraging responses of thick-billed murres to ocean conditions appear to be robust, and may apply to other piscivorous seabirds such as black-legged kittiwakes and common murres *Uria aalge* (Paredes et al. 2014, Will & Kitaysky 2017).

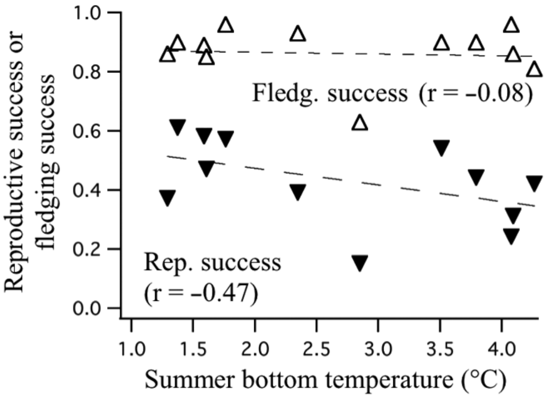

Fig. 6. Reproductive success (▼) and fledging success (△) of thick-billed murres at St. George Island in relation to summer bottom temperature between 2003 and 2015. Reproductive success (number of chicks fledged/number of nests with eggs) and fledging success (number of chicks fledged/number of nests with chicks hatched) were based on biological monitoring study by US Fish and Wildlife Service and were extracted from Tappa et al. (2015, their Table 23). No significant effects of summer bottom temperature were detected (Pearson correlation coefficient: r = –0.47, p = 0.12 for reproductive success; r = –0.08, p = 0.80 for fledging success)

The breeding population of thick-billed murres at St. George Island appeared to increase from the mid-1980s to 1999–2002, and then remained relatively stable during 2002 to 2014 (Tappa et al. 2015). Reproductive parameters of thick-billed murres did not show any clear responses to climate conditions in a previous study (Renner et al. 2014). Indeed, reproductive and fledging success were relatively stable over a range of warm and cold conditions during our study period (Tappa et al. 2015, our Fig. 6), which was in contrast to the clear responses we observed in the behavioral and physiological parameters. This suggests that murres buffer the effect of inter-annual climate variability on reproductive parameters via changes in their fine-scale foraging behavior. Such 'behavioral buffering' has been documented in various seabird species, and appears to be a common response to changes in foraging conditions (Harding et al. 2007, Grémillet et al. 2012, Einoder et al. 2013). However, our concurrent corticosterone data suggest that there may be some associated costs to parents of this behavioral buffering. We suggest that a combined study of seabird foraging behavior and physiological stress is an effective integrative approach to examining the impact of environmental changes on breeding seabirds (Piatt et al. 2007, Kitaysky et al. 2007, 2010, Satterthwaite et al. 2012).

Our results showed that thick-billed murres decreased foraging effort and incurred less nutritional stress in warm years, indicating that warming conditions are currently beneficial due to the availability of juvenile pollock on the continental shelf. Warming conditions appear to benefit black-legged kittiwakes in the southeastern Bering Sea (Satterthwaite et al. 2012), which, combined with our results, suggest that the availability of forage fish on the continental shelf increased from surface strata to the mid-water column in warm years. However, this pattern may be specific to the continental shelf regions of the southeastern Bering Sea that experience seasonal ice cover. On Bogoslof Island, Aleutian Islands, where murres rely on ocean basin habitat for foraging, common and thick-billed murres incurred less nutritional stress in cold years (Barger & Kitaysky 2012), which is in contrast to our results. This suggest that a better understanding of region-specific ecological processes (on-shelf availability of pollock in warm years, in our case) are needed to fully assess the impact of ocean climate changes on the southeastern Bering Sea ecosystems. Moreover, studies suggest that recruitment of age-0 pollock to age-1 was lower in warm years on the continental shelf due to poor body condition of juvenile pollock in the fall (Mueter et al. 2011, Heintz et al. 2013) and increased mortality due to predation and/or cannibalism (Coyle et al. 2011). In addition, oscillations of warm and cold oceanographic conditions between years may be a prerequisite to support the high productivity of this ice-influenced continental shelf ecosystem (Hunt et al. 2011). Whether continued warming of the southeastern Bering Sea would be beneficial or detrimental to piscivorous seabirds breeding on the continental shelf needs further investigation.

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Contribution to the Theme Section 'Seabird responses to a changing Bering Sea'

Timing of sea-ice retreat affects the distribution of seabirds and their prey in the southeastern Bering Sea

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ABSTRACT: The potential impacts of future climate warming on marine ecosystems can be assessed by examining the effects of present-day variation in climate. Here we report how the cross-shelf distributions of seabirds and their potential prey responded to interannual variation in the timing of sea-ice retreat in the southeastern Bering Sea. We expected that in years of early sea-ice retreat, prey resources would be scarce over the shelf and that seabird species would concentrate in frontal regions where availability of zooplankton and forage fish might be enhanced. To test this hypothesis, we used a 40 yr database of the distribution of marine birds and recently available data on the distribution of zooplankton and forage fish. We found that although there were substantial changes in the distribution of seabird species between years with early and late sea-ice retreat, there was no overall shift into frontal regions. Instead, in years with early sea-ice retreat, there was a strong tendency for seabird species that foraged off the shelf to move toward, or onto, the shelf, whereas inshore-foraging species shifted seaward. Further, the cross-shelf centers of abundance of the copepod *Calanus marshallae*/*glacialis* shifted seaward, but there was little change in the cross-shelf distributions of *Neocalanus* spp. copepods, euphausiids (primarily *Thysanoessa* spp.), and age-0 pollock *Gadus chalcogrammus*. Shifts in seabird distributions, as demonstrated in this study, indicate the importance of sea-ice retreat for structuring trophic interactions and could present both opportunities and challenges for central-place-foraging breeding seabirds and long-distance migratory species.

KEY WORDS: Climate variability · Southeastern Bering Sea · *Calanus glacialis* · *Calanus marshallae* · *Gadus chalcogrammus* · *Neocalanus* spp. · *Thysanoessa raschii*

> '*Seabirds are like graduate students; they go where the food is.*'

Comment by Bob Paine on the occasion of an after-dinner talk on Seabirds as Feathered Oceanographers

INTRODUCTION

Marine ecosystems respond to climate forcing at a variety of temporal scales, from those of storm events, to periods of cooling and warming lasting millennia. While seasonal variability in heat and light is manifested in the ocean by changes in production and by migration of organisms to more favorable locations, changes in climate forcing lasting multiple years and longer may result in major reorganizations of food webs and ecosystem structure (e.g. Drinkwater 2006, Beaugrand & Kirby 2010, Sydeman et al. 2015). In the

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southeastern Bering Sea, unusually warm or cold years have resulted in shifts in ecosystem components, including the relative abundance of phytoplankton cells of different sizes (Eisner et al. 2016), zooplankton (Coyle et al. 2011), the abundance of euphausiids (Hunt et al. 2016), the diets and lipid content of age-0 and age-1 pollock (Coyle et al. 2011, Heintz et al. 2013), the survival of these young pollock to age-3 (Hunt et al. 2011, Eisner & Yasumiishi 2016), and changes in the distributions of fish species (Mueter & Litzow 2008). Some studies indicate that climate change may have a greater impact through affecting biotic linkages than through the direct impacts of warming (e.g. Drinkwater et al. 2010, Søreide et al. 2010, Ockendon et al. 2014).

An indication of the potential impacts of future climate warming on marine ecosystems can be obtained by investigating the effects of present short-term (years to decades) variations in climate. In this paper, we compare and contrast the cross-shelf distributions of southeastern Bering Sea seabirds and their prey in years with early and late sea-ice retreat to see how this ecosystem may respond to climate warming.

The eastern Bering Sea is noted for the interannual variability of its marine conditions (Stabeno et al. 2001, 2012, Hermann et al. 2013). Located at the southern terminus of the winter arctic sea-ice extent in the Pacific Arctic, the southeastern Bering Sea experiences strong interannual variability in spring sea-ice cover. This is manifested in variability in sea-ice extent, percent cover, and the timing of sea-ice retreat (Niebauer 1998, Stabeno et al. 2001). The timing of sea-ice retreat affects the availability of ice-associated algae and possibly the timing, intensity, and duration of the spring bloom (Alexander & Niebauer 1981, Stabeno et al. 1998, Hunt et al. 2002b, 2011, Brown & Arrigo 2013).

Variations in the timing of sea-ice retreat affect food availability for zooplankton in spring (Smith & Vidal 1986, Niebauer et al. 1990, Napp et al. 2002) and thereby the potential for transfer of energy to fish, seabirds, and marine mammals. Recent work has shown that the distribution and abundance of large crustacean zooplankton and forage fish respond to variability in the timing of sea-ice retreat and/or water temperatures (Baier & Napp 2003, Coyle et al. 2011, Hunt et al. 2011, 2016, Eisner et al. 2014, Coyle & Gibson 2017). In particular, there is considerable information on changes in the abundance of large copepods (Coyle et al. 2011, Eisner et al. 2014, 2015), euphausiids (principally *Thysanoessa* spp.) (Ressler et al. 2012, 2014, Hunt et al. 2016), juvenile walleye pollock *Gadus chalcogrammus* (hereafter 'pollock'), and Pacific cod *G. macrocephalus* (Hunt et al. 2002b, 2008, Farley et al. 2016, Sigler et al. 2016), as well as the survival of the pollock to age-1 or age-3 (Mueter et al. 2011, Heintz et al. 2013, Sigler et al. 2016), in relation to the timing of sea-ice retreat. In warm years, when sea-ice retreat occurs early in the spring, there are reduced abundances of the large, lipid-rich copepods and middle shelf euphausiids and usually weaker year classes of pollock and Pacific cod.

Associations between seabirds and their prey occur at spatial scales, from those of ocean basins, to Langmuir circulation cells and individual prey (reviewed in Hunt & Schneider 1987, Hunt et al. 1999). Seabirds respond to changes in the distribution or abundance of their prey by shifting their foraging distributions (e.g. Takahashi et al. 2015, Nishizawa et al. 2017; Will & Kitaysky 2018, Will et al. 2018, both this Theme Section), although relatively few studies have simultaneous measures of seabird foraging activity and the abundance of prey (e.g. Hunt & Harrison 1990, Kokubun et al. 2008, Suryan et al. 2016). The distribution and abundance of seabirds over the southeastern Bering Sea shelf has been a topic of research since the mid-1970s. Initially, the emphasis was on large-scale static distributions (e.g. Hunt et al. 1981, Schneider et al. 1986, 1987), as time series were not available, or on small-scale process studies where interactions between the behavior of prey and physical processes result in concentrations of prey (e.g. Coyle et al. 1992, Hunt et al. 1996, Jahncke et al. 2005). In particular, seabirds respond to prey accumulations in frontal regions, either because of convergences or divergences (e.g. Coyle et al. 1992, Hunt et al. 1998), or because of enhanced or prolonged primary production (e.g. Jahncke et al. 2005).

Recently, as a substantial time series of pelagic observation of seabirds has become available, there has been more emphasis on changes in distribution or abundance at decadal time scales or longer, both in the eastern Bering Sea (e.g. Jahncke et al. 2008, Kuletz et al. 2014, Renner et al. 2016) and in the adjacent Chukchi Sea (Gall et al. 2017). The finding of strong seasonal signals in both abundance (Schneider et al. 1986) and distribution (Hunt et al. 2014) has raised interest in the possibility that seabird distributions across the southeastern Bering Sea shelf might vary at a multi-annual time scale in response to variation in the abundance or availability of prey.

In this paper, we examine interannual patterns of seabird distribution across the southeastern Bering Sea shelf, and relate these patterns to spatial and temporal variability in the marine environment, including timing of sea-ice retreat and the distribution and abundance of potential prey such as large crustacean zooplankton and forage fish. We use a 40 yr data set of pelagic seabird observations from the eastern Bering Sea to assess changes in the cross-shelf distribution of seabirds and potential prey organisms to test the hypothesis that shifts in seabird distribution reflect temporal variability in the distribution of their prey, which in turn, may have been affected by the timing of sea-ice retreat.

We hypothesized that seabirds would shift their centers of distribution toward frontal areas when conditions were such that large lipid-rich copepods and euphausiids and forage fish were scarce in the inner and middle portions of the shelf. Because large, lipid-rich crustacean zooplankton were expected to be less abundant in years with early sea-ice retreat, and thus, perhaps, the only concentrations might be available near fronts with strong surface expressions (the Inner Front and the Shelf-break Front, see 'Study area and hydrology' below), we expected use of frontal areas by seabirds to be greatest in years with early sea-ice retreat. We did not anticipate a shift toward the Middle Front, because its surface expression is weak (Coachman 1986), and Schneider et al. (1987) had found that if seabirds aggregated at fronts, it was the fronts with a strong surface expression that were attended. Alternatively, if age-0 pollock were most abundant in the Middle Shelf Domain in years with early sea-ice retreat, it could be expected that seabirds that depend on them might increase their foraging in this region.

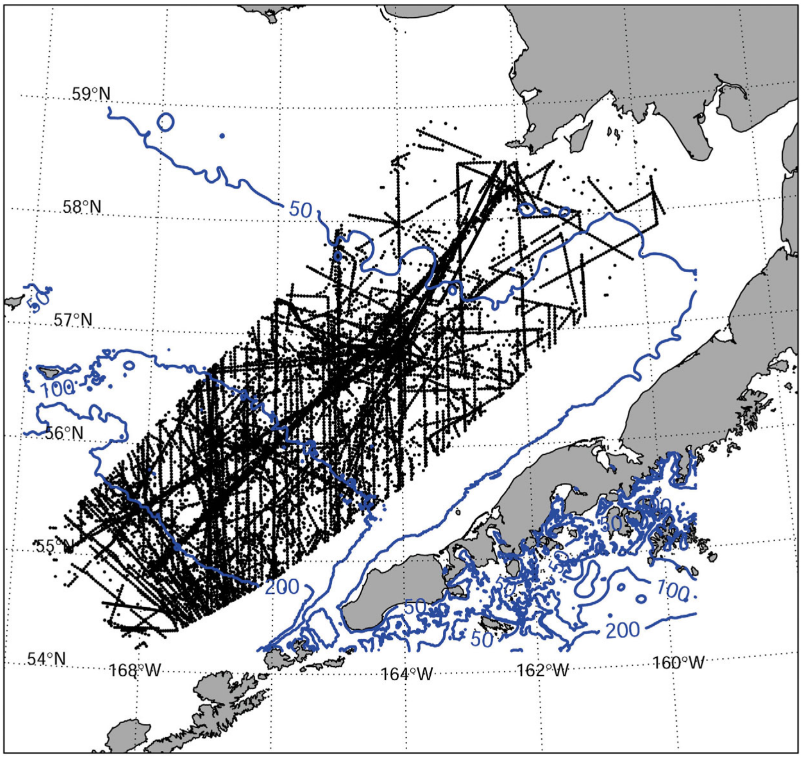

Fig. 1. Study area on the southeastern Bering Sea shelf showing location of survey effort from 1975 to 2014 (small black dots show location of each 1 km^2 transect). The 50, 100, and 200 m isobaths are delineated in blue

BACKGROUND AND METHODS

Study area and hydrology

Our study area encompassed a portion of the southeastern Bering Sea shelf from a depth of about 20 m to the shelf edge and beyond over the shelf slope to waters of 2500 m depth, closely following the area used by Schneider et al. (1986), Hunt et al. (2014), and Renner et al. (2016) (Fig. 1). The northwest and southeast sides of our study area were selected to minimize the impact of nesting seabirds foraging out from the major colonies of the Pribilof Islands (Jahncke et al. 2008), and to avoid proximity to the Alaska Peninsula and its shallow coastal waters. We assumed that the ecosystem within our study area is largely homogeneous along isobaths, and that the main ecological gradient is depth or is depth-related (Hunt et al. 2014). We therefore based our analysis on bathymetry and regarded samples along an isobath as replicates.

During summer, the waters of the southeastern Bering Sea shelf are characterized by 4 hydrographic domains, the Inner Shelf Domain (depth 0 to ~50 m), the Middle Shelf Domain (~50 to ~100 m), and the Outer Shelf Domain (~100 to ~200 m) (Kinder & Schumacher 1981, Coachman 1986). Here we also identify a Shelf-slope Domain (~200 to ~2500 m), where there is an abrupt shift from the very gradual increase in depth from the shore to the shelf edge to a rapid increase in depth toward the deep Aleutian Basin (Kinder & Coachman 1978, Mizobata et al. 2008). These domains are separated by fronts with the degree of surface expression varying temporally and spatially. In summer, the Inner Front separates the well-mixed waters of the Inner Shelf Domain from the waters of the Middle Shelf Domain, which are strongly stratified in summer (Schumacher et al. 1979, Kachel et al. 2002). The Middle Front (Coachman & Charnell 1979, Coachman 1986) separates the 2-layer Middle Shelf Domain from the more oceanic-influenced Outer Shelf Domain and is largely coincident with a northwestward flow along the 100 m isobath (Reed & Stabeno 1996, Stabeno et al. 2016). The Middle Front has its strongest expression at depth (Coachman & Charnell 1979). The Shelf-break Front separates the Outer Shelf Domain from the Shelf-slope Domain (Kinder & Coachman 1978) and its associated flows along the shelf slope (Johnson et al. 2004, Okkonen et al. 2004, Ladd 2014).

For the purposes of this paper, we defined the location of the Inner Front as waters of 45 to 55 m depth, as this front moves significantly depending on tidal strength and wind mixing (Kachel et al. 2002, Jahncke et al. 2005). We defined the Middle Front as waters between 85 and 105 m depth, and the Shelf-break Front as between 175 and 250 m depth. These definitions encompassed the range of depths over which the physical expression of these fronts occurs, and provided sufficiently wide regions to capture an adequate sample of seabird observations in the regions of the fronts.

Seabird prey in the southeastern Bering Sea

To understand seabird responses to years with early and late sea-ice retreat, we needed to know the species composition of their prey and how these prey might change in distribution or abundance in response to the timing of sea-ice retreat. The diets of seabirds in the southeastern Bering Sea are known primarily from samples obtained from breeding birds at colonies (e.g. Sinclair et al. 2008, Dorresteijn et al. 2012, Renner et al. 2012, Paredes et al. 2014), but in a few cases, samples have been obtained from birds collected while foraging at sea (e.g. Schneider et al. 1986, Hunt et al. 1996, Jones et al. 2014). Although a wide variety of prey were used by the birds, the most important prey types identified were large copepods (*Neocalanus* spp., *Calanus marshallae*) for least auklets (for Latin names of seabirds, see Table 1); amphipods (*Themisto libellula*) for thick-billed murres and black-legged kittiwakes; euphausiids (*Thysanoessa raschii* and *T. inermis*) for black-legged kittiwakes, thick-billed murres, and short-tailed shearwaters; squid for northern fulmars, black-legged kittiwakes, and thick-billed murres; myctophids for black-legged and red-legged kittiwakes; and juvenile pollock (age-0 or age-1) for short-tailed shearwaters, common murres, thick-billed murres, and black-legged kittiwakes (references above).

For black-legged kittiwakes, thick-billed murres, and short-tailed shearwaters, there has been sufficient pelagic sampling of foraging birds to detect spatial patterns in prey use. For example, black-legged kittiwakes and thick-billed murres sampled near the Pribilof Islands and Bogoslof Island had strong interannual and regional differences in prey used, with murres showing strong spatial patterns (Jones et al. 2014). Both kittiwakes and murres took more deep-water pelagic fish species and squid when foraging in the outer shelf-slope and in deep off-shelf waters (Jones et al. 2014). Short-tailed shearwater diets varied regionally and perhaps seasonally, with euphausiids, in particular *T. raschii*, as the principal prey around the Pribilof Islands and in the Middle Shelf Domain, and sand lance *Ammodytes hexapterus* as an important prey in the near shore Inner Shelf Domain of Bristol Bay in spring (see Appendix) (Hunt et al. 1996, 2002a). In some summers, these shearwaters also took age-0 pollock at, and just seaward of, the Inner Front (Hunt et al. 2002a). For the most part, there are broad dietary overlaps among seabird species in the southeastern Bering Sea and, without collecting a bird, we rarely had a way of knowing what any individual bird at sea had been eating.

Selected prey types

The zooplankton communities of the southeastern shelf vary by hydrographic domain. The biomass of large, lipid-rich copepods of the Middle Shelf Domain is dominated by *C. marshallae/glacialis* (termed *C. marshallae* for brevity), whereas *Neocalanus* spp. predominate in the Outer Shelf Domain and over the deeper waters of the Shelf-slope Domain and the Aleutian Basin (Cooney & Coyle 1982, Smith & Vidal 1986, Napp et al. 2002, Coyle et al. 2008). Similarly, the dominant species of euphausiids differ between the Outer Shelf Domain (*T. inermis*) and the Middle and Inner Shelf domains (*T. raschii*) (Smith 1991, Coyle & Pinchuk 2002b, Coyle et al. 2008, Pinchuk & Coyle 2008). The outer and middle shelf species of euphausiids and copepods differ in life history characteristics and requirements for successful recruitment.

In particular, both of the dominant large zooplankton species in the Middle Shelf Domain, *T. raschii* and *C. marshallae*, require food in early spring if they are to produce strong cohorts (Baier & Napp 2003, Hunt et al. 2016). Both consume ice algae (Baier & Napp 2003, Wang et al. 2015, Campbell et al. 2016) and, when the ice retreat is late, there is little or no gap in the availability of ice-associated algae and the spring bloom (Brown & Arrigo 2013, Hunt et al. 2016). Thus, years with late sea-ice retreat are likely to be favorable for the recruitment of large cohorts of *C. marshallae* and *T. raschii* over the Inner and Middle Shelf Domains (Baier & Napp 2003, Coyle et al. 2008, 2011, Hunt et al. 2008, 2011, Eisner et al. 2014), but see Coyle & Gibson (2017) for an argument that poor over-winter survival of diapausing copepods is responsible for the low biomass of *C. marshallae* in warm years. The biomass of *C. marshallae* in early sea-ice retreat years was only 5% of that in years with late sea-ice retreat (Renner et al. 2016). Although they live in generally ice-free waters, the shelf-slope and basin-dwelling copepods, *Neocalanus plumbchrus/flemingeri* and *N. cristatus,* also appear to be more abundant in cold years with late ice retreat (Ohashi et al. 2013, Eisner et al. 2014). Renner et al. (2016) showed that *Neocalanus* spp. biomass in years with early sea-ice retreat was 64% lower than in years with late sea-ice retreat.

Ressler et al. (2014) used acoustic surveys of the southeastern Bering Sea shelf conducted between 2004 and 2010 to establish that there was a greater abundance of euphausiids over the Outer and Middle Shelf Domains in years with colder water temperatures. Similarly, Bi et al. (2015), Hunt et al. (2016), and Renner et al. (2016) provided evidence that *T. raschii* is less abundant overall in years with early sea-ice retreat. The overall impact of these changes is a severe decrease in the abundance of large, lipid-rich zooplankton over the middle and possibly the outer shelf in years with early sea-ice retreat.

In contrast to *C. marshallae* and *T. raschii* in the Middle Shelf Domain, production of age-0 pollock, an important prey for seabirds and the most abundant ground fish in the study area, is stronger in years with early sea-ice retreat and surface waters that are warmer (0 to 4°C, versus −0.5 to −2.7°C) when pollock eggs and larvae are present. Pollock eggs thrive in water that is above 0°C (Blood 2002), and the early life survival and growth of pollock in the Bering Sea is higher in warmer years (e.g. Quinn & Niebauer 1995, Napp et al. 2000, Coyle & Pinchuk 2002a,b). The result is a large cohort of age-0 pollock in the spring of 'warm' years. Many of these small age-0 pollock remain in near-surface waters (upper 20 m) into late summer/early fall, particularly in years with early sea-ice retreat (Moss et al. 2009, Parker-Stetter et al. 2013, 2015, Eisner et al. 2015), and would thereby be more vulnerable to predation by a wider array of seabirds. There is also evidence that in years with early sea-ice retreat and warm surface-layer temperatures, there are more age-0 pollock in the upper mixed layer than in cold years with late sea-ice retreat (Moss et al. 2009, Eisner et al. 2015), which may reflect higher survival of eggs and larvae in warm years.

Years with early vs. late sea-ice retreat

Several metrics have been used to define warm or cold years, or years with heavy or light sea-ice cover (e.g. Stabeno et al. 2012, Eisner et al. 2014, Hunt et al. 2016, Renner et al. 2016, Sigler et al. 2016). Because mounting evidence supports the hypothesis that the timing of sea-ice retreat is critical for the transfer of primary production to large lipid-rich zooplankton (Coyle et al. 2011, Hunt et al. 2011, 2016, Sigler et al. 2016, but see Coyle & Gibson 2017 for an alternative view), we elected to base our contrast of years on the timing of sea-ice retreat within our study area, per Renner et al. (2016) (Fig. 1). Within the study area, the southern edge of the sea ice is determined by a combination of wind forcing and melting (Pease 1980, McNutt 1981, Zhang et al. 2010). In spring, depending on wind direction, the ice may either surge southward or retreat northward, only to return a few days later (Sullivan et al. 2014). Thus, there is no clearly defined date of ice retreat. Therefore, to characterize the timing of ice retreat, we used the proportion of ice cover within the study area, between the 50 and 500 m isobaths, during the month of April. Using this metric, a low proportion of ice cover in April would equate to a year with early sea-ice retreat. Conversely, a high proportion of sea-ice cover in April would equate to a year with late sea-ice retreat. Although years with late sea-ice retreat are usually characterized by cool upper water column temperatures, this relationship does not always hold (for example, a late sea-ice retreat was followed by exceedingly warm sea surface temperatures in late spring and early summer of 1997) (Napp & Hunt 2001).

We used 2 sources of sea-ice data to determine sea-ice concentrations within the study area. For the period 1972–1994, we obtained weekly sea-ice concentrations, on a 0.25° × 0.25° grid, from the Joint US–Russian Sea Ice Atlas (Environmental Working

Group 2000). Overlapping that dataset, from 1978 to the present, we used the National Snow and Ice Data Center Bootstrap algorithm on a 25 km grid (Comiso 2017). The ice data were reported semi-daily before 1987, and daily since then. Using these data sources, we calculated the daily mean sea-ice concentration in the study area from the ice concentration data points within it. For data before 1987, we used a linear extrapolation of semi-daily or weekly data to provide an estimate of daily sea-ice cover within the study area. Years were then grouped into those with early and late sea-ice retreat, with 80% of sampled years in the early and late categories (16 yr each) and 20% as intermediate (Fig. 2).

We found autocorrelation in the timing of sea-ice retreat between years up to a time lag of 1 to 2 yr. We do not consider autocorrelation an issue for our study of the summer distribution of seabirds, because migration, dispersion, and displacement by sea ice will have resulted in a fresh re-distribution each year. Thus, for the seabirds, each year was assumed to be an independent sample.

Copepod and age-0 pollock sampling

The sampling of potential prey for seabirds was done within the study area and the years of the study, but for different purposes. Therefore, not all seabird prey types were sampled, nor were all dates in summer and locations sampled.

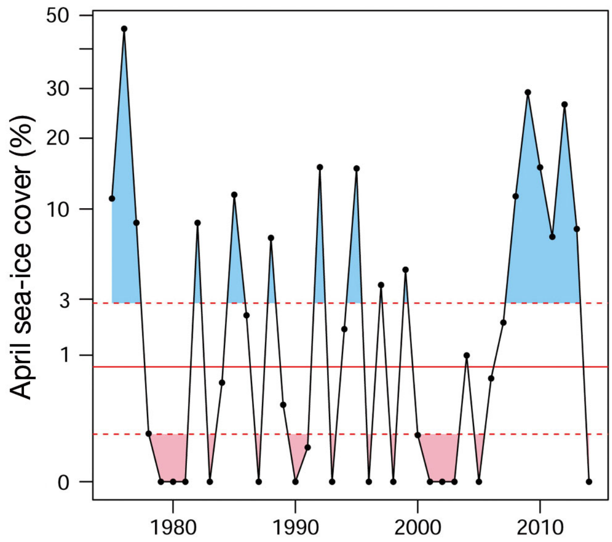

Fig. 2. Classification of years (1975–2014, black dots) as those with early (red) or late (blue) sea-ice retreat based on the 40% of years with the least ice (early), or 40% with the most ice (late) present in April. The solid red line is the mean ice cover for April; years between the dashed red lines (40 and 60% quantiles) were considered intermediate in terms of the timing of sea-ice retreat

Large copepods and age-0 pollock were sampled during the Bering Arctic Subarctic Integrated Surveys (BASIS) on the southeastern Bering Sea shelf during mid-August to September 2003–2010 (see Fig. 1 in Hunt et al. 2016) following methods in Eisner et al. (2014) and Moss et al. (2009) for zooplankton and fish, respectively. Briefly, large copepods were collected with a 60 cm bongo frame with 505 µm mesh, towed obliquely from near bottom to the surface, and preserved in 5% formalin buffered with seawater. Samples were sent to the Polish Plankton Sorting and Identification Center (Szczecin, Poland) (2003–2004) or to the University of Alaska (Coyle et al. 2008) (2005–2010), sorted, and counted to estimate abundances (no. m^{-2}) of *Calanus marshallae* and *Neocalanus* spp.

All stages were combined for *C. marshallae* and *Neocalanus* spp. abundance estimates. During August and September, *C. marshallae* are almost completely comprised of late copepodite stages (C5) in late sea-ice years (Eisner et al. 2018), but can have higher proportions of earlier stages in years with early sea-ice retreat (A. I. Pinchuk pers. comm.). The size and amount of lipid increase with stage. Therefore, in early-ice years, not only were there fewer *C. marshallae*, but those that were present may have been less lipid-rich on average (and poorer prey) due a lower percentage of C5 stages. *Neocalanus* spp. are found in low abundances in August and September compared to earlier months (spring months, in particular) (Eisner et al. 2017). Therefore, these late summer abundances may not accurately reflect their availability over the spring and early summer growing season.

Copepods and age-0 pollock were sampled over the survey area at 13 to 68 stations yr^{-1} (mean ± SD = 34 ± 17) from 2003 to 2010, which included 2 early sea-ice retreat years (2003, 2005), 3 intermediate years (2004, 2006, 2007), and 3 late ice retreat years (2008, 2009, 2010; Fig. 2). Note that 2004 has been considered a 'warm' year, and 2007 a 'cold' year by others (e.g. Stabeno et al. 2012). In the case of this paper, the difference was the result of sampling more years. Stations were sampled primarily over the Inner, Middle, and Outer Shelf Domains with few offshore stations. Station spacing and area covered varied somewhat from year to year, particularly over the Outer Shelf Domain (e.g. in 2008, no Outer Shelf Domain stations were sampled) (Eisner et al. 2015).

Pelagic fish (e.g. age-0 pollock) were captured with a midwater rope trawl with a mean horizontal spread of 55 m, configured to sample the top 15–35 m of the

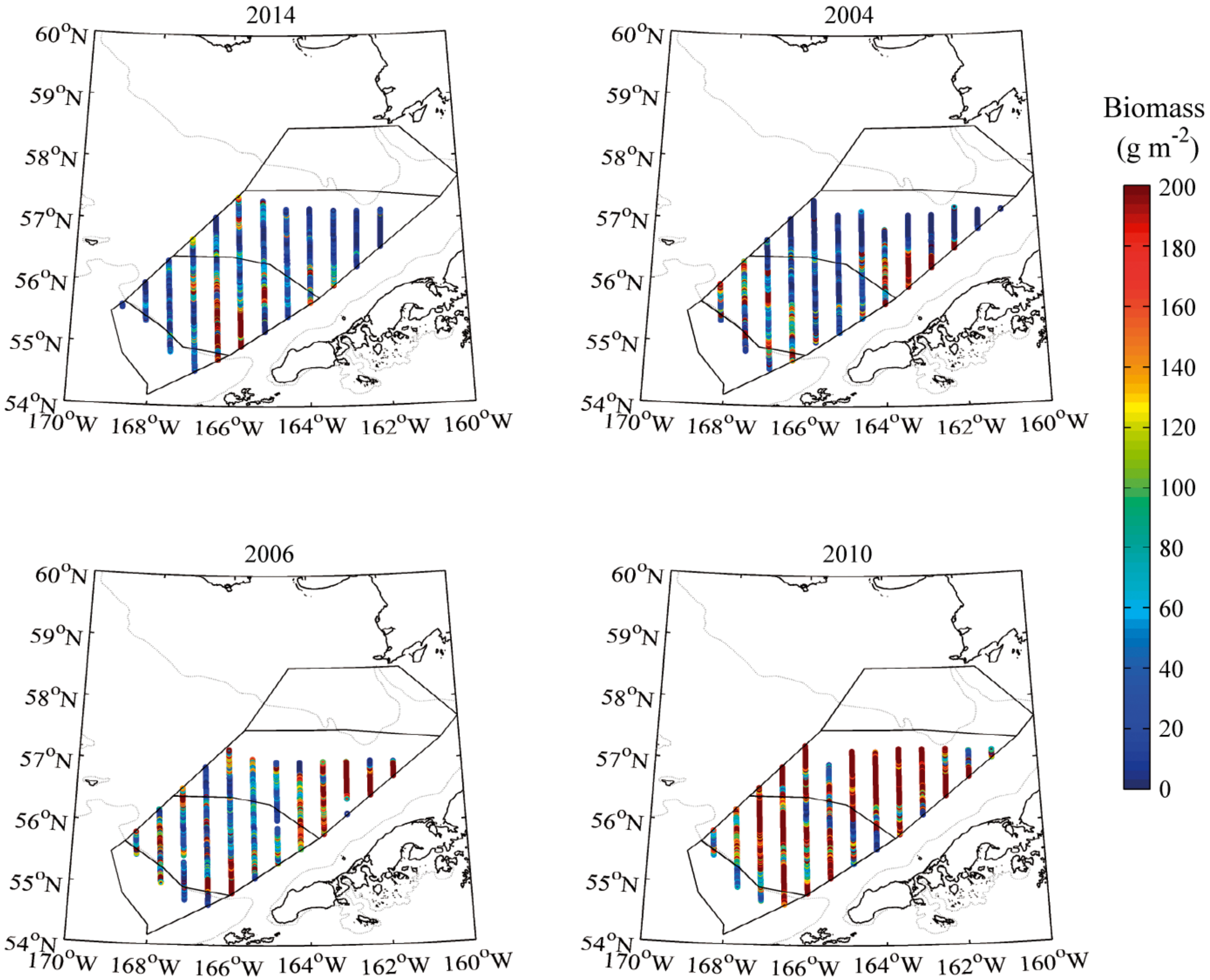

Fig. 3. Acoustic survey effort and euphausiid biomass (g m^{-2}) within Inner, Middle, Outer, and Shelf-slope Domains (black polygons) for years of different sea-ice retreat: 2014 (early), 2004 (neutral), 2006 (neutral), and 2010 (late) (see Fig. 2). 2004 occurred in the middle of a series of warm years with early sea-ice retreat, 2006 was a year of transition from a series of years with mostly early sea-ice retreat to years of later sea-ice retreat, 2010 was in a series of cold years with later sea-ice retreat. 50 and 200 m isobaths are shown in light gray

water column. The net had a 1.2 cm mesh cod liner and hexagonal mesh wings. Trawls were towed at 3.5–5.0 knots (6.5–9.3 km h^{-1}) for 30 min. The catch was immediately sorted to separate age-0 pollock from other species and life stages, and pollock were counted to estimate abundances (no. km^{-2}). Age-0 pollock were sampled from the surface layer (~0–20 m). Therefore, pollock located deeper in the water column were not included. Some seabirds can access prey below the surface layer; this potential food source and its relationship to individual seabird distributions was not evaluated in our study.

Euphausiid sampling

Ressler et al. (2012) computed the abundance of euphausiids on the middle and outer shelf of the eastern Bering Sea using multi-frequency acoustic backscatter and Methot trawl data from 2004–2014 surveys of midwater pollock (Fig. 3). Methot trawl samples from acoustically detected euphausiid layers were preserved in 5% formalin:seawater solution and enumerated to determine abundance, size, and species composition at the Polish Plankton Sorting and Identification Center (Szczecin, Poland).

Estimated euphausiid biomass (wet weight, g m^{-2}) along acoustic survey transects was vertically integrated over the water column and averaged in 0.926 km (0.5 nautical mile [n mile]) bins along north–south survey transects (see Hunt et al. 2016, for updated methodology). Euphausiid biomass in cross-shelf 25 m depth bins in years with early and late sea-ice retreat was computed selecting 0.5 n mile acoustic survey intervals and then computing the simple average for a given bin.

Euphausiid survey data were available in 2004, 2006, 2007–2010, 2012, and 2014. The coverage of the study area from approximately 50 to 1000 m bottom depth was similar in all years (see Fig. 1 in Hunt et al. 2016). Euphausiid data were not available prior to 2004 due to differences in equipment and data collected.

Determination of seabird distributions

We extracted data from the North Pacific Pelagic Seabird Database (NPPSD; US Geological Survey et al. 2015), excluding aerial surveys contained therein. These data were collected by a variety of researchers conducting visual surveys for marine birds from a wide variety of vessels. For this study, we selected 4855 records from the 'summer'(15 June to 31 August 1975–2014), as the summer should be a period with minimum migratory bird passage through the study area, and the area is ice free (Hunt et al. 2014). We classified seabird species by foraging method, as either surface-seizing or pursuit-diving (Table 1). The sub-set of pelagic data used provided observations over the study area from waters with a depth of about 10 m to about 2500 m, with the majority having been obtained between about 30 and 2000 m (Fig. 4). The spatial coverage of the study area was similar in both scenarios, e.g. years with early or years with late sea-ice retreat. The overall number of samples was lower for the years with early sea-ice retreat (Fig. 4).

Records in the NPPSD were developed from counts of seabirds along 300 m strip transects from directly ahead of a vessel to 90° off the side with the best visibility. Over time, 2 methods for recording seabird observations have been used. Most recent surveys used the snapshot method (Tasker et al. 1984), thereby addressing the issue of biases from the motion of flying birds relative to the ship. Older surveys in the Bering Sea counted all flying birds, which would lead to an inflated density estimate, if not corrected. We corrected surveys counting all flying birds for flux as - described by Renner et al. (2013) and listed in Appendix 1 of Hunt et al. (2014). We thus merged density data from the NPPSD from the 2 different methods applied to flying birds. Known biases remain. We made no correction for vessel attraction (although observers attempted to avoid repeated counts of ship-following birds), vessel avoidance, or detectability. However, we have no reason to believe that these biases changed across our study area, or were different in years with early or late sea-ice retreat.

Analyses

The analyses of seabird distribution and abundance followed the approach used by Hunt et al. (2014) and Renner et al. (2016). We first identified outliers in the seabird records and adjusted them, then calculated the abundance (density) of seabirds, by species, in 3 km segments. The 3 km segment densities were then averaged within domains to obtain mean density estimates for each depth-defined domain across the shelf (see below). These densities were then used to examine cross-shelf distributions of seabirds in years with early and late sea-ice retreat. For comparison, the average cross-shelf distribution of prey groups was determined by computing a biomass-weighted mean bottom depth for each prey group, and a bootstrap was used to compute a 95% confidence interval on the difference in mean bottom depth between years with early and late sea-ice retreat.

Data preparation

Seabirds identified only to higher taxonomic levels were prorated according to the following: if an unidentified bird could belong to species A, B, or C, we modeled the relative proportion of species A within the sum of identified individuals of species A, B, and C as a smooth function of bathymetry, month, and year using a binomial error distribution with a logistic link-function and no interactions. The level of smoothing was determined through generalized cross-validation (Wood et al. 2008). Prorating was applied sequentially, first to the smallest groups of unidentified species and then to more inclusive groups, as detailed in Appendix 2 of Hunt et al. (2014). We aggregated short-tailed shearwater *Ardenna tenuirostris* and sooty shearwater *A. griseus* records into 'dark shearwater'. We assumed that the vast majority of shearwaters were short-tailed shearwaters, because that is by far the predominant spe-

Table 1. Seabird species included in this study, listed by 4-letter code (as used in the figures), their overall density in the study area, their foraging mode (after Ashmole 1971), and their major prey in the southeastern Bering Sea as known, not including offal. For seabird species lacking diet information in the southeastern Bering Sea, we indicate UNDT and provide an indication of diets known from elsewhere, with preferred prey reported by (1) Hunt et al. (1981), (2) Hunt et al. (1996), (3) Hunt et al. (2000), and (4) Schneider et al. (1986). Zoop: zooplankton; krill: euphausiids; deca: decapods; poly: polychaetes

Abbreviation	Common name	Latin name	Density (ind. km^{-2})	Foraging mode	Preferred prey
ALTE	Aleutian tern	*Onychoprion aleuticus*	0.00303	Surface	UNDT, fish (4)
ANMU	Ancient murrelet	*Synthliboramphus antiquus*	0.358	Diver	UNDT, fish, zoop, krill (4)
ARTE	Arctic tern	*Sterna paradisaea*	0.0582	Surface	UNDT, fish (4)
BFAL	Black-footed albatross	*Phoebastria nigripes*	0.00817	Surface	UNDT, fish, squid (3)
BLKI	Black-legged kittiwake	*Rissa tridactyla*	0.999	Surface	Fish, krill, zoop (1)
CAAU	Cassin's auklet	*Ptychoramphus aleuticus*	0.0255	Diver	UNDT, zoop (3)
COMU	Common murre	*Uria aalge*	0.893	Diver	Fish (1)
CRAU	Crested auklet	*Aethia cristatella*	0.0143	Diver	Zoop (1), krill (4)
DCCO	Double-crested cormorant	*Phalacrocorax auritus*	0.00000532	Diver	UNDT, fish (4)
FTSP	Fork-tailed storm-petrel	*Oceanodroma furcata*	1.68	Surface	Zoops, squid (3)
GLGU	Glaucous gull	*Larus hyperboreus*	0.00239	Surface	UNDT omnivore (4)
GWGU	Glaucous-winged gull	*Larus glaucescens*	0.0667	Surface	UNDT omnivore (4)
HEGU	Herring gull	*Larus argentatus*	0.00111	Surface	UNDT omnivore (4)
HOPU	Horned Puffin	*Fratercula corniculata*	0.022	Diver	Fish, zoop (1)
KIMU	Kittlitz's murrelet	*Brachyramphus brevirostris*	0.0284	Diver	UNDT, fish, krill, amphipods (4)
LAAL	Laysan albatross	*Phoebastria immutabilis*	0.0268	Surface	UNDT, squid (4)
LEAU	Least auklet	*Aethia pusilla*	0.0563	Diver	Zoop (1)
LESP	Leach's storm-petrel	*Oceanodroma leucorhoa*	0.000356	Surface	UNDT
LTJA	Long-tailed jaeger	*Stercorarius longicaudus*	0.00309	Surface	UNDT
MAMU	Marbled murrelet	*Brachyramphus marmoratus*	0.18	Diver	UNDT; fish, amphipods (4)
MOPE	Mottled petrel	*Pterodroma inexpectata*	0.00286	Surface	UNDT
NOFU	Northern fulmar	*Fulmarus glacialis*	5.21	Surface	Squid, fish (1), (4)
PAAU	Parakeet auklet	*Aethia psittacula*	0.0631	Diver	Fish, krill, zoop (1)
PAJA	Parasitic jaeger	*Stercorarius parasiticus*	0.0101	Surface	UNDT fish (4)
PECO	Pelagic cormorant	*Phalacrocorax pelagicus*	0.00188	Diver	UNDT fish (4)
PIGU	Pigeon guillemot	*Cepphus columba*	0.000518	Diver	UNDT fish, deca, poly (4)
POJA	Pomarine jaeger	*Stercorarius pomarinus*	0.0202	Surface	UNDT, fish (4)
REPH	Red phalarope	*Phalaropus fulicarius*	0.243	Surface	UNDT zoops, krill (4)
RFCO	Red-faced cormorant	*Phalacrocorax urile*	0.00017	Diver	Fish, deca (1)
RHAU	Rhinoceros auklet	*Cerorhinca monocerata*	0.000081	Diver	UNDT fish (4)
RLKI	Red-legged kittiwake	*Rissa brevirostris*	0.115	Surface	Fish (1), krill
RNPH	Red-necked phalarope	*Phalaropus lobatus*	0.0199	Surface	UNDT zoop, krill (4)
SAGU	Sabine's gull	*Xema sabini*	0.00423	Surface	UNDT
STAL	Short-tailed albatross	*Phoebastria albatrus*	0.00279	Surface	UNDT squid, fish (4)
TBMU	Thick-billed murre	*Uria lomvia*	0.401	Diver	Fish, krill, poly (1)
THGU	Thayer's gull	*Larus thayeri*	0.000129	Surface	UNDT fish, krill (4)
TUPU	Tufted puffin	*Fratercula cirrhata*	0.326	Diver	Fish, poly (1)
UNSH	Dark shearwaters	*Ardenna* spp.	27.6	Diver (1)	Krill, fish (2), squid (4)

cies of shearwater in the region (Howell 2012), and all shearwaters collected at sea were this species (Hunt et al. 1996, 2002a). We excluded loons, grebes, and ducks because they use the area primarily as a migration corridor, but only rarely for foraging, at least in summer.

To avoid having a small number of observations with unusually high densities affect the analyses, we used the following conditions to identify an outlier: (1) >1000 individuals of that particular species had to be observed, and (2) the observation had to be >10 SD above the mean density for that particular species. Outliers were not removed, but rather their value was set to the maximal value observed within the remaining records of that species. This procedure affected 2 records of black-legged kittiwakes.

Examination of bird data by depth interval

To examine how the cross-shelf use of the southeastern Bering Sea by seabirds might differ between years with early or late sea-ice retreat, we divided the southeastern shelf into bands of differing bathy-

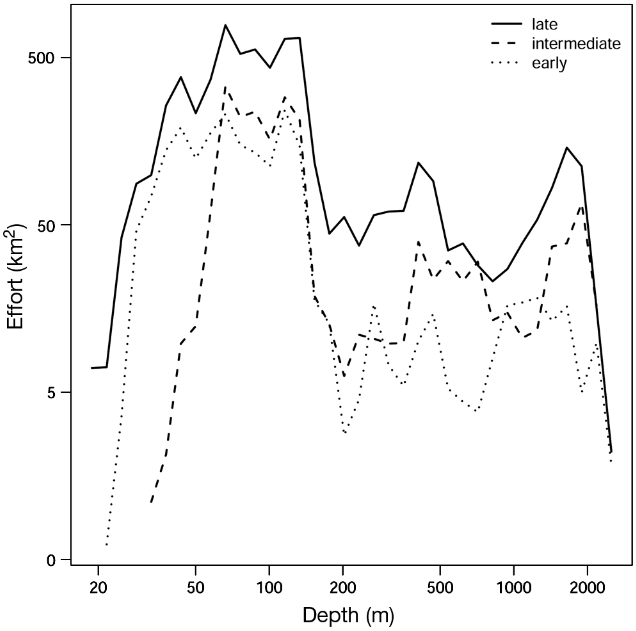

Fig. 4. Seabird survey effort by depth across the study area in years with early, late, or intermediate timing of sea-ice retreat

metry (depth). Bathymetry data were extracted from the Alaska Ocean Observing System (AOOS) bathymetry database (http://portal.aoos.org/#module-metadata/8c6e4afa-4294-11e2-920a-00219bfe5678, accessed 30 January 2013). To smooth some of the fine-scale local variation in the 1 km high-resolution bathymetry which was unlikely to be relevant to seabirds, we applied a 9 km × 9 km moving average filter.

From northeast to southwest, the ocean floor is gently down-sloping over much of the study area, but then drops rapidly at the continental slope (Fig. 1). We sought a trade-off between sufficient seabird samples within each bathymetry band and spatial resolution. A logarithmic division of bathymetry was chosen rather than linear intervals, because with the inclusion of the shelf break, there were regions (shelf slope) with very rapid changes in bathymetry as compared to the very gradual changes in depth across the shallower portions of the shelf. Therefore, we defined bands to be evenly spaced on a log-scale of depth so that the bounding isobaths would each be 1.15 times deeper than the previous respective isobath (see Fig. 2, top, in Hunt et al. 2014). Because our sampling of seabird distributions was uneven in space and time, the data available were not sufficient to calculate the mean bathymetry–depth distributions of seabird species on an annual basis. To account for variation in the sampling effort among bathymetry bands (Fig. 4), we averaged the density (birds km^{-2}) of each species within each band.

Use of frontal areas

For each seabird species in our study, we calculated the difference of the proportion of that species that was at the Inner, Middle, and Shelf-break Fronts between years with early sea-ice retreat and years with late sea-ice retreat. We used the change in annual proportions rather than an absolute increase or decrease in a frontal region because the total numbers of a species present in the study area often differed significantly between years with early sea-ice retreat and years with late sea-ice retreat (Renner et al. 2016).

RESULTS

Shifts in the cross-shelf distributions of potential seabird prey

In years with early sea-ice retreat, the middle and inner shelf copepod *Calanus marshallae* shifted the center of its distribution toward the deeper waters of the Outer Shelf Domain (Table 2). The shelf-slope copepods *Neocalanus* spp. and euphausiids appeared to shift their centers of cross-shelf distribution very

Table 2. Shifts in the cross-shelf distributions of selected zooplankton and age-0 walleye pollock within the study area. Confidence intervals (CI) on the difference between the bathymetry centroids (early minus late years) were calculated from 5000 bootstrap replicates

Prey species/group	Depth (m) at location of centroid		Difference and 95 % CI	Years of data
	Years with early sea-ice retreat	Years with late sea-ice retreat		
Neocalanus spp.	142	129	13 (−1, 33)	2003–2010
Euphausiid spp.	120	108	12 (9, 14)	2004, 2006, 2007–2010, 2012, 2014
Calanus marshallae	130	78	52 (37, 65)	2003–2010
Age-0 *Gadus chalcogrammus*	83	84	−1 (−29, 19)	2003–2010

little, with the euphausiids showing about a 10% depth shift from the inner edge of the Outer Shelf Domain to the middle of that domain in years with early sea-ice retreat (Table 2). Age-0 walleye pollock, which were found chiefly in waters of the Middle Shelf Domain, showed little or no shift in cross-shelf distribution (Table 2).

Use of frontal areas by seabirds

In our test of the hypothesis that seabird species should increase their use of frontal areas in years with early sea-ice retreat, we found no clear pattern of increased use of the Inner, Middle, and Shelf-break Fronts in years with early sea-ice retreat (Figs. 5 & 6). In years of early sea-ice retreat, 13 of 34 species increased their proportional use of these 3 fronts, whereas 21 decreased their proportional use of these fronts (Figs. 5 & 7). Among pursuit-diving seabirds, 8 of 15 species decreased their proportional use of the Inner and Shelf-break Fronts in years with early sea-ice retreat, whereas 7 species increased the proportional use of these fronts. Surface-foraging seabird species showed a lesser use of these fronts in years with early sea-ice retreat: 6 of 19 species increased their proportional use of the Inner, Middle, and Shelf-break Fronts, and 13 species showed a decreased proportional use. Three surface-foraging species (red phalarope, red-necked phalarope, and Laysan albatross) showed increased use of the Middle Front in years with early sea-ice retreat (Fig. 5).

With the exception of the 3 species mentioned above, none of the fronts showed a strong attraction for seabird species in years with early sea-ice retreat, although somewhat more species showed a shift of their centers of distribution to the Inner Front (Fig. 6). In years with early sea-ice retreat, only 3 of the 20 most common species (least auklet, red-necked phalarope, and Arctic tern) had concentrations in the region of the Inner Front (as demarked by steep increases in their cumulative frequency distributions in the region of the front), while glaucous-winged gull, tufted puffin, northern fulmar, and fork-tailed storm-petrel had concentrations in the Shelf-break Front (Fig. 5). In years with late sea-ice retreat, parakeet auklets, least auklets, and Arctic terns had concentrations in the area of the Inner Front, while Arctic terns, fork-tailed storm-petrels, and Laysan albatrosses had concentrations in the Shelf-break Front region (Fig. 5). For none of these species did the elevated numbers within these frontal areas demark the centers of their abundances across the shelf.

Cross-shelf distributions of seabirds

Despite the lack of increases of seabird densities in frontal areas in years with early sea-ice retreat, there were considerable differences in seabird cross-shelf distributions between years with early and late sea-ice retreat (Fig. 5). Among the 20 most abundant seabird species in the study area, 7 species shifted their distributions toward deeper water in years with early ice retreat, and 12 species showed shifts toward shallower waters (Fig. 5). In years with early sea-ice retreat, seabird species with mean bathymetry distributions that were shallow tended to move toward deeper waters, whereas those with mean distributions that were at or beyond the shelf edge tended to move toward shallower waters (Fig. 8). When examined by foraging guild, surface-foraging species showed larger shifts in distribution between years with early and late sea-ice retreat than pursuit-diving species, as predicted, but the 95% confidence intervals overlapped broadly (Fig. 8).

Of the seabird species with the deepest average depth distributions and the strongest shift toward shallower waters in years with early sea-ice retreat, short-tailed albatross (Fig. 8) and Laysan albatross (Figs. 5 & 8) stand out. These 2 species are surface (or near-surface) foragers, as is the parasitic jaeger (Fig. 8), which also showed a strong shift toward shallower waters. Other offshore surface foragers shifting toward shallower waters in years with early sea-ice retreat included fork-tailed storm-petrel (Figs. 5 & 8), Leach's storm-petrel (Fig. 8), long-tailed jaeger (Fig. 8), and red-legged kittiwake (Figs. 5 & 8); the latter is a myctophid specialist when breeding. In contrast, black-footed albatross (Fig. 8) tended to shift farther off the shelf, as did the mottled petrel (Fig. 8), a relatively rare species (Table 1). No pursuit-diving species had a strong shift from deep water to the shelf; thick-billed murres (Figs. 5 & 8) had a center of distribution off the shelf and shifted shelf-ward, but not onto the shelf, in the years with early sea-ice retreat.

In contrast to the 'deep-water' species, seabirds with the centers of their distributions over the middle or inner shelf showed both shifts to deeper water and shifts to shallower waters in years with early sea-ice retreat (Figs. 5 & 8). Least auklets (planktivores) shifted the center of their distribution inshore from the waters of the Outer and Middle Shelf Domains to offshore of the Inner Front, whereas shearwaters (omnivores) shifted their center of distribution to just inshore of the Inner Front

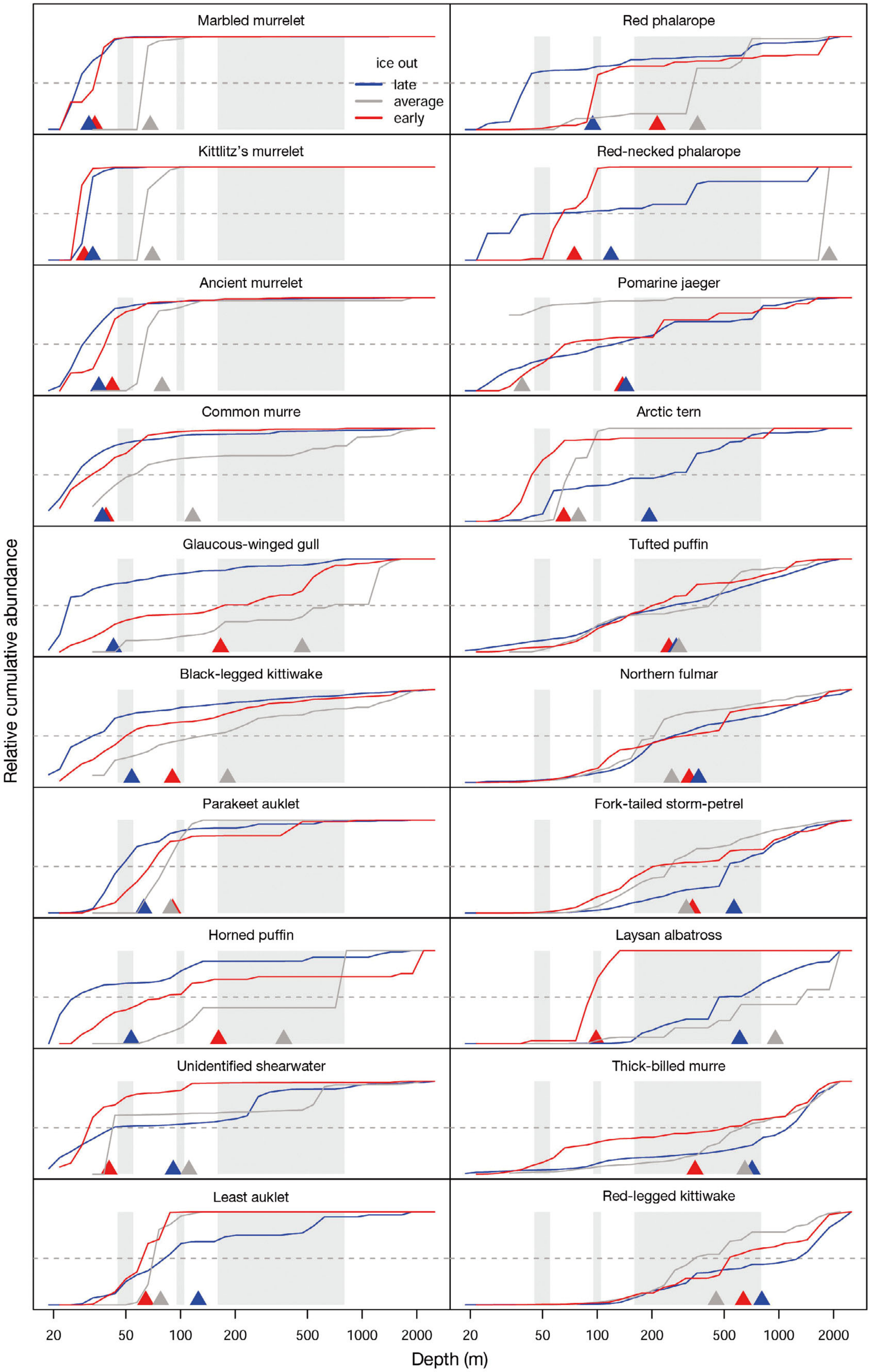
Marbled murrelet
ice out
late
average
early
Red phalarope
Kittlitz's murrelet
Red-necked phalarope
Ancient murrelet
Pomarine jaeger
Common murre
Arctic tern
Glaucous-winged gull
Tufted puffin
Black-legged kittiwake
Northern fulmar
Parakeet auklet
Fork-tailed storm-petrel
Horned puffin
Laysan albatross
Unidentified shearwater
Thick-billed murre
Least auklet
Red-legged kittiwake
Relative cumulative abundance
20
50
100
200
500
1000
2000
20
50
100
200
500
1000
2000
Depth (m)

Fig. 5. Cross-shelf cumulative density distributions of the 20 most abundant seabird species in summers of years with early, late, and intermediate timing of spring sea-ice retreat. The Inner Front (45–55 m), the Middle Front (85–105 m), and the Shelf-break Front (160–800 m) are delineated with grey shading. The grey dotted lines denote 50 % of the cumulative frequency distribution. The triangles are the centers of the distribution of a species in years with early (red), late (blue), and intermediate sea-ice retreat (grey). Panels are arranged as species with predominately shallow-water distributions to those with predominately deep-water distributions

(Appendix, Figs. 5 & 8). Horned puffins, black-legged kittiwakes, and glaucous-winged gulls (all piscivores) shifted their distributions offshore from near the Inner Front to near the shelf edge (Figs. 5 & 8). Others, such as marbled murrelets, Kittlitz's murrelets, ancient murrelets, and common murres, all of which are piscivorous pursuit divers, showed little variation in their depth distributions (Figs. 5 & 8).

DISCUSSION

Seabird distributions in years with early and late sea-ice retreat

It has become increasingly clear that the timing of sea-ice retreat in the southeastern Bering Sea, and/or sea temperatures there, have a profound impact on its marine food webs (e.g. Coyle et al. 2011, Hunt et al. 2011, 2016, Duffy-Anderson et al. 2016, 2017, Farley et al. 2016, Gann et al. 2016, Sigler et al. 2016, Coyle & Gibson 2017). In our paper, we focused on expanding our understanding of how seabird distributions over the southeastern Bering Sea shelf respond to variations in the timing of sea-ice retreat and the resulting variation in the location and abundance of their prey. Knowledge of how seabirds are dispersed under different climate conditions is a first step in the identification of present areas of importance to seabirds, and how the distribution of these areas may change with climate warming. There may be different sea-ice/warming pressures influencing offshore and onshore seabirds, as well as different impacts on resident breeders vs. migrants. The stability of regional foraging grounds near seabird colonies will be critical for breeding birds, while migrants may have to keep moving to other seasonal foraging grounds.

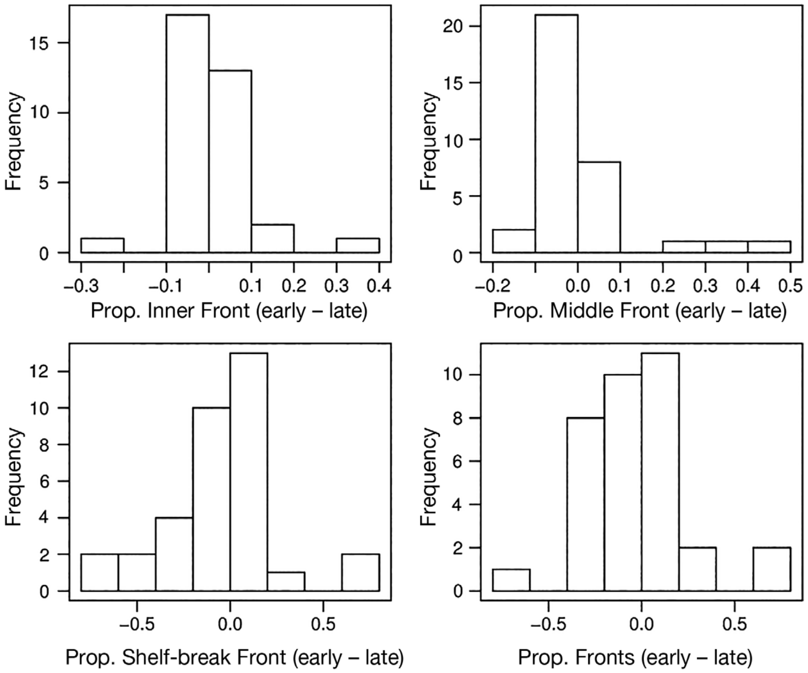

Fig. 6. Frequency distributions of change in the proportion (prop.) of seabirds (all species) using the Inner, Middle, Shelf-break and total Fronts in years with early sea-ice retreat minus years with late sea-ice retreat

Frontal shift hypothesis

We investigated the hypothesis that seabirds in years of early sea-ice retreat, given a significant reduction in the biomass of both large, lipid-rich copepods (e.g. *Calanus marshallae*) and euphausiids (Coyle et al. 2011, Hunt et al. 2011, 2016, Renner et al. 2016), would shift their centers of distribution to the Inner Front and the Shelf-break Front, as these fronts typically are areas of high rates of production in summer (Springer et al. 1996, Kachel et al. 2002, Jahncke et al. 2005). We had also assumed that there would be a seaward shift in the cross-shelf distributions of both *C. marshallae* and euphausiids, as we expected that their abundances in the Middle Shelf Domain would decline in years with early sea-ice retreat to a greater degree than would occur over the outer shelf (Hunt et al. 2016, Renner et al. 2016,

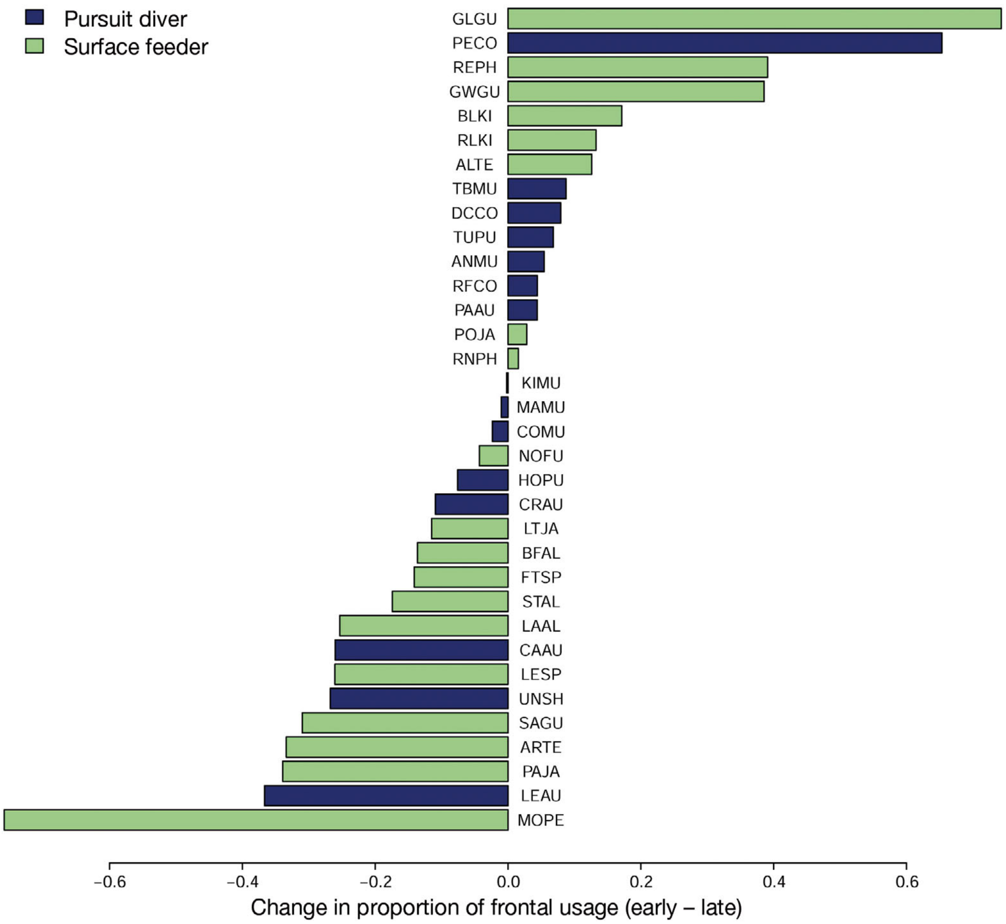

Fig. 7. Change in proportion of a species using of frontal areas (Inner and Shelf-break Fronts, combined), comparing years with late and early sea-ice retreat. See Table 1 for full species names

Sigler et al. 2016). Although, as predicted, we found a significant shift in the center of distribution of *C. marshallae* from the Middle Shelf Domain toward the outer shelf, the cross-shelf shift in the distribution of euphausiids was unexpectedly small. Contrary to our predictions, there was no cross-shelf shift in the centers of distribution of seabirds from the Middle Shelf Domain toward either the Inner Front or the Shelf-break Front, or to the Outer Shelf Domain. Instead, the most notable cross-shelf shift in seabird distributions was to the Middle Shelf Domain.

In developing our hypothesis of a shift to frontal regions, we had focused on the impacts of the timing of sea-ice retreat on the distribution and abundance of zooplankton and had overlooked the potential impact on the distribution and abundance of age-0 pollock. Earlier work had shown that age-0 pollock were significantly more abundant in surface (0–20 m) waters of the Middle Shelf Domain in 'warm' years (e.g. Moss et al. 2009). Recent work has shown that age-0 pollock were about 50× more abundant in surface waters of the Middle Shelf Domain in years with early sea-ice retreat as compared to years with late sea-ice retreat (Renner et al. 2016), although the proportions of the age-0 pollock over the middle and outer shelves remained similar, despite the increase in abundance. Blood (2002), Smart et al. (2012), and others have shown that early life stages of pollock fare better in 'warmer' waters, with higher survival and faster growth. Additionally, age-0 pollock preflexion larvae, late larvae, and juveniles are expected to shift inshore onto the shelf in warm years compared to cold years (e.g. a decrease in offshore density of juveniles was observed in warm years), based on modeled results for 1988–2009 (Smart et al. 2012). Most of the seabird species that shifted their centers of distribution into the Middle Shelf Domain are surface foragers that take forage fish as a component of their diet. It is likely that the shift of these seabirds to the middle shelf was motivated by an increased availability of age-0 pollock there in years with early sea-ice retreat.

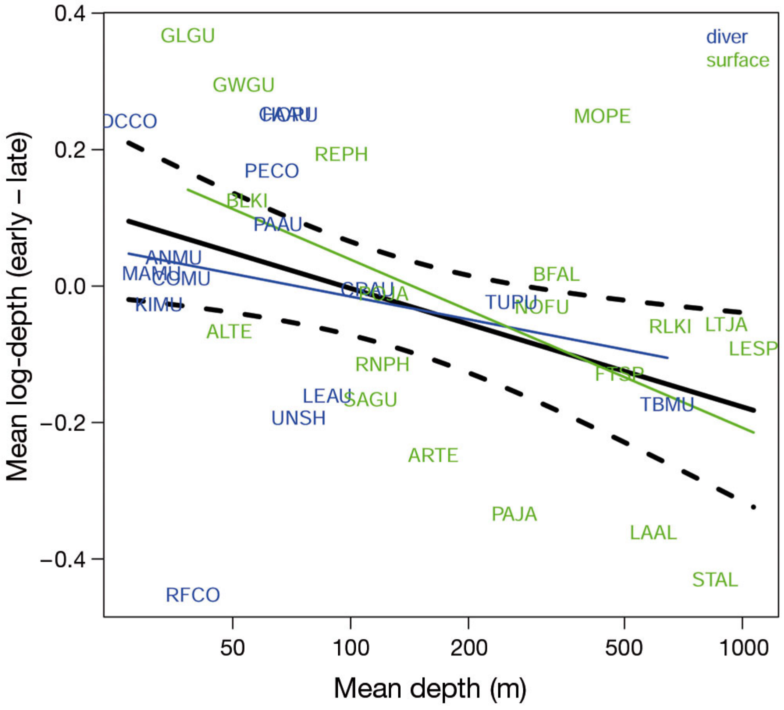

Fig. 8. Extent of change in depth relative to mean depth distribution of seabird species in summers of years with early and with late sea-ice retreat. Species with values below 0.0 mean log depth (early – late) moved shoreward, those above the line moved seaward. The overall effect (black line) is statistically significant at p = 0.019. Black dashed lines are 95% confidence intervals. As expected, surface-foraging species appear to have somewhat greater movements than pursuit diving species, although the difference is not statistically significant (p = 0.26). See Table 1 for full species names

Shifts of seabirds from the basin to the outer and middle shelf

Overall, cross-shelf shifts in seabird distributions between years with early and late sea-ice retreat were of the same order of magnitude as the distribution shifts between spring and summer seasons reported by Hunt et al. (2014) (Fig. 9) or between summer and fall as reported by Suryan et al. (2016). One of the most striking patterns was the shift of most seabird species with off-shelf centers of distribution in years with late sea-ice retreat to shallower distributions in years with early sea-ice retreat, which resulted from both a decrease in use of off-shelf waters and an increase in the use of shelf waters (See Fig. 1c in Renner et al. 2016). While 3 of the species (red-legged kittiwake, thick-billed murre, and fork-tailed storm-petrel) moved from the outer edge of the 'greenbelt,' a region of high productivity offshore of the shelf (Springer et al. 1996) to the top of the slope, Laysan albatrosses and Arctic terns shifted the center of their distributions well into the Middle Shelf Domain. All of these species, except the thick-billed murre, are surface foragers. The food habits of this group are quite diverse (Table 1), but at least 2 species, i.e. Laysan albatross and the fork-tailed storm-petrel, are unlikely to have been attracted to upper slope and shelf waters by age-0 pollock.

An alternative hypothesis is that the deep waters of the outer slope region may become more strongly stratified in warm years than in cool years. Increased heating of the upper mixed layer in warm years could lead to stronger stratification, and an earlier shut down of primary production (see Brown et al. 2011 for a discussion of the impact of warming on primary production over the shelf), but data are lacking to test this hypothesis. If upper mixed-layer productivity dropped, vertically migrating zooplankton and fish might be expected to remain at depth and become less accessible or inaccessible to surface- and near-surface foraging seabirds. In contrast, mixing at the shelf edge (Mizobata et al. 2008), and provision of iron there through the melting of sea ice, could result in a longer, more intense outer shelf bloom in years when sea ice reaches the shelf edge (Aguilar-Islas et al. 2008), consequently resulting in more robust *Neocalanus* spp. populations. Panteleev et al. (2012) related the Pacific Decadal Oscillation (PDO) signal to eddy kinetic energy in the Bering Sea basin, and Zhang et al. (2010) modeled a strong correlation between the PDO and sea-ice cover over the eastern Bering Sea shelf. It remains unclear how interannual variation in the eddy kinetic energy or sea-ice cover over the shelf may affect variation in seabird prey availability over the basin. This is an area requiring further study.

Little work has been done in slope and near-slope basin waters, but if the productivity of off-shelf surface waters shuts down early in 'warm' years, it could have a strong impact on both fish and seabirds dependent on food resources in the upper mixed layer there. On-shelf shifts in seabird distribution will also likely increase the interactions between the seabirds and the long-line fisheries, with the inevitable result of increased seabird mortality. This increased mortality will be of particular concern in the case of the 3 albatross species that presently, in the eastern Bering Sea, are found mostly near the shelf-slope, as

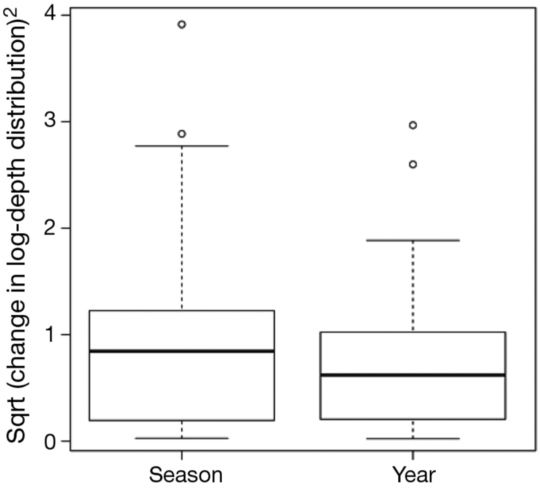

Fig. 9. Comparison of the change in median depth range of seabird species between spring and summer seasons (all years) and between years with early and late sea-ice retreat. Boxes are median with first and third quartiles. Whiskers are 1.5 times interquartile range. Circles are outliers

well as off-shelf, especially given trends toward more frequent ‘warm’ years.

Inshore shift of shearwaters

Shearwaters, for the most part short-tailed shearwaters, are the most abundant species of seabird in the southeastern Bering Sea (Hunt et al. 2014, Kuletz & Labunski 2017). Their distribution pattern changed radically between years with late sea-ice retreat and years with early sea-ice retreat (Renner et al. 2016, this study). Not only did their distribution center shift from the Outer Shelf Domain to just inside the Inner Front, but their numbers were lower in the years of early sea-ice retreat by comparison with years of late sea-ice retreat (Renner et al. 2016). In the years with late sea-ice retreat, shearwaters were spread across much of the shelf, from the shelf-slope region to the Inner Shelf Domain (Renner et al. 2016, this study). However, in the years of early sea-ice retreat, they were concentrated inshore of the Inner Front. Although there are insufficient data to know what attracted shearwaters so far inshore during years with early sea-ice retreat, earlier work has shown that they consume both the shelf euphausiid *Thysanoessa raschii* and age-0 pollock in the vicinity of the Inner Front (Hunt et al. 2002a, Baduini et al. 2006). The biomasses of euphausiids and age-1 pollock were significant predictors of shearwater abundance in the southeastern Bering Sea during 2008–2010 (Suryan et al. 2016).

Impacts on seabirds breeding on the Pribilof Islands

At-sea distributions of prey impact the reproductive ecology and physiology of breeding seabirds. In the southeastern Bering Sea, interannual variability in the availability of both large, lipid-rich zooplankton and age-0 pollock affects the productivity and physiology of seabirds nesting on the Pribilof Islands. Evidence is accumulating that in years with early sea-ice retreat and warm water, black-legged kittiwakes have lower levels of stress hormones, which have been associated with higher reproductive performance, than they do in years characterized by cold water (Satterthwaite et al. 2012, Yamamoto et al. 2016). There is also evidence that some seabird species nesting on the Pribilof Islands shift the region in which they forage between years with early and late sea-ice retreat. For example, Yamamoto et al. (2016) found that pursuit-diving thick-billed murres reduced their foraging in off-shelf waters in years with late sea-ice retreat compared to years with early sea-ice retreat, whereas red-legged kittiwakes did not shift foraging areas. Murres also changed their diets between ‘warm’ and ‘cold’ water years, with juvenile pollock and sand lance predominating in 2004, a warm year with intermediate sea-ice retreat, and cephalopods, pollock, and sculpins in 2007, a cold year also with intermediate timing of sea-ice retreat (Kokubun et al. 2010). Although the levels of the stress hormone corticosterone did not differ between years in red-legged kittiwakes, in thick-billed murres corticosterone levels were higher in a year with late sea-ice retreat. Corticosterone levels in planktivorous least auklets nesting on the Pribilof Islands were higher in years with early sea-ice retreat and a reduced proportion of *Neocalanus* spp. in their diets, suggesting that their preferred prey, i.e. large, lipid-rich copepods, were scarce in these ‘warm’ years (Dorresteijn et al. 2012).

Implications

In the short term, occasional periods of warm conditions with early sea-ice retreat may have beneficial effects for seabird species that consume small forage fish such as age-0 pollock. For example, the improved nutritional state of seabirds nesting on St. George Island, such as black-legged kittiwakes and thick-billed murres (e.g. Renner et al. 2012, 2014; Kokubun et al. 2018, this Theme Section), and the increases in the pelagic abundances of some seabird species, as reported by Renner et al. (2016), support the hypothesis that the increased abundance of age-0 pollock in surface waters provides a valuable resource for seabirds. On the other hand, most seabird species present in the study area during summer were less abundant during the years of early sea-ice retreat (Renner et al. 2016). Additionally, the advantage of having abundant age-0 pollock in surface waters may be only temporary; during prolonged periods of years with early sea-ice retreat, successive years of small year classes of pollock occur, with a consequent decline in the biomass of pollock (Ianelli et al. 2016). The reduction in the abundance of the large, lipid-rich zooplankton, *Calanus marshallae/glacialis* and *Thysanoessa raschii,* over the southeastern Middle Shelf Domain in years with early sea-ice retreat is likely to have a severe impact not only on pollock and cod recruitment (e.g. Farley et al. 2016, Sigler et al. 2016), but also on seabirds and marine mammals dependent directly on these zooplankton, e.g. least auklets nesting on the Pribilof Islands (Dorresteijn et al. 2012). The likely resultant decline in forage fish, not only juvenile pollock, but also capelin and sand lance (Andrews et al. 2016), can be expected to negatively impact piscivorous seabirds and marine mammals in a warming Bering Sea.

The strong shift in the distribution of surface-foraging seabird species from the deep waters of the basin to the Shelf-slope and Outer Shelf Domains in warm years with early sea-ice retreat was not expected. This shift could reflect either the documented increased availability of age-0 pollock in surface waters of the middle shelf in early sea-ice retreat years (e.g. Moss et al. 2009, Renner et al. 2016, this paper), or the hypothesized decline in the near-surface availability of prey over deeper waters. The abundance and distribution of squid species may also be influencing seabird distribution in the eastern Bering Sea. Squid distributions and abundances remain largely unknown in the eastern Bering Sea. We require new information on squid as well as on the abundance and near-surface availability of large, lipid-rich zooplankton such as *Neocalanus* spp., and forage fish, including myctophids, over the deep basin and shelf slope to test these hypotheses. If the shifts in the seabird distributions in years with warm surface waters are indicating a decline in prey resources over the basin, then there are potential long-term implications for the salmon and other large predators that forage in these waters.

CONCLUSIONS

This study has shown that the cross-shelf distribution of seabirds in the southeastern Bering Sea is related to the timing of sea-ice retreat in spring. Our work supports the hypothesis that these shifts in seabird distributions are likely in response to changes in the distribution, abundance, and availability of their prey. Over the shelf, changes in prey distributions and abundances are related to the reproduction and recruitment of large, lipid-rich copepods and euphausiids and the effects of their availability on the production and vertical distribution of age-0 pollock. Many seabird species shifted the cross-shelf centers of their distributions to the middle shelf region in years with early sea-ice retreat (‘warm’ years), likely because age-0 pollock were more abundant in surface (<20 m) waters than in years with late sea-ice retreat (‘cold’ years). This result suggests that in future, warmer years, the abundance of these age-0 pollock will be able to support abundant seabird populations. However, other recent studies have shown that the abundances of seabirds in warm years with early sea-ice retreat drop significantly (Renner et al. 2016). Possibly, the declines in large, lipid-rich copepods and shelf euphausiids have a greater negative impact on the seabirds, such as euphausiid-eating shearwaters, foraging over the shelf than the advantages provided by an abundance of lipid-poor age-0 pollock.

We found no general shift of seabirds to the frontal areas during years with early sea-ice retreat, and in fact, concentrations of most seabird species declined in frontal areas under warmer conditions. However, one particularly abundant taxon of seabirds, i.e. dark shearwaters (primarily short-tailed shearwaters), did shift its cross-shelf center of distribution from the outer shelf to inshore of the Inner Front, an area demonstrated to have persistent production throughout summer. This may indicate that the Inner Front is important for sustaining zooplankton and age-0 pollock populations in years with early sea-ice retreat.

In years with early sea-ice retreat, several seabird species moved the centers of their distributions from the deepest waters that we surveyed to well onto the shelf. This distribution shift may have reflected surface warming (and possible increased stratification) in the deep, offshore waters, as well as higher levels of production over the shelf edge and outer shelf (Brown et al. 2011). It will be important to test these hypotheses, as the implication is that in future warm years, productivity in the upper mixed layer of the

Bering Sea basin may be reduced, thereby affecting fish populations, such as salmon species, that forage there.

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Appendix. Prey taken by short-tailed shearwaters collected in the southeastern Bering Sea. PROBES refers to birds collected during the PROBES study (McRoy et al. 1986) in an area roughly congruent with the study area encompassed in the present study. % occ.: percent of samples in which prey type occurred; % wt.: percent of the mass of all samples combined; %vol.: percent of the volume of all samples combined; % num.: percent of items of a particular group divided by the number of all items present

Year	Season	Area	*Themisto libellula*	*Thysanoessa raschii*	Other euphausiids	Zoeae	Fish	Reference
1970s	Unknown	North of Pribilofs	66.7 % wt.	99.4 % occ. 20.5 % wt.			Capelin/pollock 12.6 % wt.	Ogi et al. (1980)
1981	Spring	PROBES		82 % vol.				Schneider et al. (1986)
1982	Spring	PROBES		100 % vol.				Schneider et al. (1986)
1989	Summer	Around St. Paul Is.		100 % num.			0.00 % vol.	Hunt et al. (1996)
1997	Spring	Inner Front		100 % num.				Hunt et al. (2002a)
1997	Fall	Inner Front		41 % num.	50 % num.	Zoeae 8 % num.	1 % vol. pollock	Hunt et al. (2002a)
1998	Spring	Inner Front		99 % num.			20 % vol. sandlance	Hunt et al. (2002a)
1998	Fall	Inner Front		19 % num.	10 % num.	Zoeae 61 % num.	77 % vol. pollock	Hunt et al. (2002a)
1999	Spring	Inner Front		49 % num.	51 % num.		41 % vol. pollock	Hunt et al. (2002a)
1999	Fall	Inner Front		96 % num.			59 % vol. pollock	Hunt et al. (2002a)

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Contribution to the Theme Section 'Seabird responses to a changing Bering Sea'

Persistent annual migration patterns of a specialist seabird

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ABSTRACT: Specialization can make animals vulnerable to rapid environmental changes. For long-lived seabirds, foraging specialization may make individuals especially sensitive, as climatic changes are currently occurring over the course of one lifetime. The Bering Sea is a dynamic subarctic and arctic ecosystem where windblown sea ice mediates annual productivity and subsequent pathways to upper trophic levels. Red-legged kittiwakes *Rissa brevirostris* are endemic surface foraging seabirds specializing on myctophid fishes during reproduction. Their degree of specialization outside the breeding season is less understood. We examined their non-breeding ecology (migration, distribution, isotopic niche) during 4 winters with varying sea ice extent. Although we found annual variation in core distributions, diets (as reflected in feather stable isotope signatures), and outbound migratory timing, the winter range of red-legged kittiwakes was restricted to the western regions of the Bering Sea and North Pacific. Contrary to expectations, sea ice did not limit distributions in the Bering Sea in 3 yr: e.g. sea ice associations (<100 km) were infrequent (8.7 % mo^{-1}). Yet, their wintering range often overlapped with areas of seasonal ice cover, suggesting range-wide use of sea ice ecosystems. Stress levels measured by corticosterone in feathers were generally low. However, birds that concentrated in the Bering Sea in February had higher stress levels and fed at a lower trophic level than those in the western Aleutians and western subarctic. As conditions change, this persistence in wintering locations, while incurring differential stress levels, may contribute to rapid population fluctuations as has been observed in the recent past.

KEY WORDS: Feather corticosterone · Life-history trade-off · Geolocation · Migration · Net-squared displacement · Stable isotopes · Red-legged kittiwake · *Rissa brevirostris*

INTRODUCTION

Specialization in habitat use, diet, or behavior can make animals vulnerable to rapid environmental changes (Colles et al. 2009, Clavel et al. 2011). If specialists are long-lived animals, they may be particularly vulnerable to anthropogenically driven climate change, as individuals are now experiencing significant environmental changes over the course of their lifetime (Henson et al. 2017). Specialization can occur

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at individual, population, and species levels. The degree of specialization can be considered on a continuum (Bolnick et al. 2003). For instance, foraging strategies and habitat are often linked, and this may result in seasonal or annual variation in diet (e.g. Hückstädt et al. 2012). Yet, within a season, individuals may continually specialize on the same prey (Elliott et al. 2009). Conceivably, narrow dietary preferences for certain prey could limit foraging in the midst of what appear to be ample resources. Specialization can occur in tandem with flexibility in other behaviors, such as the ability to adjust breeding or migratory phenology. Understanding how individuals of specialized populations alter or maintain migratory behavior in the face of differing annual conditions may help to further our understanding of how they might fare under future climatic conditions.

Foraging or migratory specialists are presumed to be employing a predictably beneficial strategy, yet changing conditions could alter the cost of strategies over both the short and long term. In seabirds, including red-legged kittiwakes *Rissa brevirostris*, the stress hormone corticosterone can be used as a proxy to measure relative exposure to nutritional stress (Kitaysky et al. 2001, 2007) and provides a mechanistic link between food shortages and reproductive timing, success, and survival (Goutte et al. 2011, Nelson et al. 2015). Furthermore, corticosterone is incorporated into feathers, providing an integrated measure of the nutritional stress experienced during feather growth (Bortolotti et al. 2008, Will et al. 2014). Therefore, feathers can be collected during the breeding season and provide insight into the nutritional history of a bird's preceding migration that can be related to concurrent tracking data. The combination of spatial and physiological information allows for a representation of the 'stress landscape' experienced by individuals during the molting period.

The Bering Sea is a dynamic marine ecosystem situated at the boundary of the subarctic and arctic biomes, and in recent years anthropogenic climate change has driven changes in environmental conditions and dependent ecosystem components (Grebmeier et al. 2006, Litzow et al. 2014, Springer & van Vliet 2014). The eastern Bering Sea is dominated by a shallow shelf that in some years is covered by windblown sea ice (Brown et al. 2011). Running the south–north length of the Bering Sea, the shelf break is often termed the 'Green Belt' for its high productivity (Springer et al. 1996). Likewise, the narrow shelf in the western Bering Sea is associated with high productivity (Brown et al. 2011, Belkin 2016). In contrast, the northern arctic portion of the Bering Sea is supported by benthic-based food webs (Grebmeier et al. 2006). Framed by these shelf ecosystems, the Bering Sea basin is dominated by an anticyclonic current and eddies that concentrate prey for seabirds and seals (Nordstrom et al. 2013, Paredes et al. 2014). In the eastern Bering Sea, the duration, timing, and extent of sea ice over the shelf interact to influence primary productivity, and distributions of upper trophic organisms such as fish and seabirds (Wyllie-Echeverria & Wooster 1998, Renner et al. 2016). The relationship between sea ice and species that primarily use the waters of the Bering Sea basin is less understood. The contemporary Bering Sea, particularly the eastern shelf region, oscillates between years dominated by warmer water temperatures and less sea ice, contrasted by years of colder temperatures (Overland et al. 2012). In simple terms, these oscillations provide a natural experiment for how long-lived upper trophic level organisms may react to fundamental changes in prey type and availability that occur with annual changes in sea ice extent.

Red-legged kittiwakes are surface-foraging seabirds endemic to the Bering Sea, nesting at only a few colonies along the Aleutian Islands, in the Commander Islands, and in the Pribilof Islands, where >70% of the entire population nests on the tall cliffs of St. George Island (~235 000 pairs; Byrd et al. 2008a, Goyert et al. 2017). Red-legged kittiwake populations at St. George Island experienced a significant decline in the 1980s leading to an IUCN 'Vulnerable' designation (BirdLife International 2017). In summer, red-legged kittiwakes are more specialized in diet and habitat use than their congener, the black-legged kittiwake *R. tridactyla*, foraging almost exclusively (by volume) on myctophid fishes and squid that are found at the surface at night in waters over the slope and basin (Sinclair et al. 2008, Kokubun et al. 2015). Both kittiwakes breeding on St. George Island have similar overall productivity (fledglings nest^{-1}), but red-legged kittiwakes typically have higher fledgling success (chicks fledged per number of eggs laid) than black-legged kittiwakes (Byrd et al. 2008b, Springer & van Vliet 2014), providing evidence that they are employing a foraging strategy that is usually profitable.

Although foraging specialization of red-legged kittiwakes in the breeding season is well documented, little is known about their specialization during nonbreeding. In comparison to black-legged kittiwakes, red-legged kittiwakes have a narrower dietary niche (quantified by stable isotope values of feathers) and occupy a substantially smaller wintering range, both as a group and individually (Orben et al. 2015a).

However, these earlier results were based on a single winter of tracking, and distributions could shift annually (Orben et al. 2015b). Red-legged kittiwake tracking data and at-sea observations indicate the use of shelf habitats in both the northern and eastern Bering Sea, where their summer prey are not typically found (Tanimata et al. 2005), which suggests seasonal dietary flexibility. Additionally, the use of the northern Bering Sea during the autumn suggests the potential for sea ice-associated foraging, although due to the coarseness of geolocation tracking data, the exact degree of fine-scale spatial overlap is unknown (e.g. roosting, foraging in leads, avoidance; Orben et al. 2015a). Regardless, tracking individual movements across multiple years with differing sea ice conditions could help disentangle the degree to which red-legged kittiwakes are consistently associated with sea ice at broad spatial scales. Multiple years of tracking data will also further our understanding of the extent that red-legged kittiwakes are restricted in range during the winter, potentially a form of spatial or habitat specialization, and the degree to which migration timing is consistent. Feather stable isotopes can provide evidence for dietary specialization, in terms of similarity between individuals, during the period of feather growth (Thompson & Furness 1995). For red-legged kittiwakes, the period just before the birds return to the colony region could be expected to correspond to a period of food shortages when winter food resources are depleted and prior to the onset of spring productivity. This is also when birds undergo costs of growing feathers during their prenuptial molt and may need to regain/maintain body condition in preparation for breeding. Thus, this is a key time period during which to assess nutritional stress experienced during migration.

We tracked red-legged kittiwakes with geolocation data loggers during 4 winter migrations with variable sea ice conditions to better understand the degree to which these birds can be considered population-level migratory specialists during this timeframe. Given their consistency in foraging behavior during breeding, we predicted that specialization during the remainder of the year would also be apparent. The aims of our study were as follows: (1) to quantify between individual and among-year variation in wintering distributions, stable isotope inferred niches, and migratory timing; (2) to evaluate whether red-legged kittiwakes are consistently associated with sea ice at a broad scale; and (3) to test if differences in habitat use and migratory behavior correspond to winter stress levels, and if there is spatial structure in these values. These results provide the first look at changes in wintering behavior over a relatively long period (albeit still a short-term time period for this long-lived seabird).

MATERIALS AND METHODS

To study red-legged kittiwake wintering ecology, geolocation loggers that record light and wet/dry data were deployed on 96 red-legged kittiwakes in 2010 (Mk9, Mk19, British Antarctic Survey), 2013 and 2014 (Mk3, Biotrack), and 2015 (C-65, Migrate Technology) at St. George Island (56° 36′ N, 169° 33′ W) in the Pribilof Islands, Alaska, USA (Table 1). In successive years, 72% of birds were recaptured, and 59 complete wintering trips were obtained (Table 1). Loggers were attached to plastic leg bands using zip-ties and weighed 1–2.5 g. Although we cannot discount tagging effects, all loggers represented 0.2–0.8% of the birds' body weight (n = 107; 375 ± 29 [SD] g, min. = 305 g, max. = 470 g), a percentage below that at which minor negative effects have been recorded for smaller-bodied seabirds (Quillfeldt et al. 2012). Birds were caught at their nest sites using

Table 1. Sample sizes of red-legged kittiwakes deployed and retrieved with geolocation loggers from St. George Island, Alaska, USA. In total, 59 complete wintering trips were recorded (1 September to 15 April). In all years, additional birds were seen but not recaptured. Higher recapture rates in 2013–2014 and 2014–2015 are due to 3 and 2 yr of recapture effort, respectively. Only 1 yr of recapture effort occurred for the 2010–2011 birds

	Tag type	Tag mass (g)	Deployed (D)	Recaptured (R)	Complete tracks (C)	% Re-captured (R/D)	% Tag failure (R –C)/R	% Overall success (C/D)
2010–2011	Mk9/Mk19	2.5	23	16	15	69.6	6.3	65.2
2013–2014	Mk3	2.5	19	16	12	84.2	25	63.1
2014–2015	Mk3	2.5	20	14	9	70.0	35.7	45
2015–2016	C-65	1	34	23	23	67.6	0	67.6
Total			99	69	59	71.9	14.5	59.6

noose poles, foot snares, or a handheld CO_2 powered net gun (2011 recaptures only; Super Talon Animal Catcher; Advanced Weapons Technology). Head feathers (side of head), grown during the pre-nuptial molt from February to March (Gabrielson & Lincoln 1959), were collected at recapture.

Geolocation processing

To estimate locations, we first identified the timing of twilight associated with sunrise and sunset, and then twilight estimations were automatically selected (github.com/slisovski/twGeos). We used a light threshold of 0.5 for all tracks, but adjusted the sun angle selection window for each tag type to reduce the north–south spread of points (Mk19: –3 to 0; Mk9: –5 to 0, Mk3: –6 to 0; C-65: –7 to –1). Tracks were estimated using an iterative forward step selection process by computing the weighted probability for a cloud of possible locations (number of particles at each time step = 10 000) and selecting a potential location (Merkel et al. 2016). To calculate a median geographic track, this process was iterated along the track for 200 iterations (Merkel et al. 2016). A land mask (0.25° × 0.25°, NOAA OI SST V2 High Resolution Dataset) prevented the selection of points on land; however, this did not prohibit tracks from crossing land, particularly the Kamchatka ($n = 14$) and Alaska Peninsulas ($n = 3$), which are narrow enough for a kittiwake to cross in one 12 h period. Estimated travel speed of each individual was included for dry (in flight) (max = 22.22 m s^{-1}, mean ± SD = 10.6 ± 5.3 m s^{-1}; Paredes et al. 2012, Elliott et al. 2014) and wet (on water) (max = 1.7 m s^{-1}, SD = 0.25 m s^{-1}, optimal = 0.5 m s^{-1}; Conners et al. 2015) activity bins. Double tagging with GPS data loggers indicates that a median error in locations associated with this method (calculated at similar latitudes) is 185 km for the solstice and 145 km for equinox periods (Merkel et al. 2016). Two individuals were tracked for 2 complete consecutive winters; however, as black-legged kittiwakes show some site fidelity in their winter migrations (Orben et al. 2015b), and this appears to be the case for red-legged kittiwakes as well, only the first track recorded was used to characterize migratory behavior.

Distributions and migratory behavior

Utilization distributions (UDs) were calculated annually and for each bird from October through March (Calenge 2006), using a grid size of 50 km and a bivariate normal kernel. We estimated the scale of first peak in variance of first-passage time (FPT, 176 km) to determine a smoothing factor (h = 88 km; Lascelles et al. 2016). Tracks were projected using a Lambert azimuthal equal-area projection. Areas were calculated for the 95% and 50% UDs to compare range and core areas of use, respectively. Because the number of individuals tracked can influence area of UDs, we iteratively calculated area (1000 iterations) at increasing sample sizes for each year (Hindell et al. 2003). To provide metrics of similarity and space use sharing, we calculated Bhattacharyya's affinity (BA) as a metric of overall similarity between UDs, where 0 indicates no overlap and 1 indicates complete overlap for the 100% UD, and 0.50 indicates complete overlap for the 50% UD (Fieberg & Kochanny 2005).

To identify annual differences in the presence, duration, and timing of rapid long-distance migratory movements, we fitted non-linear models to the daily net-squared displacement (NSD) of each track (squared great-circle distance between each point and the breeding colony). Each track was fitted to a resident (logarithmic model), nomadic (linear model), disperser (single sigmoidal model), and 2 migratory models (double sigmoid), following Eq. (1):

$$\mathrm{NSD} = \frac{\delta}{1+\exp\left(\frac{\theta-t}{\varphi}\right)} + \frac{\delta * \zeta}{1+\exp\left(\frac{\theta+2*\varphi+2*\varphi_2+\rho-t}{\varphi_2}\right)} \quad (1)$$

where the distance between summer and winter ranges (δ) was either held constant (migratory, $\zeta = 1$) or allowed to vary (mixed migratory) (Bunnefeld et al. 2011, Spitz et al. 2017). The fit of each model type was assessed using Akaike's information criterion (AIC; Bunnefeld et al. 2011). In Eq. (1), t is time along the track, θ is the midpoint of migratory movements, φ quantifies the duration of the outbound migratory movement (φ_2 indicates the inbound leg) and ρ is the length of time spent on the winter range. We allowed flexible starting points along the first 60 d of each movement trajectory by first fitting models sequentially and minimizing AIC to find the best fit starting point (Spitz et al. 2017). We chose 60 d, as this encompasses the autumn equinox period and the time frame prior to migration. We found this approach particularly helpful due to inherent error in geolocations and kittiwake behavior, as some individuals made short excursions or moved slowly away from the colony before making the rapid long-distance movements characterized with this method. The inclusion of the mixed migratory model allowed for different end points, corresponding to wider ranging, yet colony centric, distributions in the spring pre-laying period. Additionally, we tested for annual differences in the cumulative distance traveled and the maximum distance from the colony attained by each bird.

Bathymetry and sea ice

Bathymetry was extracted from ETOPO1 (Amante & Eakins 2009) as the average depth within a 0.5 × 0.5° grid cell and then each point was categorized into bathometric habitats as follows: oceanic (>3000 m), slope (>1000–3000 m), shelf break (>200–1000 m), and continental shelf (≤200 m). Annual seasonal trends in bathymetric habitat use were assessed using generalized additive mixed models (GAMMs) with individual as a random effect and a quasi-Poisson log link function (Wood & Scheipl 2014). Smoothers were included for each year, and then years were sequentially combined to identify the model with the lowest AIC. Models were assessed through residual plots and checked for overdispersion.

Sea ice concentrations were extracted from daily remote-sensed sea ice data from passive microwave sensors for each location from a 50 × 50 km grid cell (Cavalieri et al. 1996). The minimum great circle distance to the sea ice edge (MASIE-NH, 4 km resolution; National Ice Center & National Snow and Ice Data Center 2010) was extracted as a second metric of sea ice association. These 2 datasets were combined to identify locations where kittiwakes were associated with sea ice.

Laboratory analyses

Stable isotopes

Due to enrichment with each trophic transfer, stable isotope ratios of nitrogen provide an estimation of trophic level, while stable isotope ratios of carbon reflect geographic gradients in carbon sources (Hobson et al. 1994). Therefore, quantification of isotope space provides an integrated assessment of niche width along the axes of diet and habitat during the time feathers are grown. To quantify winter niche space, we sampled head feathers from prenuptial plumage. Feathers were washed in a 2:1 chloroform: methanol solution, cut into small pieces, and weighed to the nearest mg in tin capsules. Samples from 2011 were analyzed using a Carbo-Erba elemental analyzer interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, UCSC). Feathers from 2014–2016 were analyzed at the University of Alaska Fairbanks Stable Isotope Facility using continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Delta+XP isotope ratio mass spectrometer (Thermo Electron) interfaced with an EA Costech ECS 4010. UCSC internal standards (pugel) were run at the University of Alaska Fairbanks Stable Isotope Facility and found to be comparable (Will et al. 2018, this Theme Section).

Stable isotope ratios are reported in delta notation as parts per thousand (‰) deviation from the international standards $\delta^{13}C_{\text{PeeDee Belemnite}}$ and $\delta^{15}N_{\text{air}}$, as follows: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. To compare core isotopic area occupied each year, we calculated standard ellipse areas (SEAs) within a Bayesian framework that is robust to small sample sizes and convex hulls to represent the total niche area occupied (Jackson et al. 2011).

Corticosterone

We measured corticosterone concentrations in head feathers (hereafter fCORT) to test for differences in stress levels accrued by birds during the prenuptial molt. In most cases, we analyzed 3 head feathers obtained from each bird (n = 58); for 3 birds, only 2 head feathers were available, and a single head feather was available for 2 individuals. Each feather length was measured (to the nearest 0.5 mm, 25.5 ± 3.5 [SD] mm), and all feathers in a sample were weighed collectively (to the nearest 0.1 mg, total sample mass: mean = 3.4 ± 1.4 mg) to account for weight and size variability in feathers (Lattin et al. 2011, Will et al. 2014). Feather samples were cleaned in a 1 min wash in isopropanol (HPLC-grade, Sigma-Aldrich) (Will et al. 2018) and extracted in 5 ml of HPLC-grade methanol (Fisher Scientific), which involved sonication for 60 min at 50°C followed by overnight incubation in a 50°C water bath (Bortolotti et al. 2008) and filtering via solid phase extraction with commercially available C18 columns. To control for loss of hormone during extraction, we added 2000 cpm of H^3-labeled corticosterone (NET399 Perkin Elmer), and adjusted final fCORT titers for % recovery of each individual sample (mean ± SD, 93.6 ± 4.67%). Feather extracts were air-dried, reconstituted in phosphate-buffered saline with gelatin, and analyzed using radioimmunoassay with a Sigma-Aldrich antibody (C 8784). All samples were analyzed in 2 assays, with intra- and inter-assay CV less than 2%. For statistical analyses, fCORT titers were standardized by feather length (pg mm^{-1}). We also found a significant relationship between fCORT titers and sample mass ($F_{1,59}$ = 11.73, p = 0.001); therefore, in all statistical analyses we used fCORT concentrations (pg mm^{-1}) de-trended for sample mass (Will et al. 2014).

Statistical analyses

To assess the influence of migratory behavior on fCORT, we used linear models with fCORT as the response and departure or return date from the colony as predictors. To test for spatial structure in birds relative to fCORT concentration in head feathers, we scored all individual samples based on a deviation of fCORT concentrations relative to average fCORT (1.64 pg mm^{-1}). We excluded birds with intermediate levels of fCORT (within 3% of the mean, 16% of birds) from the subsequent analysis grouping birds by low and high fCORT. We then calculated the BA between the 50% UD for high fCORT and low fCORT birds across the migration period (1 November to 1 March), for an interval of 25 d (approximately the amount of time it takes a feather to grow at 1–2 mm d^{-1}, A.S. Kitaysky unpublished) to determine potential temporal windows of spatial separation. Next, we randomized the group identity of these individuals across potential windows of spatial separation, for intervals of 14–30 d to identify BA significantly different than random (Breed et al. 2006).

All analyses and data processing were done in R (3.3.1, R Core Development Team 2016), significance was considered to be $p < 0.05$, and Bonferroni adjusted p-values were used in pairwise comparisons. Means are given ± SD to emphasize variation within groups.

RESULTS

Distributions

From October through March, red-legged kittiwakes used areas in the northern Bering Sea, western Bering Sea, Kuril Islands, and western subarctic gyre with core areas on the shelf in the northwestern Bering Sea and near the Kamchatka Strait in the

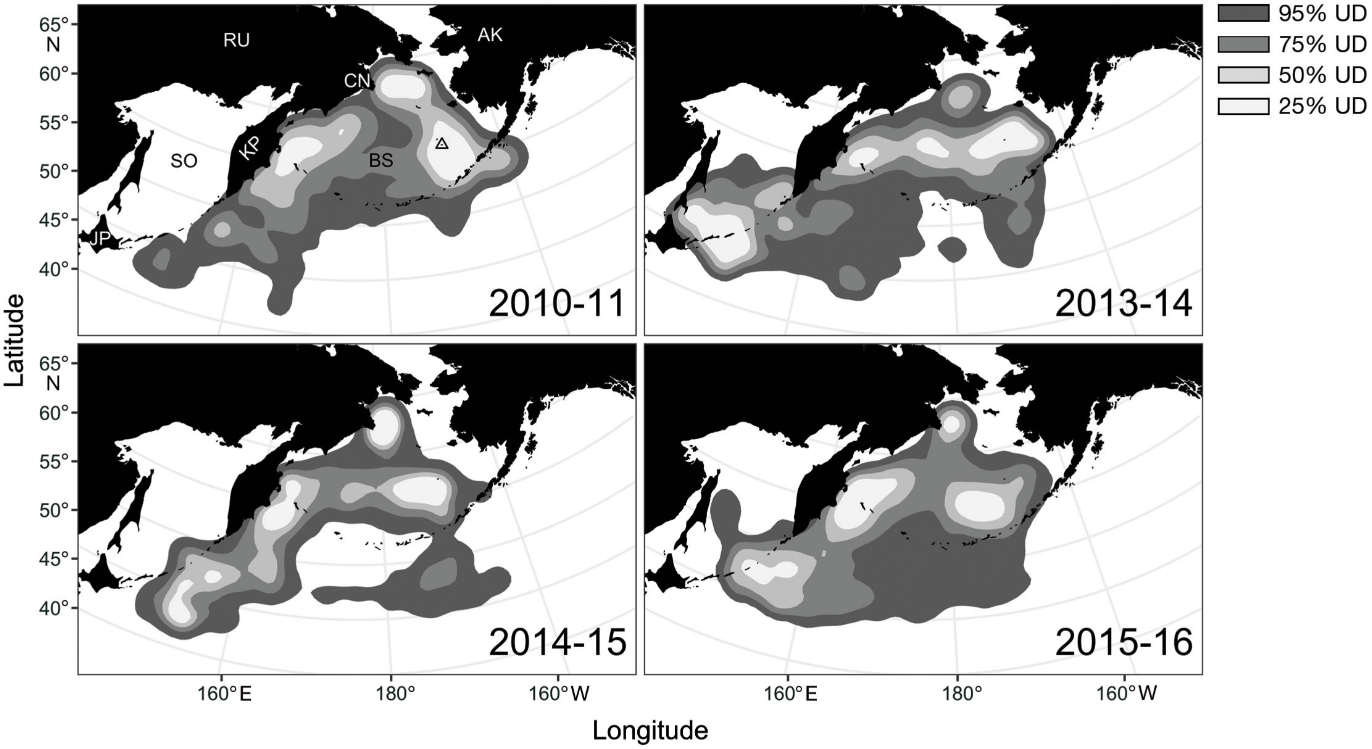

Fig. 1. Annual at-sea utilization distributions (UDs) of red-legged kittiwakes from October through March. St. George Island is indicated by a triangle, and place names are as follows: Alaska (AK), Russia (RU), Japan (JP), Sea of Okhotsk (SO), Kamchatka Peninsula (KP), Cape Navarin (CN), and Bering Sea (BS). Smoothing factor h = 88 km

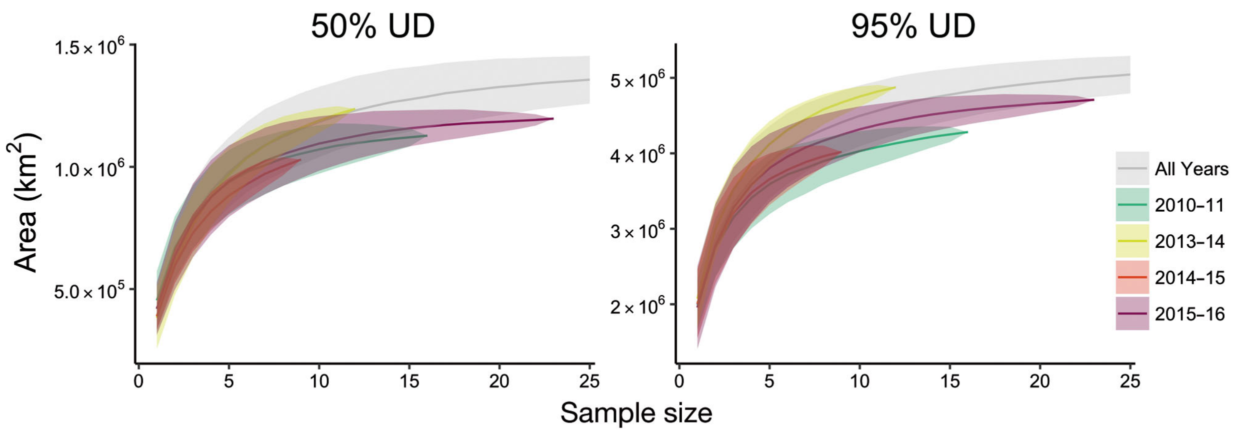

Fig. 2. Cumulative area of the 50 % and 95 % utilization distributions (UDs) for increasing sample sizes of red-legged kittiwakes. The shaded area is the standard deviation for each sample size from 1000 iterations

vicinity of the Commander Islands (Fig. 1). Across all years, 39 % of birds visited the northern Bering Sea shelf near Cape Navarin, Russia, and this did not differ significantly among years (multiple comparison chi-squared test, $p > 0.05$). In the 3 latter winters, birds visited the Sea of Okhotsk (47 %), and the percentage of birds visiting this region was the greatest in 2013–2014 (67 %). The randomized cumulative area curve of individuals tracked in all years appears to reach an asymptote even with the relatively small number of individuals tracked each year (Fig. 2). This indicates that our sample sizes are large enough to capture common high-use areas. The area of individual core and range UDs did not differ among years (Table 2).

Among years, BA indicated little overlap in core areas (0.240 ± 0.044) and relatively similar ranges (0.755 ± 0.035). Among individuals in the same year, the BA between the 95 % UDs was significantly higher in 2010–2011 (0.412 ± 0.16, post hoc $p = 0.003$) than all other years (pooled: 0.360 ± 0.009), indicating medium similarity of individual ranges; however, there was more homogeneity in ranges among birds in 2010–2011 (Table 2). The BA of individual core areas did not differ among years and indicates low similarity (Table 2).

Table 2. Yearly comparison of distribution, migration, and physiological parameters from red-legged kittiwakes deployed and retrieved with geolocation loggers from St. George Island, Alaska, USA. Stable isotope values and corticosterone concentrations (fCORT) are from head feathers grown in late winter (February to March), and sample sizes for these measurements are given in parentheses. Yearly samples sizes from geolocation-derived parameters are $n_{2010\text{-}11} = 15$, $n_{2013\text{-}14} = 12$, $n_{2014\text{-}15} = 9$, $n_{2015\text{-}16} = 23$. BA: Bhattacharyya's affinity, UD: utilization distribution. Means are given ± SD; significant values ($p < 0.05$) are shown in **bold**

	2010–2011	2013–2014	2014–2015	2015–2016	*F*	p
Area of individual 50 % (km^2)	456000 ± 131087	383750 ± 127540	393056 ± 60799	420326 ± 107013	1.113	0.296
Area of individual 95 % (km^2)	2036167 ± 355951	2090833 ± 394736	2018611 ± 490550	1976522 ± 562618	0.148	0.702
BA among individual 50 % UD	0.090 ± 0.008	0.050 ± 0.009	0.081 ± 0.013	0.076 ± 0.005	2.758	0.096
BA among individual 95 % UD	0.412 ± 0.016	0.321 ± 0.02	0.378 ± 0.027	0.368 ± 0.011	4.143	**0.042**
Outbound migration timing (d)	Nov 29 ± 37	Nov 10 ± 30	Nov 24 ± 18	Nov 7 ± 28	8.053	**0.006**
Arrival on wintering grounds	Jan 20 ± 21	Dec 31 ± 33	Jan 6 ± 26	Jan 9 ± 35	1.265	0.265
Departure from wintering grounds	Feb 17 ± 18	Feb 3 ± 25	Feb 14 ± 17	Feb 18 ± 16	1.637	0.206
Return to colony region	Mar 5 ± 16	Mar 1 ± 27	Mar 7 ± 36	Mar 15 ± 16	1.637	0.206
Duration (d) on wintering grounds (ρ)	30.9 ± 32	38 ± 35.8	42 ± 29.7	43.7 ± 31.6	1.573	0.215
Outbound migration duration (φ)	11.8 ± 6.4	11.5 ± 5.4	9.8 ± 7.4	14.5 ± 7.7	0.807	0.373
Return migration duration (φ)	3.6 ± 3.7	5.8 ± 5.3	4.7 ± 6.5	5.6 ± 4.7	1.384	0.244
Maximum distance from colony (km)	2337 ± 486	2858 ± 624	2688 ± 416	2451 ± 517	0.567	0.455
Day at maximum location	Feb 5 ± 16	Jan 15 ± 32	Jan 22 ± 27	Jan 23 ± 32	2.017	0.161
Cumulative distance traveled (km)	27287 ± 3413	26558 ± 1771	25210 ± 1637	26630 ± 2680	1.074	0.304
δ^{15}N (‰)	16.00 ± 0.48 (17)	15.45 ± 0.54 (7)	15.23 ± 0.42 (9)	15.53 ± 0.40 (23)	13.69	**<0.001**
δ^{13}C (‰)	−18.30 ± 0.18 (17)	−18.29 ± 0.27 (7)	−18.50 ± 0.22(9)	−18.55 ± 0.20 (23)	14.86	**<0.001**
fCORT (pg mm^{-1})	1.61 ± 0.263 (17)	1.731 ± 0.190 (7)	1.686 ± 0.414 (9)	1.665 ± 0.402 (28)	0.107	0.745

Migration movements

All red-legged kittiwake tracks fit to a migratory model based on net-squared displacement from the colony (migratory n = 9, mixed migratory n = 50). The initiation of the outbound migration (10% of migratory movement) occurred in October through December, and was significantly different among years (Table 2), as outbound migration occurred later in 2015–2016 than in 2010–2011 (post hoc p = 0.026). The timing of arrival on the wintering grounds was not significantly different among years, nor was departure from the wintering grounds, the duration of time spent in the wintering areas, time when birds returned to the colony, or the duration of each migratory leg (Table 2). However, the outbound migration was significantly longer than the inbound migration (paired *t*-test, p < 0.001). In general, these migratory patterns resulted in relatively constrained autumn (September to November) and spring (March to May) distributions in the eastern Bering Sea, with a short wintering period in the western Bering Sea and subarctic (Fig. 3). Overall, the maximum distance from the colony was not significantly different among years, nor was the time when birds arrived there, or the cumulative distance traveled from October through March (Table 2).

Habitat use

Red-legged kittiwakes predominantly used oceanic habitats (51 ± 14%), although the use of these habitats was typically highest from January to March (Fig. 4).

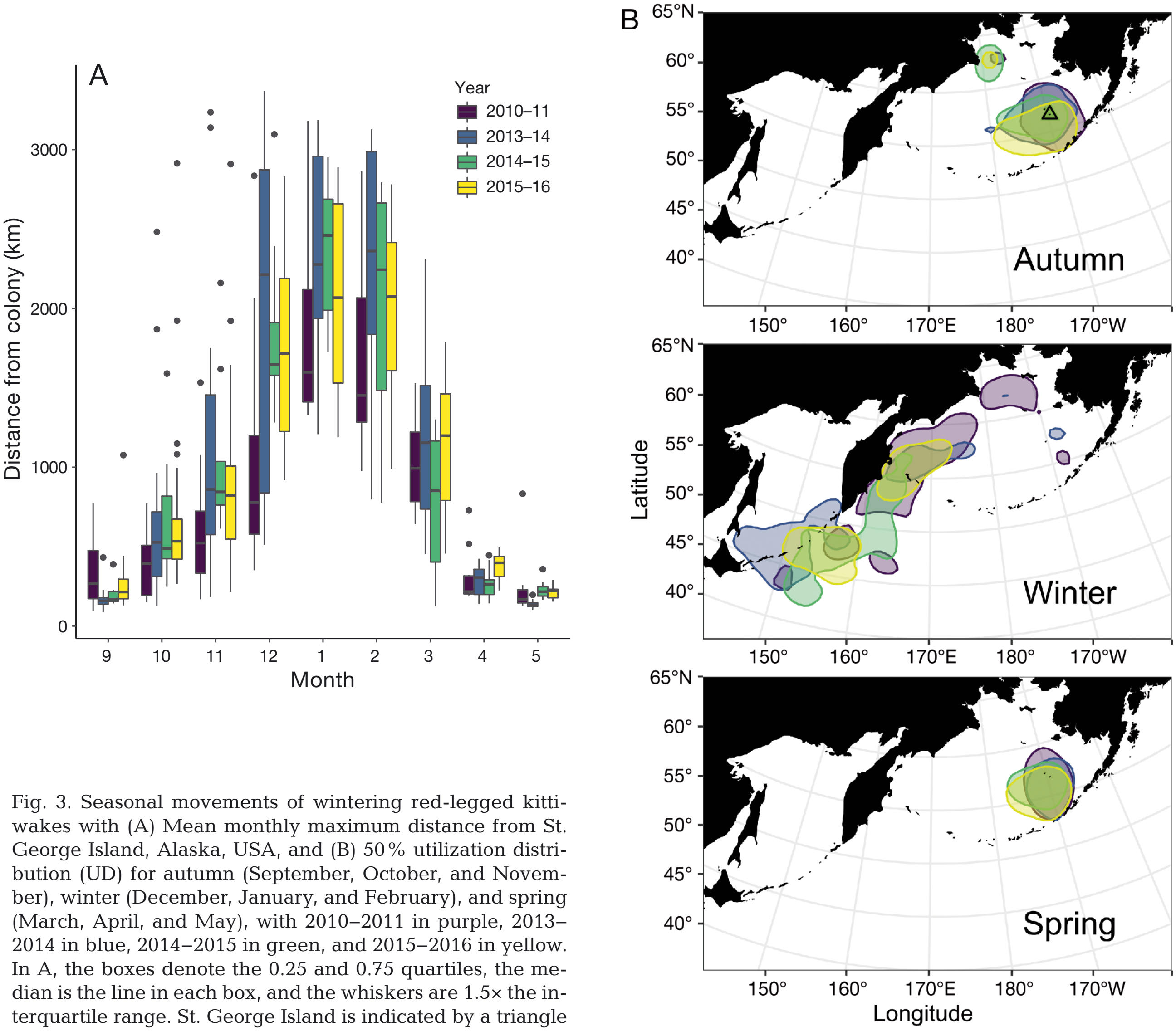

Fig. 3. Seasonal movements of wintering red-legged kittiwakes with (A) Mean monthly maximum distance from St. George Island, Alaska, USA, and (B) 50% utilization distribution (UD) for autumn (September, October, and November), winter (December, January, and February), and spring (March, April, and May), with 2010–2011 in purple, 2013–2014 in blue, 2014–2015 in green, and 2015–2016 in yellow. In A, the boxes denote the 0.25 and 0.75 quartiles, the median is the line in each box, and the whiskers are 1.5× the interquartile range. St. George Island is indicated by a triangle

Annually, the seasonal use of oceanic habitats was relatively similar between the later 3 years, while the inclusion of a separate smoother for 2010–2011 improved AIC scores (Table S1 in the Supplement at www.int-res.com/articles/suppl/m593p231_supp.pdf). Seasonally, the overall pattern of shelf use was similar (Fig. 4), and the lowest AIC score resulted from a 2-group model with 2010–2011 and 2013–2014 combined. Shelf use was highest in 2010–2011 (2010–2011: 36 ± 8%) and lowest in 2015–2016 (16 ± 8%). The annual percentage of time birds spent using the shelf break was minimal and did not differ by year (ANOVA: 5.2 ± 3.0%, $F_{1,57}$ = 0.002, p = 0.968); the lowest AIC score resulted from the model with all years combined. Seasonal use of the slope had a unique pattern in 2013–2014, and AIC values were reduced with 1 smoother for 2013–2014, and a second smoother for the other years, but overall use of the slope did not differ by year (ANOVA: 17.9 ± 6.4%, $F_{1,57}$ = 1.16, p = 0.286, Fig. 4).

From November to May, red-legged kittiwakes spent on average 8.7% of each month overlapping with, or within 100 km, of the sea ice, and 2010–2011 had significantly more sea ice interactions than the other 3 years (LMM: $F_{3,59}$ = 7.04, p < 0.001). There was no significant difference in sea ice interactions between the other 3 years (LMM: $F_{2,44}$ = 0.44, p = 0.6467, Fig. 5). Both the cumulative maximum extent of sea ice and the location of kittiwake–ice interactions shifted annually, occurring across the Bering Sea shelf, along the coast of Kamchatka, the Kuril Islands, and in the Sea of Okhotsk (Fig. 5).

Period of pre-nuptial molt

The $\delta^{15}N$ values from red-legged kittiwake feathers ranged from a minimum of 14.37‰ to a maximum of 17.05‰, and within this range there were differences among years, with $\delta^{15}N$ significantly higher in 2011 than in all other years (post hoc p = 0.006, Fig. 5), likely indicating a higher trophic level diet during this year. $\delta^{13}C$ values (min. = −19.01, max. = −17.97) were significantly different between all year combinations except 2011 and 2014 (p = 0.903) and 2015 and 2016 (p = 0.691; Table 2). As determined by maximum likelihood estimates of the SEA, the size of the 2-dimensional isotopic niche space did not significantly differ among the 4 winters (Fig. 6).

Concentrations of corticosterone in feathers were not significantly different among study years (Table 2). Likewise, within-year variance was not different among years (p > 0.05). We did not find a significant linear relationship between migratory parameters and fCORT (p > 0.05). Average fCORT was 1.64 pg mm^{-1}; 14 birds comprised the high fCORT group (18.9 ± 10.5% above the mean), 22 birds were in the low fCORT group (−13.1 ± 6.5% below the mean), while 7 birds had average concentrations of fCORT (within 3% of the mean) and were excluded from subsequent analysis looking at spatial separation. Across the migratory period, the only timeframe with spatial separation between birds with high and low fCORT occurred in February, corresponding to the estimated period of feather growth (Gabrielson & Lincoln 1959). Birds with high and low fCORT values

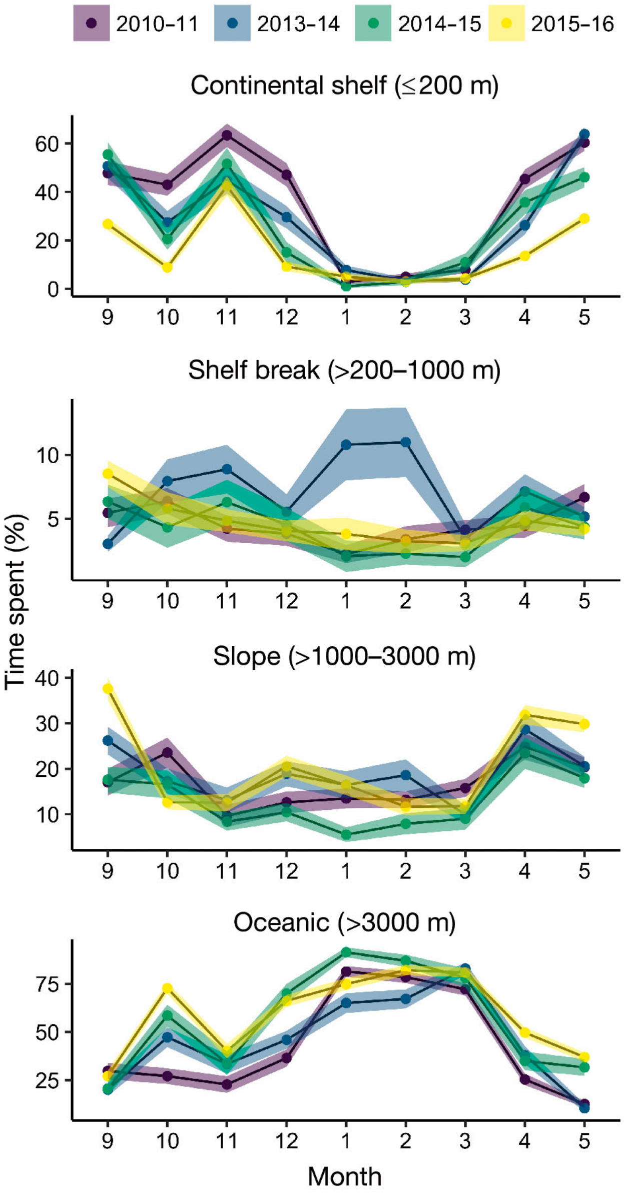

Fig. 4. Monthly percentage of time spent in bathymetric habitats of the North Pacific by wintering red-legged kittiwakes. The shaded area is the standard error for each month

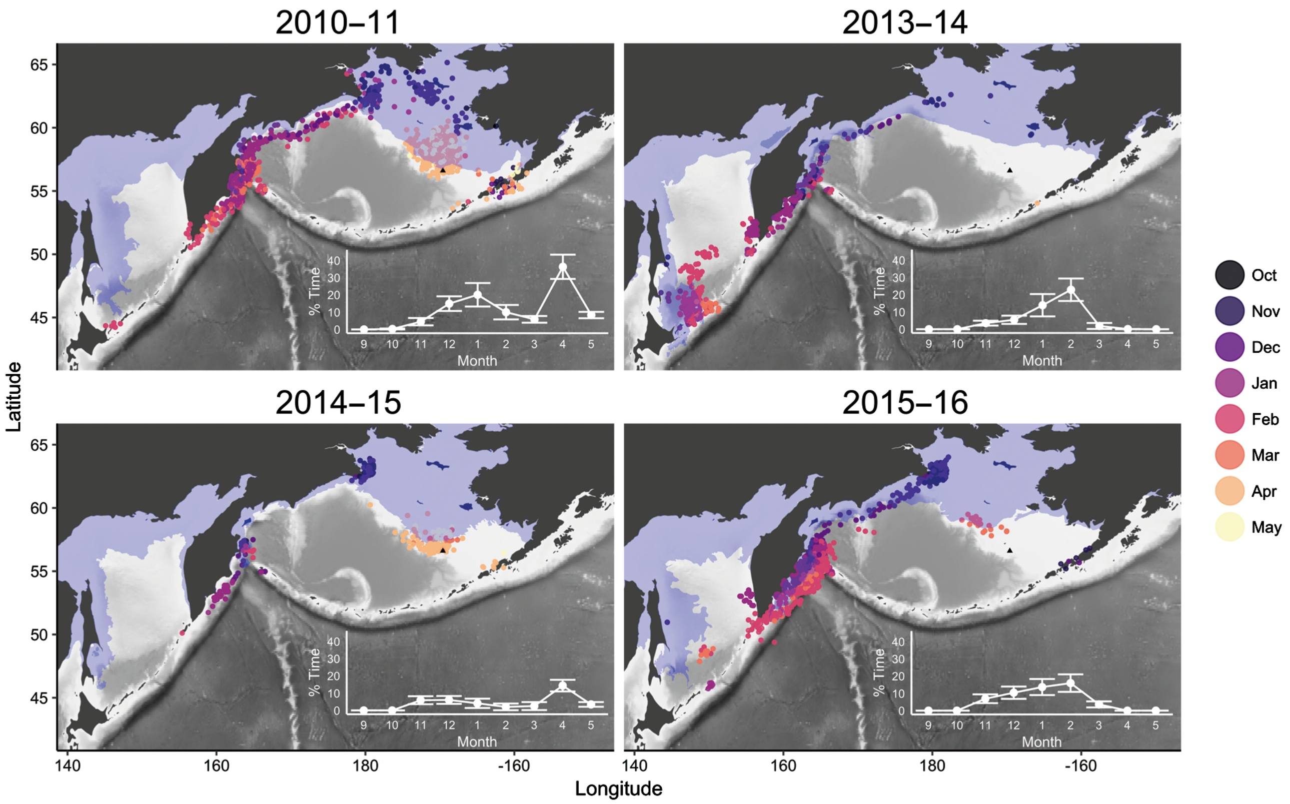

Fig. 5. Association of red-legged kittiwakes with sea ice. Twice daily locations of red-legged kittiwakes within 100 km of the sea ice edge (and within the sea ice) overlaid on the cumulative maximum sea ice extent for each year (in lavender). Locations are colored by month. Inset into each map is the percentage of time each month birds were associated with sea ice. Error bars indicate ± SD. St. George Island is indicated by a small black triangle

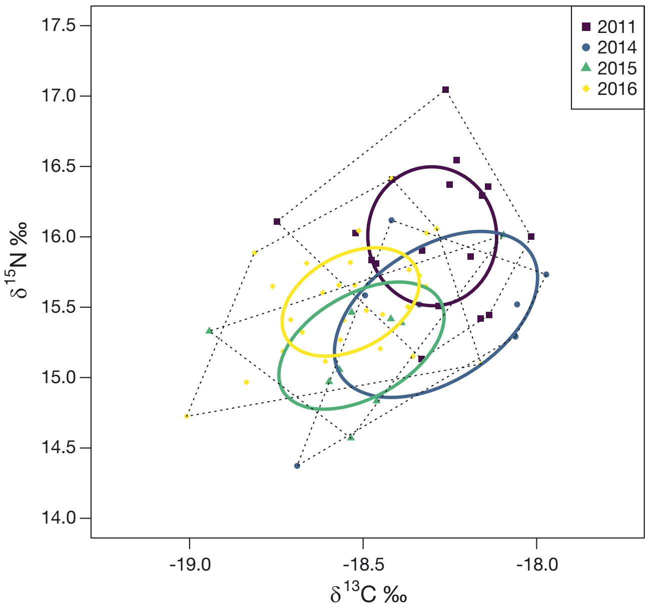

Fig. 6. Annual stable isotope values from nape feathers of red-legged kittiwakes (n = 61), overlaid with convex hulls (dashed lines) and small sample-size corrected 40% standard ellipses (SEAc)

had significantly spatially separated 50% UD, determined via BA, from early February to early March (Fig. 7). Reinforcing this spatial separation, carbon stable isotope values were also significantly different between birds of high and low fCORT (δ^{13}C, High fCORT = −18.35 ± 0.25‰, Low fCORT = −18.45 ± 0.19‰, $F_{1,34}$ = 18.09, $p < 0.001$). Moreover, birds with higher fCORT were foraging at a significantly lower tropic level than their counterparts with lower fCORT (δ^{15}N, High fCORT = 15.49 ± 0.43‰, Low fCORT = 15.84 ± 0.53‰, $F_{1,34}$ = 10.87, $p = 0.002$).

DISCUSSION

Across 4 yr, red-legged kittiwakes consistently returned to the same general regions of the Bering Sea and western North Pacific during their winter migrations. Within this region, core areas changed annually, and individuals varied in where and when they moved between bathymetric habitats, especially in the autumn. Since long-distance migratory movements were initiated roughly 2 mo after the breeding

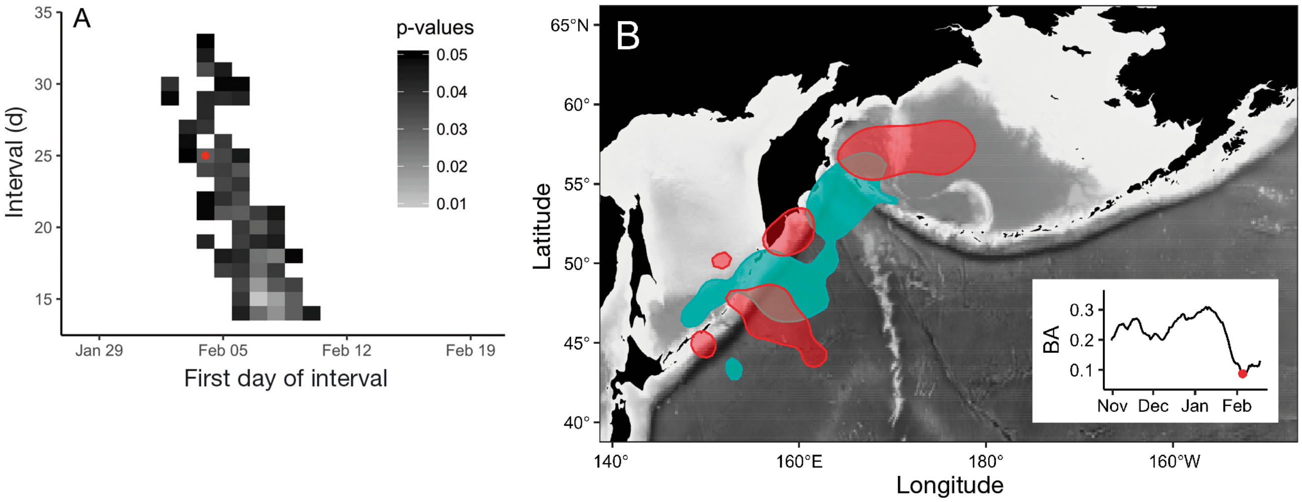

Fig. 7. Spatial separation between red-legged kittiwakes with above and below average corticosterone concentrations in head feathers grown at the end of the wintering period (fCORT). (A) Significant p-values for intervals beginning on 30 January to 18 February, with intervals from 14–35 d. The red dot corresponds to the day and interval shown in panel B. (B) Representative kernel density plot (50 % utilization distribution, UD) from the significant time period, with birds with high fCORT levels in red and low fCORT levels in turquoise (Bhattacharyya's affinity [BA] = 0.0873, p = 0.03). Inset: BA between the 2 groups for the 50 % UD from 1 October to 18 February for a sliding interval of 25 d. The representative interval is highlighted with a red dot

season ended, the timing likely relates to local environmental conditions rather than life-history drivers. Kittiwakes used multiple oceanographic habitats, but the majority of their time was spent in deep pelagic waters, followed by time spent foraging over shallow shelf waters of the eastern Bering Sea. Annually, the relatively cooler year of 2010–2011 was unique, as birds stayed on the southeastern Bering Sea shelf longer, had higher δ^{15}N, and slightly higher homogeneity among individual wintering areas. Birds were more likely to visit the Sea of Okhotsk in 2013–2014, whereas distributions were the most pelagic in 2015–2016. Associated with these differences in migration behavior, we found no significant annual difference in feather corticosterone. Nonetheless, we found a significant spatial separation between birds with relatively high and low fCORT across all years, indicating specific regions where and when individual red-legged kittiwakes consistently experienced lower prey availability (as reflected in elevated fCORT). Our evidence of a 'stress landscape' suggests that regions in the Bering Sea basin consistently had lower prey availability, at least in February, suggesting why it may be beneficial for red-legged kittiwakes to migrate out of the Bering Sea.

Red-legged kittiwakes wintered in the western Bering Sea and western subarctic regions. Yet, birds could have headed east, as 1 bird did in November of 2015, taking a short trip to the Gulf of Alaska. This is not unprecedented, as a flock of juvenile red-legged kittiwakes was observed once in southeast Alaska (Siegel-Causey & Meehan 1981), suggesting that the tendency to head west may be learned, or may be a phenomenon of our study years. Preference for western regions of the North Pacific is also exhibited by the widely ranging wintering black-legged kittiwakes that breed on the Pribilof Islands (Orben et al. 2015b), and has been observed during at-sea surveys of marine mammals and birds (Shuntov 1974, Springer et al. 1999). The western subarctic regions have higher primary productivity, along with a higher diversity of mesopelagic fishes than the eastern subarctic (Beamish et al. 1999, Springer et al. 1999). The most abundant myctophid species in the North Pacific, *Stenobrachius leucopsarus,* is thought to spawn sometime from December through March (Smoker & Pearcy 1970). This is also the species recorded in summer diets of red-legged kittiwakes (Sinclair et al. 2008). If spawning behaviors make myctophids vulnerable to predation, this would provide consistent winter foraging opportunities for kittiwakes. Myctophids are thought to be vulnerable to being trapped at the surface by currents (Flynn & Williams 2012). The western subarctic has more eddies than the eastern portion (Bograd et al. 1997), and wintering red-legged kittiwakes appear to be concentrated in areas of strong currents: Cape Navarin, Kamchatka Strait, and along the Kuril Islands.

Ocean fronts and eddies concentrate prey for marine predators, and are especially important for surface-feeding seabirds (Bost et al. 2009, Scales et al. 2014). For instance, instead of foraging over slope regions, chick-rearing black-legged kittiwakes forage in more distant deep waters, targeting eddies (Paredes et al. 2014). Starting in the northern Bering Sea, red-legged kittiwakes consistently occupied the region to the southwest of Cape Navarin where along-shelf currents and the western Bering Sea Current converge to flow up over the shelf (Stabeno et al. 1999). Further investigation is needed to understand what mechanisms make this region profitable for kittiwakes and other marine predators in the autumn. The regions between Cape Navarin and the Karaginsky Gulf were not often frequented by wintering kittiwakes, while the associated basin areas appear to be associated with higher levels of stress incurred by birds in late February. In the western Bering Sea, fronts are often closer to each other than in the east due to the narrow continental shelf (Belkin 2016), perhaps limiting foraging opportunities. Instead, core areas associated with lower stress levels were located over the deep waters of Kamchatka Pass and Near Straight, where surface currents move out of the Bering Sea at up to 100 cm s^{-1}, some of the fastest current speeds in the Bering Sea (Stabeno et al. 1999, 2005). This region was a consistent hotspot, and due to its proximity to colonies in the western Aleutians and Commander Islands, there is the potential for high overlap between birds from multiple colonies. Red-legged kittiwakes did not appear to frequent the other Aleutian passes, even though 3 of their 4 breeding colonies are within or proximate to this island chain. The passes through the Kuril Islands were not consistently used by wintering red-legged kittiwakes, nor was the southern Sea of Okhotsk where the East Sakhalin Current moves towards the Kuril Island chain (Andreev & Shevchenko 2008). This selective use of areas might be due to kittiwake reliance on both ample prey resources and the need for physical processes, such as currents, to then make prey available at the surface.

Red-legged kittiwakes encountered sea ice across their range and throughout the non-breeding period. Due to the spatial resolution of our geolocation data, we cannot shed light on the direct nature of how, or if, red-legged kittiwakes use the marginal ice zone. Certainly, compared to a pagophilic species like Mandt's black guillemot *Cepphus grylle mandtii*, their use of sea ice is minimal (Divoky et al. 2016). Considering the seemingly low level of spatial association with sea ice, it is somewhat surprising that red-legged kittiwake reproductive timing and productivity, and wintering condition (fCORT, isotopic niche) appeared to be related to sea ice dynamics (Byrd et al. 2008b, Zador et al. 2013, Will et al. 2018). However, there is a spatial association between red-legged kittiwakes and regions of seasonal sea ice, predominantly in the late autumn and winter, that could perhaps help to explain possible links between sea ice, and breeding parameters and foraging ecology of red-legged kittiwakes. For instance, the higher association of red-legged kittiwakes with sea ice in 2010–2011 may be an artifact of higher abundances of prey species on the shelf, such as amphipods, due to consecutive cold years of higher ice abundance and the associated shift in trophic dynamics (Pinchuk et al. 2013). In all years, red-legged kittiwakes returned to the eastern Bering Sea in March, emphasizing the importance of prey resources in this region for kittiwake pre-laying condition (e.g. Shultz et al. 2009, Renner et al. 2014), and potentially dampening the influence of migration quality on subsequent reproductive success.

We found no significant differences in fCORT levels among our study years, although in some cases our annual sample sizes were fairly small. In context, the birds we tracked had some of the lowest fCORT values seen in the last century (Will et al. 2018). Although we found annual and individual variability, at the broad scale we found distributions, migrations, and stable isotopes to be relatively consistent among winters. This could explain why fCORT values were similar as well. Yet, we found significant spatial separation in birds with high and low fCORT across all years. Surprisingly, birds continued using the deep oceanic waters of the Bering Sea basin despite experiencing apparent food limitation here and consuming a lower trophic level diet. This may be indicative of individual allostatic loads (e.g. Schultner et al. 2013 and references therein), consistency in wintering movements, and/or that availability of prey in deep water ocean areas might be high under certain environmental conditions, but our relatively short time series of observations failed to detect such variability. This is also a period of the annual cycle when red-legged kittiwakes spend the majority of their time sitting on the water (Orben et al. 2015a), and this sedentary tendency might accentuate the observed stress landscape. A persistent use of the same wintering ground regardless of local feeding conditions might make red-legged kittiwakes vulnerable to climate-associated changes in those areas.

Are red-legged kittiwakes employing a specialist strategy during the winter? Compared to black-legged kittiwakes, they do appear to be more specialized during the winter, as red-legged kittiwakes consistently occupied a smaller, somewhat restricted wintering area and isotopic niche space (Orben et al. 2015a,b). However, there is still much more to understand about the exact nature of their wintering foraging ecology, individual consistency, and seasonal shifts in diets. Red-legged kittiwakes should certainly not be considered extreme migratory specialists, as they showed the capacity to annually adjust timing of outbound migrations, and high diversity between individual core use areas within their wintering range. Yet, across our 4 study years, they employed a relatively consistent wintering strategy, along with an apparent willingness to incur higher stress levels in specific regions. If red-legged kittiwakes are targeting spawning myctophids or squids across their wintering range, this would provide further evidence of foraging specialization, that in most years is likely highly profitable. There is some evidence that through the 1990s, the abundances of myctophids in the subarctic North Pacific increased (Beamish et al. 1999), potentially corresponding to upward population trends in red-legged kittiwakes and the stability of the ecosystem's apparent carrying capacity for this marine predator (Goyert et al. 2017).

IMPLICATIONS

Our 4 years of tracking highlight the persistence in wintering areas and behaviors in a surface foraging seabird species that is capable of traversing the entire North Pacific, like its congener the black-legged kittiwake (Orben et al. 2015b). Therefore, potential threats and risks to this population should be considered within the context of this putatively specialized spatial behavior, especially given that climate change is expected to continue to have large-scale impacts on marine ecosystems over the next decades (Henson et al. 2017). Though not considered at risk for direct or indirect fishery interactions, the winter range of red-legged kittiwakes does overlap in space and time with fisheries in the western Bering Sea and Kuril regions, and further investigation is warranted, as cumulative impacts can act in synergy (Maxwell et al. 2013). Our evidence for a consistent 'stress landscape' pattern could compound these impacts. We were able to track birds during 4 winters, but it is important to note that red-legged kittiwakes can live upwards of 25 yr (The North American Bird Banding Laboratory, Patuxent Wildlife Research Center), so for an individual bird, 4 yr represents only ~17 % of its adult life. As the next step, and given that other seabirds show both individual fidelity and flexibility in migratory behavior, it would be informative to track individual birds during multiple winters to understand the degree of flexibility individuals may have. This is particularly pertinent, as a chick hatched in 2017 could live until 2040+, facing life in a rapidly changing ecosystem altered by multiple climate-driven stressors (Henson et al. 2017). In light of past declines in red-legged kittiwake populations, we can expect similar population volatility as marine communities restructure in the arctic and subarctic North Pacific, as this seabird has a consistent reliance on both ecosystems.

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Contribution to the Theme Section 'Seabird responses to a changing Bering Sea'

Variability in trophic level and habitat use in response to environmental forcing: isotopic niche dynamics of breeding seabirds in the southeastern Bering Sea

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ABSTRACT: Climate-driven changes in the marine environment may affect inter- and intraspecific resource partitioning by marine organisms. When and how resources are partitioned may depend on access to diverse foraging habitats. Here we examined the variability in the isotopic niche of breeding seabirds with respect to trophic level and habitat use in years with cold and warm sea temperatures in the Bering Sea. Between 1999 and 2015 (n = 12 yr), we collected blood from black-legged kittiwakes *Rissa tridactyla*, and common *Uria aalge* and thick-billed murres *U. lomvia* breeding on St. George and St. Paul Islands on the southeastern Bering Sea continental shelf. We examined isotopic niche dynamics at the group and species levels. Stable isotope values of blood tissues corroborated published observations of seabird distributions in the region. All 3 species increased foraging on shelf-based prey during warm oceanographic conditions, in contrast to a higher reliance on oceanic-based prey during cold conditions. Under warm ocean conditions, the isotopic niche of the seabird group with access to only shelf habitat (St. Paul Island) contracted, whereas the isotopic niche of the seabird group with access to shelf, slope, and basin habitats (St. George Island) expanded. These group-level responses were associated with increased food availability. We conclude that habitat heterogeneity in the vicinity of breeding colonies may mediate how predators partition food resources in response to changes in climate-driven food availability.

KEY WORDS: Black-legged kittiwake · Murre · Stable Isotope Bayesian Ellipses in R · SIBER · Layman's metrics · Stable isotope analysis · Habitat heterogeneity · Resource partitioning

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INTRODUCTION

The southeastern Bering Sea is characterized by long- and short-term variability in oceanographic conditions. On a decadal scale, the region as a whole may be subject to either a warmer or a colder climate regime (Stabeno et al. 2012). On shorter temporal scales (1 to 3 yr), the region shifts between cold years, characterized by extensive sea ice and a late sea ice retreat, and warm years, characterized by low sea ice coverage and an early retreat (Stabeno et al. 2012). Fluctuations in annual sea ice extent and the timing of its retreat have been linked to the timing and duration of primary production (Liu et al. 2016), and the availability of large lipid-rich crustacean zooplankton over the shelf (e.g. Hunt et al. 2016, Sigler et al. 2016). It has been proposed that these oscillating oceanographic conditions affect the distribution and availability of forage fish to marine predators, including seabirds (Hunt et al. 2011). This well studied system provides a natural setting in which to address how sub-Arctic species may respond to future changes in the marine environment. We used it to examine how seabirds use and partition resources during a period when the southeastern Bering Sea experienced very cold and very warm years (1999–2016, Overland et al. 2012, Stabeno et al. 2012).

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Resource partitioning is considered to be an important mechanism by which species are able to reduce competition for common resources and co-exist (Schoener 1974, Finke & Snyder 2008). The partitioning of food resources in the ocean may be dynamic, driven by environmental factors affecting the availability of prey (e.g. Friedlaender et al. 2011, Sabarros et al. 2012). In seabirds, sympatrically breeding species are known to partition resources horizontally (Cherel et al. 2008, Rayner et al. 2016), vertically (Navarro et al. 2015, Kokubun et al. 2016), diurnally (Barger et al. 2016), and/or by prey type (Moreno et al. 2016, Rayner et al. 2016) or size (Mancini & Bugoni 2014). The degree of partitioning can depend upon changes in food availability (Barger & Kitaysky 2012), or it can occur during energetically taxing life stages such as offspring provisioning (Cherel et al. 2008, 2014, Barger et al. 2016, Delord et al. 2016).

Habitat heterogeneity may also affect resource partitioning. Access to different types of habitat may reduce interspecific competition for resources. For example, when foraging in a complex habitat, stone crabs *Menippe mercernaria* and knobbed whelks *Busycon carica* maintain consumption rates and feed upon similar prey species because these 2 predators are able to forage in different types of habitat (Hughes & Grabowski 2006). How access to diverse foraging habitats may modify interspecific resource partitioning under different environmental conditions in seabirds is, however, not well known.

Seabirds in the southeastern Bering Sea have access to different types of habitat depending on where they breed (Fig. 1). St. Paul Island, part of the Pribilof Islands, supports a relatively small (31 000 black-legged kittiwakes *Rissa tridactyla* ['kittiwakes'], 39 000 common murres *Uria aalge*, and 115 000 thick-billed murres *U. lomvia*) multi-species seabird colony located on the continental shelf. In contrast, St. George Island supports a multi-species colony that is an order of magnitude larger (72 000 kittiwakes, 190 000 common murres, and 1 500 000 thick-billed murres) (Hickey & Craighead 1977). By being closer to the shelf edge than St. Paul Island, St. George Island affords seabirds easier access to shelf, slope, and basin foraging habitats. These 2 islands are located 60 km apart (Byrd et al. 2008a). Tracking studies have revealed that murres and kittiwakes rarely forage in the area between the 2 colonies, and that there is little overlap in their shelf and slope foraging locations (Harding et al. 2013, Paredes et al. 2014, Kokubun et al. 2018 in this Theme Section).

Stable isotope analysis is a non-invasive tool that can be used to identify shifts in diet (e.g. Karnovsky et al. 2008, Cherel et al. 2014, Kowalczyk et al. 2015) and to determine how sympatric species partition prey resources (e.g. Young et al. 2010, Barger & Kitaysky 2012, Jaeger et al. 2014). Stable isotope ratios capitalize on the differential rate that heavy and light non-decaying isotopes of elements are used in biological processes. By analyzing samples for carbon and nitrogen isotopic ratios we can construct a predator's isotopic niche (Bearhop et al. 2004, Newsome et al. 2007), which describes where (reflected in carbon, $\delta^{13}C$) and at what trophic level (reflected in

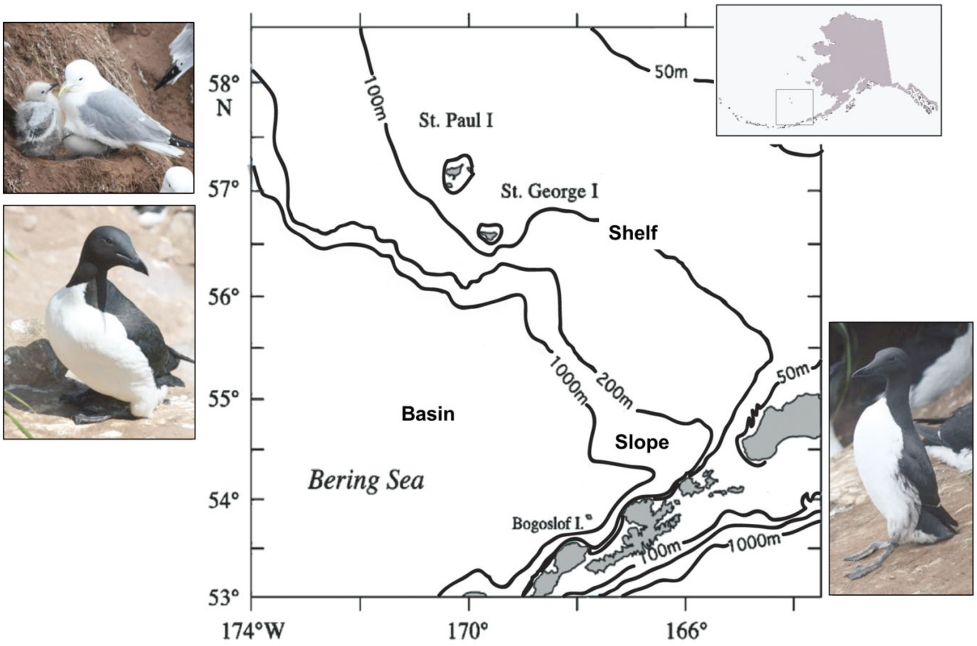

Fig. 1. Study area and focal species. St. Paul and St. George Islands are located on the continental shelf, 90 and 25 km from the shelf break, respectively. Pictured clockwise from top left are a black-legged kittiwake *Rissa tridactyla* with chick, a common murre *Uria aalge*, and a thick-billed murre *U. lomvia* (photo credit: A. Will, map adapted from Hunt et al. 2008)

nitrogen, $\delta^{15}N$) it has been foraging (Hobson et al. 1994). Isotopic niches have proven useful in discerning ecological segregation of marine species (e.g. tuna, Ménard et al. 2007; dolphins, Gross et al. 2009; myctophids, Cherel et al. 2010), mapping food webs (e.g. Linnebjerg et al. 2016), and inferring food web diversity (e.g. Yurkowski et al. 2016).

Using blood samples collected over the past 16 yr, we examined the isotopic niche dynamics of 3 piscivorous seabird species breeding on the Pribilof Islands to determine whether and how oceanographic conditions and habitat heterogeneity affected interspecific prey resource partitioning. The foraging behavior of seabirds is known to change throughout the course of the breeding season in response to the demands of their offspring (Navarro et al. 2014, Barger et al. 2016) as well as changes in prey resources (Scioscia et al. 2014, Jakubas et al. 2016). We analyzed tissues with different turnover rates to characterize the arrival (early) and chick-rearing (late) periods of the breeding season to capture seasonal prey-use dynamics.

We included 3 seabird species (1 kittiwake and 2 murre species, which we refer to as a 'group', Fig. 1) that use different parts of the horizontal and vertical foraging space. Black-legged kittiwakes are able to travel far from the breeding colony (up to 200 km, Paredes et al. 2014) at relatively low costs, yet as surface feeders, they have limited access to deeper layers of the water column. Common and thick-billed murres are, compared to kittiwakes, restricted in the distance they can travel from the colony (no more than 20 km during chick-provisioning day trips, but up to 100 km during overnight trips, Paredes et al. 2015). Both murres are pursuit-diving foragers and have access to prey throughout the water column, up to 200 m in depth (Croll et al. 1992, Orben et al. 2015). Common murres, compared to thick-billed murres, are able to fly greater distances, and the 2 species partition their use of the water column by time of day, distance from the breeding colony, and by foraging depth (Barger et al. 2016, Kokubun et al. 2016).

In cold years, murres and kittiwakes breeding on the Pribilof Islands incurred relatively high levels of nutritional stress, suggesting that food was scarce or difficult to obtain (Paredes et al. 2012, Satterthwaite et al. 2012, Kokubun et al. 2018). In warm years, however, they had relatively low levels of nutritional stress, indicating that food was abundant or more easily obtained (Benowitz-Fredericks et al. 2008, Satterthwaite et al. 2012, Harding et al. 2013, Paredes et al. 2014). When conditions are warm, the southeastern Bering Sea shelf supports large cohorts of young-of-the-year walleye pollock *Gadus chalcogramma* that remain in the upper water column (top 20 m) until early autumn (Moss et al. 2009, Hunt et al. 2011, Hunt et al. 2018 in this Theme Section). These small fish can make up a large portion of murre and kittiwake diets at the Pribilof Islands (Renner et al. 2012, Sinclair et al. 2008). In cold years, young-of-the-year walleye pollock may be less plentiful in the upper water column (Moss et al. 2009, Hunt et al. 2011, Renner et al. 2016, Hunt et al. 2018). Thus, we predicted that the isotopic niche of seabirds would vary between cold and warm conditions in response to changes in prey availability.

In the southeastern Bering Sea, there is a $\delta^{13}C$ gradient in seabird prey: prey from the continental shelf have higher $\delta^{13}C$ values compared to alternative prey from the continental slope or ocean basin (Zeppelin et al. 2015), which is also reflected in the stable isotope ratios of bird blood tissues (Dorresteijn et al. 2012). In cold conditions, when juvenile pollock are relatively scarce on the shelf, we predicted that the isotopic niche of birds with access primarily to shelf foraging habitat (St. Paul Island) would expand as species separate themselves by prey type and geographic location. In cold years, St. Paul Island kittiwakes have been observed to forage near the continental slope and in the ocean basin (Paredes et al. 2014), while murres continued to forage on the shelf near the breeding colonies (Harding et al. 2013, Paredes et al. 2015). In contrast, we predicted that the isotopic niche used by seabirds on colonies closer to the shelf break would contract during cold years. On St. George Island, all species have access to more heterogeneous foraging habitat, so during cold ocean conditions when prey availability is low on the shelf, we expected seabirds to concentrate their foraging efforts on prey inhabiting the continental slope region (Pomerleau et al. 2014, Zeppelin et al. 2015, Suryan et al. 2016).

MATERIALS AND METHODS

Study sites and sample collection

Murres and kittiwakes were captured using noose poles on St. Paul (57.18119° N, 170.266° W) and St. George (56.580507° N, 169.605925° W) Islands between 1 July and 25 August (see Table 1 for years and sample sizes). No more than 1 ml of blood was collected from the alar vein and stored on ice (for details see Benowitz-Fredericks et al. 2008). Within 12 h of collection, blood was separated via centri-

Table 1. Sample sizes by year, island, and tissue. All except 2015 plasma values are from individuals whose red blood cells were also analyzed. BLKI = black-legged kittiwake *Rissa tridactyla*, COMU = common murre *Uria aalge*, TBMU = thick-billed murre *U. lomvia*

Year	Island	Red blood cells			Plasma		
		BLKI	COMU	TBMU	BLKI	COMU	TBMU
1999	St. George	–	10	10	–	–	–
	St. Paul	10	–	10	9	–	7
2003	St. George	30	21	30	8	8	9
	St. Paul	30	18	30	10	8	10
2004	St. George	28	26	30	8	10	10
	St. Paul	31	24	25	10	8	10
2005	St. George	26	18	29	7	9	9
	St. Paul	15	8	18	5	2	7
2006	St. George	–	–	22	–	–	–
	St. Paul	–	–	–	–	–	–
2007	St. George	–	–	32	–	–	–
	St. Paul	–	–	–	–	–	–
2008	St. George	31	22	27	10	10	10
	St. Paul	30	28	30	10	10	10
2009	St. George	26	37	28	9	10	10
	St. Paul	24	26	30	10	10	10
2010	St. George	36	–	33	10	–	9
	St. Paul	35	–	39	10	–	10
2013	St. George	–	–	–	–	–	30
	St. Paul	–	–	–	–	–	–
2014	St. George	–	14	38	–	14	18
	St. Paul	–	–	–	–	–	–
2015	St. George	–	–	–	–	15	20
	St. Paul	–	–	–	–	–	–
Totals	St. George	177	148	279	52	76	125
	St. Paul	175	104	182	64	38	64

fugation into plasma and red blood cells, and then stored frozen until further analysis.

Stable isotope analysis

We used the isotopic composition of red blood cells and plasma to characterize seabird diets for the duration of the breeding season. Red blood cells reflect the diet of birds during the 2 mo (Hobson & Clark 1993) prior to the sampling date; thus our red blood cell samples captured the diets of birds arriving at the colony and initiating their clutches (hereafter referred to as the 'arrival' stage). Plasma turns over more quickly (5 to 7 d, Hobson & Clark 1993) and reflects an individual's diet during the week prior to the sampling date (hereafter referred to as the 'chick-rearing' stage). Individual's δ^{15}N values for red blood cell and plasma samples were not correlated (r = 0.086) and δ^{13}C were only moderately positively correlated (r = 0.46).

Red blood cells have a C:N ratio resembling pure protein (about 3.5, Cherel et al. 2014); therefore, no lipid extraction prior to analysis was needed. We freeze-dried a 20 µl sub-sample of red blood cells and weighed 0.1 to 0.6 mg into a tin boat for analysis. Plasma samples have a relatively high lipid content, which depletes ^{13}C and may lead to spurious results (Hobson & Clark 1992, Post et al. 2007). We delipidated a 20 µl sub-sample of plasma using a 1:4 methanol:choloroform solution (as described by Barger et al. 2016). Post-delipidation, we freeze-dried samples and weighed 0.1 to 0.6 mg into a tin boat for analysis. For delipidated samples where C:N ratios remained relatively high (>4, Cherel et al. 2005), we used the equation for aquatic organisms described by Post et al. (2007) to correct for carbon depletion ($\Delta^{13}\text{C} = -3.32 + 0.99 \times \text{C:N}$, where Δ^{13}C is the correction factor applied to the δ^{13}C values).

Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility (UAF SIF). Tin boats were loaded into an Elemental Analyzer (EA Costech ESC 4010) and processed via continuous flow isotope ratio mass spectrometry using a Delta+XP isotope ratio mass spectrometer. Ratios of $^{15}\text{N}:^{14}\text{N}$ and $^{13}\text{C}:^{12}\text{C}$ were calibrated using an internal standard (peptone: replicate measures indicated measurement errors of ±0.34‰ and ±0.08‰ for δ^{13}C and δ^{15}N, respectively) and then compared to the international standard ratios of atmospheric nitrogen and Vienna Pee Dee Belemnite using $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{15}N or ^{13}C and R is the ratio of heavy:light nitrogen or carbon. Results are expressed in delta notation as parts per thousand (Peterson & Fry 1987).

Statistical analysis

We conducted all statistical analysis in R (v. 3.2.3, R Core Development Team 2015 and v 3.4.2, R Core Development Team 2017). To determine whether years in our study had 'warm' or 'cold' oceanographic conditions, we used principal components analysis (prcomp package, R Core Development Team 2015) to assign a continuous value to each year based on measurements from 5 climate indices. We included the summer Pacific Decadal Oscillation index (PDOs, averaged for June, July, and August, www.beringclimate.noaa.gov/data/), which captures the variability in sea surface temperature across the North Pacific; the ice cover index (ICI, www.beringclimate.noaa.gov/data/), the average ice concentration January to May reported as anomalies against the long-term mean; the ice retreat index (IRI, www.beringclimate.noaa.gov/data/), the number of days after March 15 when >10% of ice disappears from near mooring M2; and the sea surface and bottom temperature (SST and Bottom) within a 150 km radius of the Pribilof Islands (Lauth 2016). These variables were selected to capture large and small scale variability and have been shown to be biologically relevant (seabirds: Dorresteijn et al. 2012, Satterthwaite et al. 2012; zooplankton and fish: Stabeno et al. 2012).

Prior to examining isotopic niche dynamics, we modeled $\delta^{13}C$ and $\delta^{15}N$ as a function of oceanographic conditions, colony, species, and season. The purpose for this was 2-fold: (1) to verify that changes in oceanographic conditions correspond to changes in $\delta^{15}N$ or $\delta^{13}C$ values; and (2) to determine how the models should be built to best describe the isotopic niche dynamics in the region. If, for example, all species in both colonies responded to oceanographic conditions similarly during both the arrival and chick-rearing period, then we would model the isotopic niches in a single model, not differentiating between colony or time during the breeding season. On the other hand, if interaction terms indicated that species responded differently on different islands and under different oceanographic conditions then we would model the isotopic niche by species, oceanographic condition, and island. We used a random intercept mixed model (lme4 package, Bates et al. 2015) and maximum likelihood estimation to model $\delta^{13}C$ and $\delta^{15}N$ separately with respect to the 2 islands (fixed effect: Colony), species (fixed effect: Species), time of the breeding season (fixed effect: Season), and oceanographic conditions (fixed effect: PC1, each year had a score). We included 2-way interaction terms and verified that candidate models did not include terms with high collinearity among non-categorical variables (vif.mer function available at https://github.com/aufrank/R-hacks/blob/master/mer-utils.R, cut-off value = 3). Since plasma and red blood samples were obtained from the same individuals, we included individual as a random factor. We included the 2-way interactions of these variables to determine whether species from different colonies behaved similarly (indicated by non-significant interaction terms) under different oceanographic conditions and/or across a breeding season. We used the corrected Akaike's information criterion (AIC_c for small sample sizes, Burnham & Anderson 2002) to select the best candidate model, which we used to determine how to structure our analysis of the isotopic niche dynamics (see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m592p247_supp.pdf). We also calculated the means and standard errors for $\delta^{13}C$ and $\delta^{15}N$ values of each species data to capture shifts in the isotopic niche at the species level.

We used the R package SIBER (Jackson et al. 2011) to analyze the stable isotope data at the group and species level. We used a Bayesian approach to calculate Layman's metrics, a set of summary statistics that describe changes in the shape, size, and concentration of points within the isotopic ellipse (Layman et al. 2007) for the combined group of seabirds. We used this same approach to calculate the 40% standard ellipse area (SEA) for each individual species under different oceanographic conditions during arrival and chick rearing, which we used for graphing purposes only. We categorized years as 'warm' or 'cold' according to our principal components analysis (described above) and included them in the model as the 'community' variable (i.e. all warm years were combined and all cold years were combined). We ran a Markov chain Monte Carlo with 3 chains drawing from a Wishart distribution, with vague normal priors, for 50000 iterations, and a burn in of 10000. Every 20th value of the posterior was retained (Jackson et al. 2011, Parnell et al. 2013). Following Jackson et al. (2011), we report the Layman's metrics for the group-level analysis including the mode, and 50% and 90% credible intervals for the total isotopic area covered as described by the d*x*_range (dC) and d*y*_range (dN), which give the range of the group along the *x*- ($\delta^{13}C$) and *y*-axes ($\delta^{15}N$), the distance to the centroid (Centroid), and the average distance to a point's nearest neighbor (NNdist). In regards to ecological interpretations: dN provides a description of trophic diversity and dC characterizes the breadth of the food web's base. The SEA.B is an estimate of the core 40% isotopic niche used by the group or species and is considered to be robust in the face of small sample sizes. 'Centroid' is a measure of the average diversity used in the food web. 'NNdist' complements Centroid by reporting the distribution of species within the total area, with a small NNdist indicating that species are foraging in a similar isotopic space.

RESULTS

Principal components analysis of climate variables

The first principal component (PC1) retained 91.34% of the variance in the component variables. All 5 components were loaded for PC1 (PDO = 0.906, ICI = –0.982, IRI = –0.98, Bottom = 0.951, SST = 0.957), and contributed a similar amount to determining the score (PDO = 17.968, ICI = 21.135, IRI = 21.019, Bottom = 19.803, SST = 20.075). The designation of 'warm' and 'cold' years based on PC1 corresponded to characterizations of the study years in the literature (Fig. 2, Stabeno et al. 2012).

Mixed model results

During warm conditions, all 3 species on both colonies foraged on more shelf-based prey; however, the relative change in carbon stable isotope ratios differed among species (Table 2, see Table S3 in the Supplement) being greatest in common murres (PC1 × Species $F_{2,28}$ = 28.255, p < 0.0001, Fig. 3). Birds breeding on St. George relied more heavily on oceanic prey species compared to St. Paul birds, a difference more pronounced during arrival than during chick-rearing (Season × Colony $F_{1,502}$ = 19, p < 0.0001, Fig. 3).

Nitrogen stable isotope ratios also changed in response to warmer conditions (Table 3, see Table S4 in the Supplement); however, the direction of the change varied between arrival and chick-rearing (PC1 × Season $F_{1,1041}$ = 26.14, p < 0.0001) and among species (PC1 × Species $F_{2,1242}$ = 18.19, p < 0.0001). For example, δ^{15}N increased in warm compared to cold conditions during chick-rearing but remained the same regardless of ocean conditions during arrival. At the species level, without taking breeding colony into account, δ^{15}N for common murres increased in warm ocean conditions, whereas the δ^{15}N for kittiwakes and thick-billed murres remained similar between warm and cold ocean conditions. Similarly, only common murres showed a decrease in δ^{15}N from arrival to chick-rearing, whereas kittiwakes and thick-billed murres had similar δ^{15}N throughout the breeding season (Season × Species $F_{2,1000}$ = 18.04, p < 0.0001), again without taking into account the breeding colony. Birds breeding on St. Paul Island fed on prey with higher δ^{15}N than birds breeding on St. George Island (Colony $F_{1,1209}$ = 358.26, p < 0.0001, Fig. 3).

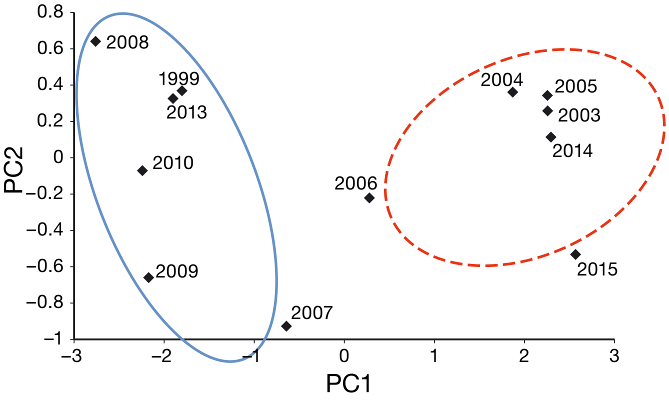

Fig. 2. Categorization of years as 'cold' or 'warm' using PC1 (the first principal component). Negative numbers correspond to cold oceanographic conditions, and positive numbers correspond to warm oceanographic conditions. PC1 is plotted against PC2 (the second principal component). The 68% ellipses indicate the cold (solid blue line) and warm (dashed red line) groupings. The year corresponding to each point is noted within the plot

Group analysis

The isotopic niche of breeding seabirds on St. George Island was larger during warm conditions (P[SEA.B cold < SEA.B warm] = 1 for both arrival and chick-rearing), and especially so early in the breeding season (Fig. 4A). In warm conditions, trophic level diversity increased (dN, Fig. 4A), as did the overall diversity of the utilized food web (Centroid mode [95% CI], cold = 0.26 [0.172, 0.358], warm = 0.601 [0.482, 0.716]).

The isotopic niche of seabirds breeding on St. Paul Island had the opposite response to warmer ocean conditions (Fig. 4C,D). Under warm ocean conditions, birds tended to forage on a smaller diversity of basal resources, likely reflecting a constricted geographic range (dC, Fig. 4C). During chick rearing, the isotopic niche of St. Paul Island breeding seabirds was smaller in warm compared to cold ocean conditions (P[SEA.B cold > SEA.B warm = 1]), which was characterized by a decrease in the diversity of trophic levels utilized (dN, Fig. 4D), and a consolidation of the foraging area (dC, Fig. 4D). Trophic diversity decreased during warm ocean conditions (Centroid, cold = 0.709 [0.529, 0.909], warm = 0.277 [0.108, 0.523]) and the trophic niche of individual species tended to converge (NNdist, cold = 0.889 [0.581, 0.909], warm = 0.355 [0.116, 0.696]). In general, birds on St. Paul Island utilized a less diverse and smaller isotopic niche in warm ocean conditions than birds on St. George Island (see Table S5 in the Supplement for full Layman's metrics).

Table 2. Corrected Akaike's information criterion (AIC_c) model selection results for $\delta^{13}C$. We report the top 2 models, as well as the single variable models and additive model. All other models had an AIC_c weight (w_i) of 0. We tested 38 models. All models include bird as a random effect. A summary for the top model (Table S3) as well as a full list of the candidate models (Table S1) are reported in the Supplement (www.int-res.com/articles/suppl/m593p247_supp.pdf)

Carbon models	k	AIC_c	ΔAIC_c	w_i
PC1 + Species + Season + Colony + PC1 × Species + Season × Colony	11	2776.95	0.00	1.000
PC1 + Species + Colony + Season + PC1 × Species	10	2794.11	17.16	0.000
PC1 + Species + Colony + Season	8	2847.39	70.44	0.000
PC1	4	3066.71	289.75	0.000
Colony	4	3087.00	310.05	0.000
Species	5	3166.42	389.46	0.000
Season	4	3185.67	408.72	0.000
Null model	3	3193.26	416.31	0.000

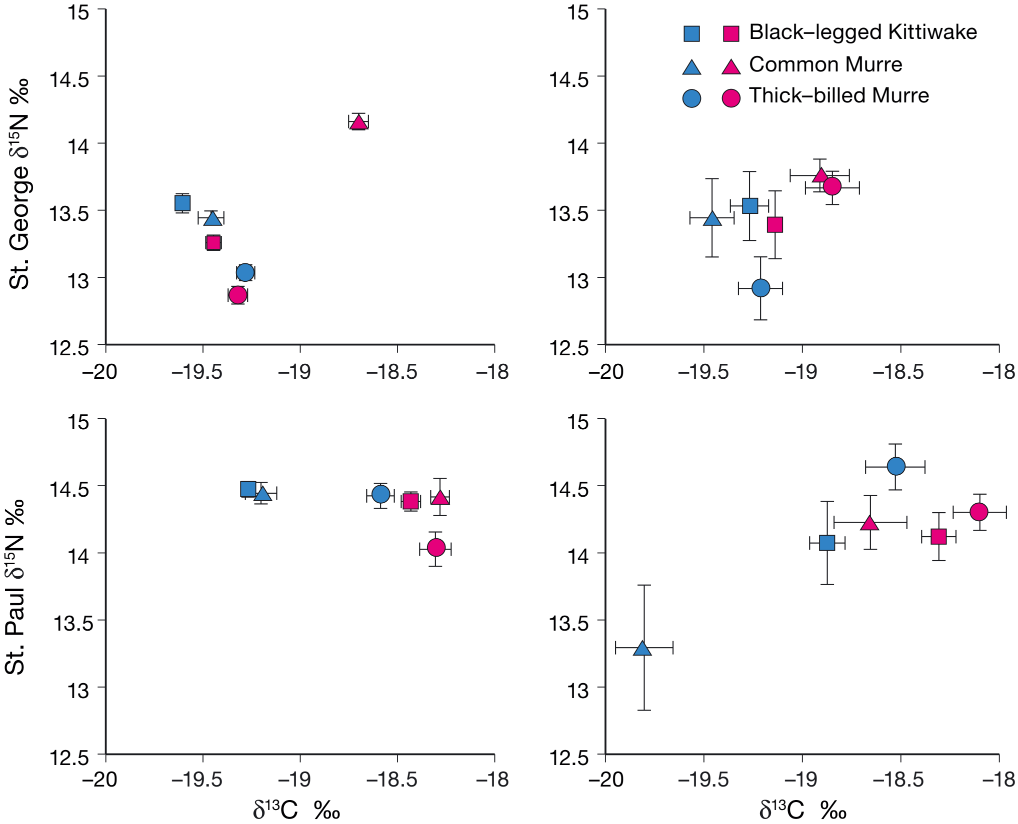

Fig. 3. Average stable isotope values for species breeding on St. George (top panel) and St. Paul (bottom panel) Islands. Mean (±SE) isotopic signatures of black-legged kittiwakes *Rissa tridactyla* and murres *Uria aalge* and *U. lomvia* shifted between cold (blue symbols) and warm (red symbols) oceanographic conditions and between the arrival (left column) and chick-rearing (right column) periods of the breeding season

Species analysis

In support of the group level analysis, St. George Island common murres had a larger niche in warm compared to cold ocean conditions (P[SEA.B cold < SEA.B warm] = 1 and 0.99 for arrival and chick-rearing, respectively). However, the isotopic niche of thick-billed murres and kittiwakes was smaller in warm compared to cold conditions (P[SEA.B cold > SEA.B warm] = 0.96, 1, and 0.6 for kittiwakes, thick-billed murres arrival, and thick-billed murres chick-rearing, respectively, Fig. 5). Seasonal dynamics of niche size differed between warm and cold ocean conditions. In warm years, the isotopic niche for all species in-

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Table 3. Corrected Akaike's information criterion (AIC_c) model selection results for $\delta^{15}N$. We report the top 2 models, as well as the single variable models and additive model. All other models had an AIC_c weight (w_i) of 0. We tested 41 models. All models include bird as a random effect. A summary for the top model (Table S4) as well as a full list of the candidate models (Table S2) are reported in the Supplement

Nitrogen models	*k*	AIC_c	ΔAIC_c	w_i
PC1 + Season + Species + Colony + PC1 × Season + PC1 × Species + Season × Species	13	3984.43	0.00	0.992
Season + Species + Colony + Season × Species + Colony × Species + Season × Colony	12	3993.95	9.53	0.008
PC1 + Species + Colony + Season	8	4066.14	81.72	0.000
Colony	4	4110.83	126.41	0.000
Species	5	4349.44	365.01	0.000
Null model	3	4391.72	407.29	0.000
Season	4	4392.07	407.65	0.000
PC1	4	4393.64	409.22	0.000

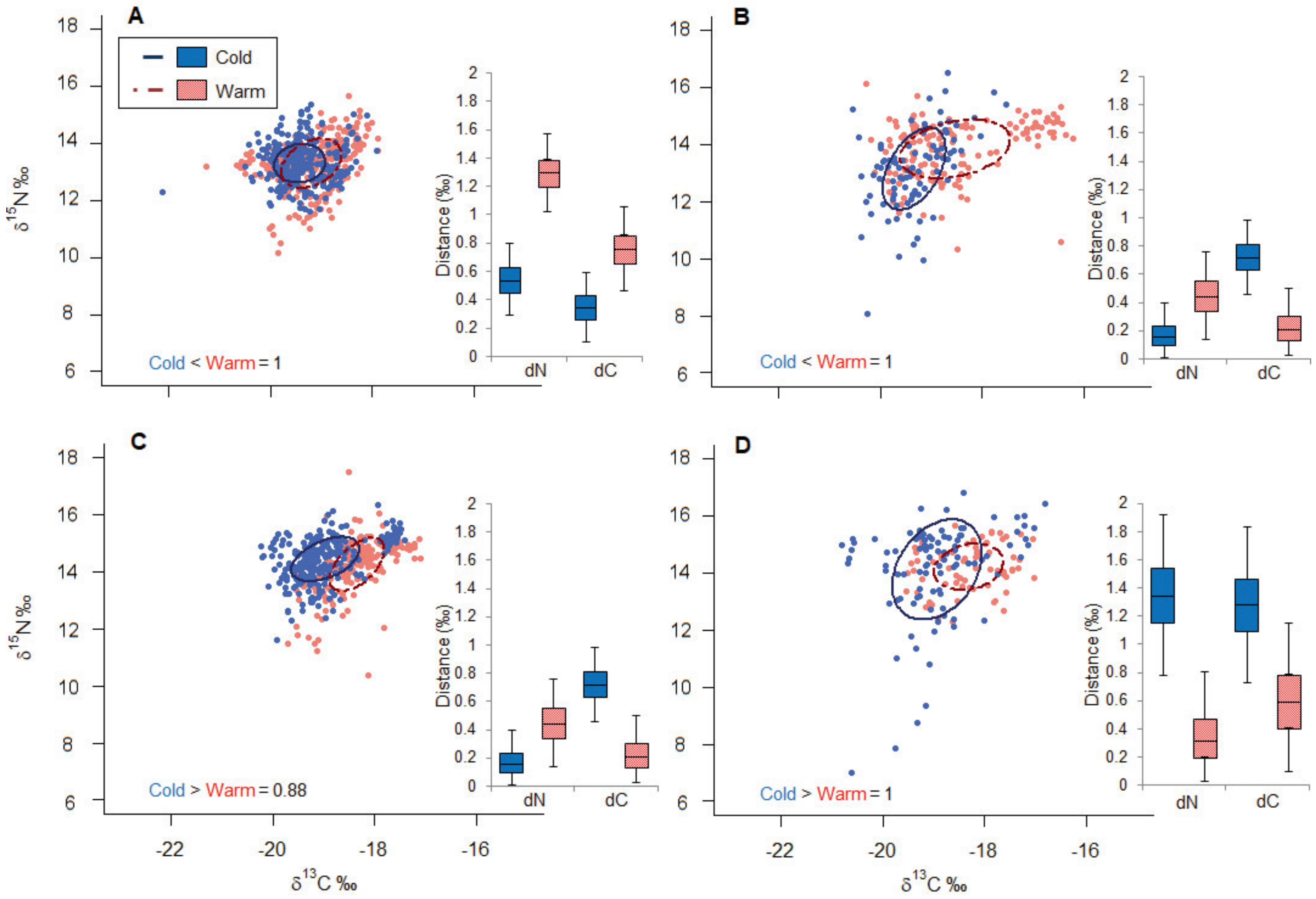

Fig. 4. Changes in the isotopic niche of black-legged kittiwakes *Rissa tridactyla* and murres *Uria aalge* and *U. lomvia* between cold and warm conditions on (A) St. George Island during arrival, (B) St. George Island during chick-rearing, (C) St. Paul Island during arrival, and (D) St. Paul Island during chick-rearing. The raw data are displayed as cold (blue points) and warm (red points), overlaid with the 40% ellipses of the seabird group in cold (blue solid line) and warm (red dashed line) ocean conditions. The posterior modes, and 50% (box) and 95% (whisker) credible intervals of the Layman's metrics dN and dC of the seabird group for cold (blue) and warm (red) ocean conditions are displayed in the inset. See 'Materials and methods' for a description of parameters; a complete set of Layman's metrics can be found in Table S5 in the Supplement

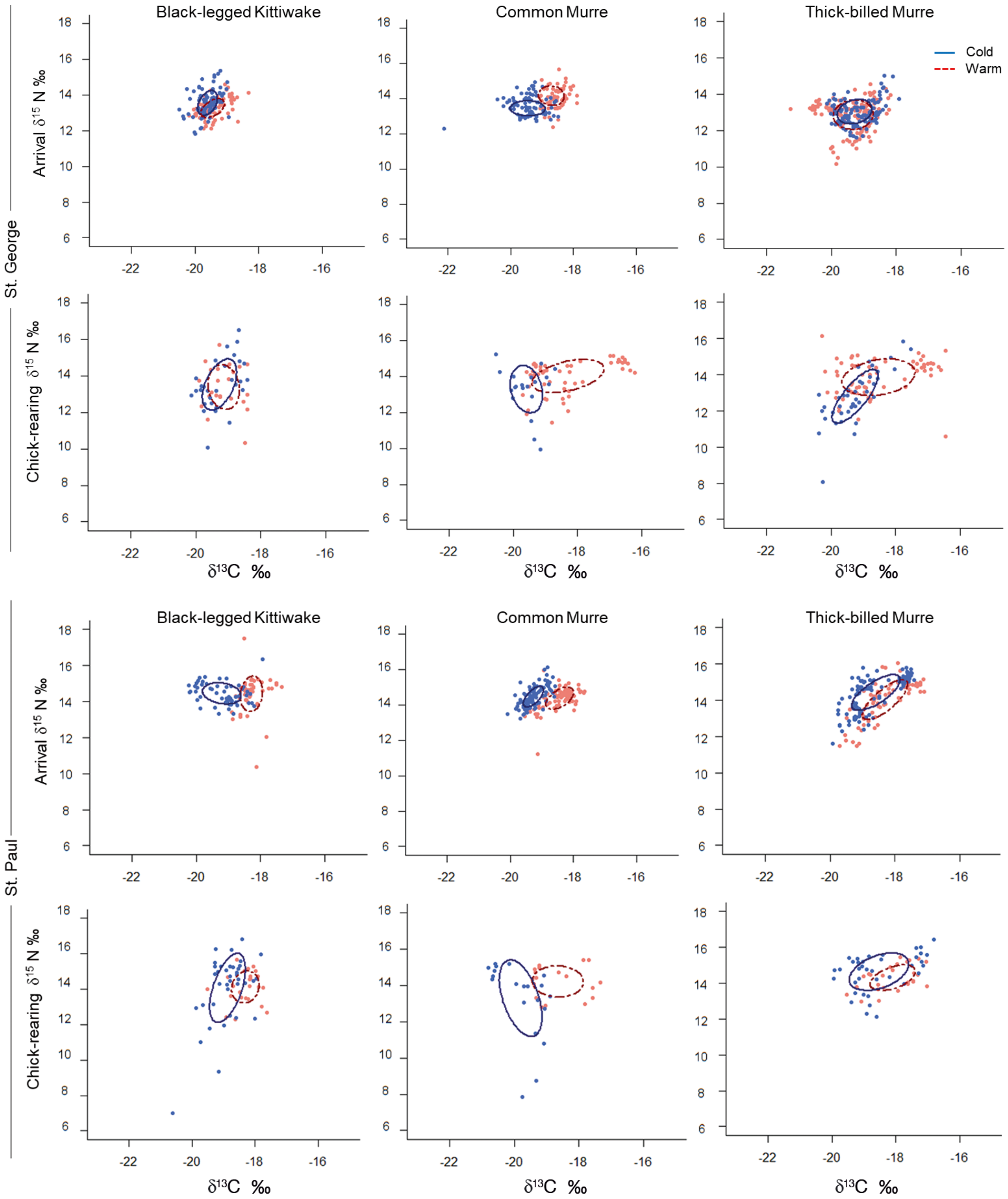

Fig. 5. Stable isotope signatures of red blood cells ('Arrival') and plasma ('Chick-rearing') for black-legged kittiwakes *Rissa tridactyla* and murres *Uria aalge* and *U. lomvia* breeding on St. George and St. Paul Islands in cold (blue) and warm (red) conditions. Superimposed are the 40% ellipses for each species during cold (blue solid line) and warm (red dashed line) conditions; a complete set of Bayesian standard ellipse areas (SEA.B) can be found in Table S6 in the Supplement

creased in size during chick-rearing compared to arrival (P[SEA.B warm-arrival < SEA.B warm-chick-rearing] = 0.97, 0.99, and 0.55 thick-billed murres, respectively), while in cold years, the niche size was smaller during chick-rearing compared to arrival (P[SEA.B cold-arrival > SEA.B cold-chick-rearing] = 0.92, 0.88, 1 for kittiwakes, common murres, and thick-billed murres, respectively, Fig. 5, see Table S6 in the Supplement for SEA.B modes and CI).

On St. Paul Island, almost all birds had smaller isotopic niches in warm compared to cold ocean conditions (P[SEA.B cold > SEA.B warm] = 0.97 to 1) with 2 exceptions: common murres during arrival and thick-billed murres during chick-rearing had larger isotopic niches in warm compared to cold ocean conditions (P[SEA.B cold < SEA.B warm] = 1 and 0.89 for common murres arrival and thick-billed murres chick-rearing, respectively). Seasonal changes in isotopic niche size were nearly consistent across oceanographic conditions and species. Niches during chick-rearing were larger than during arrival (P[SEA.B arrival < SEA.B chick-rearing] = 0.87 to 1) with 1 exception: kittiwakes during warm years had a smaller isotopic niche during chick-rearing compared to arrival (P[SEA.B arrival > SEA.B chick-rearing] = 0.99, Fig. 5).

DISCUSSION

The diets of murres and black-legged kittiwakes have been documented to be diverse, including forage fish and invertebrate species (Iverson et al. 2007, Sinclair et al. 2008, Renner et al. 2012). To date, however, efforts to detect broad relationships in this region between the diet of murres and kittiwakes nesting at the Pribilof Islands and regional climate indices have failed to find any consistent trends (Renner et al. 2012, 2014, but see Kokubun et al. 2018 for thick-billed murres). In contrast, shifting patterns in habitat use have been documented from ship-based surveys at both seasonal and inter-annual time scales (Schneider & Hunt 1984, Hunt et al. 2014, Renner et al. 2016, Suryan et al. 2016, Hunt et al. 2018). To advance the understanding of how seabirds nesting on the Pribilof Islands alter their foraging between warm and cold years, we characterized the isotopic niche of black-legged kittiwakes and common and thick-billed murres breeding on St. Paul and St. George Islands. It is expected that species engaging in similar foraging modes will partition prey when interspecific competition is more likely to occur (during food shortages or chick-rearing), and consume similar prey when it is plentiful (Hardin 1960, e.g. Barger et al. 2016). We investigated how food resources were partitioned among 3 seabird species under different oceanographic conditions and with access to different habitat types. We predicted that during cold ocean conditions, when food is less available, the diet among species would differ more than in warm ocean conditions when prey is abundant. We further predicted that this pattern of partitioning would be most apparent in seabirds breeding on St. Paul Island, a colony with more limited access to diverse foraging habitats.

Effect of oceanographic conditions on diet

Seabirds breeding on both St. Paul and St. George Islands shifted to consuming more shelf-based prey under warm oceanographic conditions. At-sea surveys have indicated that surface-feeding black-legged kittiwakes and moderately deep-diving shearwaters *Ardenna* spp. occurred in greater abundance over the shelf region in warm years (Renner et al. 2016). This may have been a response to an increased abundance of juvenile pollock on the shelf in warm years (Hunt et al. 2011, Renner et al. 2016, Suryan et al. 2016). In years with early sea ice retreat and warm sea temperatures, juvenile pollock have been observed closer to the ocean surface and found to occur at 51 times the densities recorded in cold years (Renner et al. 2016). Whether a greater abundance of pollock is also beneficial for murres has been unclear, as water masses and prey at depth may be somewhat independent of the dynamics shaping the food web available to surface foragers (Byrd et al. 2008b, Renner et al. 2016). Our results, however, indicate that common and thick-billed murres shifted towards shelf-based prey on St. George and St. Paul Islands, suggesting that they may also be feeding on juvenile pollock in warm years (Sinclair et al. 2008, Kokubun et al. 2018). Although all 3 species in both colonies took advantage of more abundant shelf-based prey in warm years in some way, we found that isotopic niche dynamics in the 2 colonies were different between warm and cold years and among species.

Isotopic niche dynamics of the seabird group

The combined isotopic niche of black-legged kittiwakes and murres nesting on St. Paul Island was heavily influenced by ocean conditions. In warm years, the group's niche area was smaller during arrival and chick-rearing. However, the diversity in foraging locations during arrival in warm conditions was comparable to that in cold conditions, as reflected in the dN and dC isotopic distances. This may be a signal that the food web on the shelf develops from a common starting point early in the breeding season, but that the trajectory of development may be determined by oceanographic conditions that result in an increasingly different foraging landscape as the season progresses (Hunt et al. 2011). Unfortunately we do not have baseline $\delta^{13}C$ or $\delta^{15}N$ values which could be used to determine whether changes in isotopic distances are due to the number of sources in a food web, to food web diversity, or simply to a relatively small plasma sample size (Layman et al. 2012, Brind'Amour & Dubois 2013). While our ability to infer inter-seasonal food web structure is limited, we found no year-associated patterns within the warm or cold isotopic values; therefore, we are able to discount the possibility that changes in baseline values alone explain the shifts in the use of the isotopic space we observed.

In warm years, the isotopic space used by seabirds on St. George Island, which is closer to the shelf break, was more diverse and larger than the isotopic space used by seabirds on St. Paul Island, which is situated farther from the shelf break. In contrast, the total isotopic spaces used at the 2 islands were similar in cold years. This may be partially attributed to the differences in colony size between the 2 islands. St. George Island supports an order of magnitude more seabirds than St. Paul Island (Hickey & Craighead 1977). Due to the population size, breeding seabirds on St. George Island may continue to use slope/oceanic foraging habitat during warm years, when shelf food resources are abundant, to avoid intraspecific competition on the shelf. The isotopic niche dynamics suggest that generalist seabirds breeding on St. George Island used oceanic-based prey, both during warm conditions when alternative shelf-based prey was available, and especially in cold conditions when it was not. The analysis of stomach contents and tracking data collected from adult birds corroborate our finding that the slope/oceanic region provides an important prey-base for St. George Island seabirds irrespective of environmental conditions (Sinclair et al. 2008, Renner et al. 2012, Harding et al. 2013). Despite the continued use of slope/oceanic prey in warm years, fledging success of thick-billed murres on both islands has been positively correlated with the occurrence of coastal/shelf-based species in chick diets (Renner et al. 2014), which may be due to the energetic savings parents make by being able to capture prey closer to the colony (Pennycuick 1997, Elliott et al. 2013).

Species level responses

In cold conditions on St. Paul Island, the trophic diversity at the species level generally increased over the course of the breeding season (i.e. the isotopic niche was larger during chick-rearing than arrival). A similar pattern of larger isotopic space utilization was also observed for seabirds breeding on St. George Island during warm ocean conditions. Intraspecific diet diversification during chick-rearing appears to have occurred and may have been due to seasonal changes in prey type and/or availability (Darimont & Reimchen 2002), or the result of an increase in energy demands associated with chick-rearing, which may lead to increased partitioning in prey among breeding seabirds (Barger et al. 2016). Alternatively, this pattern may be attributed to the development of the food web and subsequent changes in prey isotopic values as the productive season progressed rather than an actual change in types of prey consumed. If this is the case, it would still indicate that, under these conditions, the type of prey consumed by species was diverse, as prey isotopic values became more different (the niche area expanded) as the breeding season progressed.

In contrast, the isotopic area utilized by kittiwakes on St. Paul Island in warm conditions was smaller during chick-rearing than arrival. This was also observed for all 3 study species breeding on St. George Island during cold ocean conditions. A decrease in the isotopic space used over the course of the breeding season may be attributed to a reliance on more similar prey species during chick-rearing than arrival. While there may be seasonal changes in the isotopic values of prey, if murres and kittiwakes were relying on the same species throughout the breeding season we would expect there to be no difference in the size of the isotopic niche between arrival and chick-rearing.

On St. George Island, in warm ocean conditions, access to diverse habitat and the availability of on-shelf young-of-the-year pollock may facilitate prey resource partitioning (Darimont et al. 2009). During warm conditions on St. George Island, the isotopic niche of murres and kittiwakes expanded compared to cold conditions, indicating that while birds used on-shelf prey, this did not replace the use of oceanic-based prey (dC was larger in warm compared to cold conditions, Fig. 5).

Closing remarks

To summarize, we found that during warm years, piscivorous seabirds consumed prey on the shelf that was not available to them during cold years. In addition, species with access to multiple habitat types (e.g. those breeding on St. George Island) were able to exploit additional prey sources in the vicinity of their breeding colony. Consuming more prey on the shelf would potentially reduce the cost of foraging for adults during the chick-rearing period (Kokubun et al. 2018). While warm conditions in early summer have been linked to abundant young-of-the-year pollock in the upper water column of the shelf (Renner et al. 2016), warm conditions in late summer and autumn result in low recruitment of the same young pollock (Hunt et al. 2011, Mueter et al. 2011). Thus, although warm conditions may currently be associated with high prey availability near the breeding colonies, an increase in the frequency of warm years may eventually result in a negative impact on seabirds through reduced pollock populations (Mueter et al. 2011).

More generally, we demonstrated that the isotopic niche can be used to characterize how seabirds with different foraging strategies and diverse diets partition the foraging landscape in response to environmental variability. In this study, we specifically addressed whether or not having access to diverse foraging habitat modifies how seabirds partition prey resources under different oceanographic conditions. We found that knowledge of habitat type, and how prey dynamics in different habitats may change, is needed in order to correctly interpret the expansion or contraction of the isotopic niche used by a group of species as a response to changes in prey availability. In regards to the southeastern Bering Sea specifically, we conclude that changes in oceanographic conditions influenced the isotopic niche of piscivorous seabirds and that this response was mediated by foraging habitat heterogeneity.

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Contribution to the Theme Section 'Seabird responses to a changing Bering Sea'

Red-legged kittiwake feathers link food availability to environmental changes in the Bering Sea

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ABSTRACT: The largest breeding population of red-legged kittiwakes *Rissa brevirostris* has undergone a dramatic decline and subsequent recovery since 1975. The causal mechanism is hypothesized to be climate-induced food shortages during reproduction, yet little is known about how the basin ecosystem, where breeding red-legged kittiwakes primarily forage, is affected by climate variability. We examined when and under what conditions red-legged kittiwakes experienced food shortages. Head feathers (winter) and first primary feathers (summer; n = 24 and 27 yr, and 194 and 122 individuals, respectively) were collected between 1913 and 2016 on St. George Island and were analyzed for stable isotope signatures of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$). Feathers were also analyzed for corticosterone concentration (fCORT), which indicates a bird's exposure to nutritional stress during feather growth. Summer fCORT concentrations were lower when values of the annual Pacific Decadal Oscillation index were positive. Winter fCORT concentrations and $\delta^{15}N$ signatures increased when February sea-ice coverage was extensive. We conclude that, since 1913, warm conditions in the Bering Sea ecosystem have been associated with low nutritional stress in adult red-legged kittiwakes breeding on St. George Island. However, we found no strong evidence for isotopic shifts over this same period. A better understanding of the factors governing the abundance and availability of red-legged kittiwakes' prey is needed to predict the impact of anticipated warming on this species and its foraging habitat.

KEY WORDS: Historical ecophysiology · Feather corticosterone · St. George Island · Stable isotope analysis · Food shortage · Nutritional stress.

INTRODUCTION

The Bering Sea climate has historically varied between 'warm' and 'cold' states, characterized by changes in winter sea-ice dynamics, winter storminess, and summer water temperatures (Rodionov & Overland 2005). Fluctuations in the region's animal populations and community structure have been associated with these changes in climate (Hare & Mantua 2000, Litzow & Mueter 2014). In the southeastern Bering Sea, population declines observed in seabird, marine mammal, and fish populations (Hare & Mantua 2000, Litzow & Mueter 2014) during the late 1970s and 1980s are hypothesized to have been a result of changes in food availability (Anonymous 1993). How food availability changed, however, is not certain.

One hypothesis posited that a coinciding explosion in the walleye pollock *Gadus chalcogrammus* (hereafter 'pollock') population resulted in increased competition with other top predators for forage fishes (Springer 1992). Another proposed that oceanographic conditions were no longer suitable for lipid-rich forage fish species and fish lower in lipid content, such as the now abundant juvenile pollock, were inadequate to meet the energy demands of predatory fish, seabird, and marine mammal populations (Alverson 1992, the 'junk food hypothesis'). Another hypothesis, not yet tested, is that food shortages occurred during the winter and affected seabirds and marine

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mammals outside of the reproductive season (e.g. during migration or overwintering, Renner et al. 2014).

In terms of seabird responses to climate-driven food availability, much work has been done to understand how climate-associated changes in the southeastern Bering Sea continental shelf ecosystem affect prey abundance (e.g. Napp et al. 2000, Springer et al. 2007, Hunt et al. 2011) and seabird reproduction (e.g. Springer 1998, Murphy et al. 2016). How or whether these same climate patterns affect forage fish production in the Bering Sea deep water basin is less clear. Of the seabirds breeding in the southeastern Bering Sea, red-legged kittiwakes *Rissa brevirostris* are the only fish-eating seabird that relies primarily on oceanic prey (Byrd & Williams 1993). Red-legged kittiwakes forage primarily on myctophids, mesopelagic fishes, during the reproductive season (Storer 1987, Byrd & Williams 1993). Thus, red-legged kittiwakes might be somewhat independent of the food dynamics of the southeastern Bering Sea continental shelf region, which govern the diets of other seabirds breeding on the Pribilof Islands (Renner et al. 2012).

The breeding population of red-legged kittiwakes on St. George Island, where 80 % of the world's population breeds, has shown dramatic changes in its population trajectory over the past 4 decades (Tappa & Romano 2017), suggesting that the birds are experiencing changes in prey availability at some point in their annual cycle. Changes in the environment can result in food shortages that are reflected in seabird physiology (e.g. Kitaysky et al. 1999, Satterthwaite et al. 2012). Nutritional stress incurred during reproduction affects adult seabird survival (Kitaysky et al. 2007, 2010, Satterthwaite et al. 2010) and poor-quality food fed to developing offspring may produce low-quality individuals that may be unable to recruit into the population (Kitaysky et al. 2006). There is some evidence that red-legged kittiwake reproductive success may be attributed to environmental conditions (Springer 1998), but a connection between environmental variability and food availability has yet to be made. We hypothesized that further examination of the trophic ecology of red-legged kittiwakes over time might provide insight into changes in the Bering Sea basin's ecosystem in response to environmental variability.

As a step towards resolving the relationship between changes in environmental conditions and the responses of red-legged kittiwakes, we used a historical ecophysiology approach to examine the isotopic signatures and physiological response of St. George Island red-legged kittiwakes to environmental variability from 1912 to 2016. Historical ecophysiology uses analytical tools to mine ecologically relevant measures from specimens or samples collected in the past, allowing researchers to greatly extend time series and rely on unified laboratory methodologies (e.g. Charapata 2016).

Red-legged kittiwakes undergo 2 annual molts. Towards the end of the breeding season (~July–August), adults initiate their flight feather molt, a sequential molt that begins with the loss of their first primary feathers (Byrd & Williams 1993). In approximately February, adults undergo a pre-nuptial molt where they replace their non-breeding head feather plumage (Gabrielson & Lincoln 1959). To characterize foraging conditions during the breeding (summer) and non-breeding (winter) periods, we analyzed first primary ('primary') and head feathers for nitrogen, carbon, and sulfur stable isotope ratios. Based on the ratio of heavy (rare) to light (common) isotopes in an organism's tissues and differential isotopic incorporation rates, it is possible to identify the trophic level (nitrogen) and foraging location (i.e. offshore vs. onshore or benthic vs. pelagic, measured by carbon and sulfur) of the organism in a marine food web (Fry 1988).

Changes in a marine organism's nitrogen stable isotope ratio over time may indicate changes in prey species consumed (lower values indicate it is foraging on lower-trophic-level prey, Peterson & Fry 1987), changes in food web structure (the prey species may be the same but the food web has reorganized so that the trophic level it occupies changes, Grecian et al. 2016), or changes in the baseline nitrogen stable isotope ratio due to physical processes (for example, the mixed-layer depth and presence or strength of eddies can affect the amount of particulate organic matter available to nitrate-dependent phytoplankton, Yang et al. 2017). In the Bering Sea, carbon stable isotope ratios increase from the ocean basin to the continental shelf (Schell et al. 1998), and can be used to identify changes in the amount and composition of primary producers (Grebmeier et al. 2006). At the multidecadal timescale, however, carbon stable isotope values may decrease (−0.1 to −0.2‰ per decade in subpolar regions, Eide et al. 2017) due to the dilution of ^{13}C in the atmosphere by the burning of fossil fuels (the Suess effect, Revelle & Suess 1957). Sulfur stable isotope ratios are less susceptible to large changes from anthropogenic activities (Peterson & Fry 1987) and complement carbon stable isotope values in detecting shifts in sources of primary production in marine food webs (Connolly et al. 2004). In the marine system, higher sulfur stable isotope values indicate the incorporation of nutrients from more benthic habitats (Peterson & Fry 1987).

While stable isotope analysis can be used to characterize how diet and food web organization may have changed over time, it does not fully capture how seabirds may be affected by changes in the environment. A change in conditions may be detrimental to seabirds but may not be accompanied by a shift in isotopic signatures. For example, prey may become more dispersed or less available and require more energy to obtain (Will et al. 2015). Alternatively, isotopic signatures may shift when birds switch prey types but experience no change in caloric intake, or they may shift between equidistant foraging locations. Both instances would result in changes in stable isotope values but may have no effect on the birds themselves. Therefore, we also analyzed feathers for corticosterone concentration. During molt, circulating corticosterone is deposited into the growing feather and provides an integrated measure of the nutritional stress a bird experienced during the period of feather growth (Bortolotti et al. 2008). Elevated concentrations of feather corticosterone have been experimentally linked to low food intake (Will et al. 2014), validated as a proxy for low food availability (Will et al. 2015), and do not degrade over time (Bortolotti et al. 2009).

Measuring nutritional stress in tandem with stable isotope analysis makes it possible to narrow down explanations for changes in stable isotope values over time. For example, if nitrogen stable isotope ratios increase and nutritional stress decreases, the changes in nitrogen may be attributed to increased prey quality, or consumption of a higher-trophic-level prey species, and interpreted as being beneficial (Oelbermann & Scheu 2002). Conversely, if nutritional stress increases, the increase in nitrogen stable isotope ratios may be due to starvation and interpreted as detrimental (Cherel et al. 2005). We modeled changes in stable isotope values and nutritional stress in response to environmental parameters over a multidecadal timescale to determine whether red-legged kittiwakes experienced food shortages during the winter, as well as during the summer, and under what environmental conditions these shortages occurred.

MATERIALS AND METHODS

Study site and specimen origin

All samples were collected from adult red-legged kittiwakes that had been breeding on St. George Island, one of the Pribilof Islands, in the southeastern Bering Sea (56.58° N, 169.60° W, Fig. 1). We sampled live birds (n = 77), and specimens (n = 103) from the following museums: Carnegie Museum of Natural History, Natural History Museum of Los Angeles County, Museum of Southwestern Biology, James R. Slater Museum, San Diego Natural History Museum, and University of Alaska Fairbanks' Museum of the North (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m593p261_supp.pdf for museum specimen IDs).

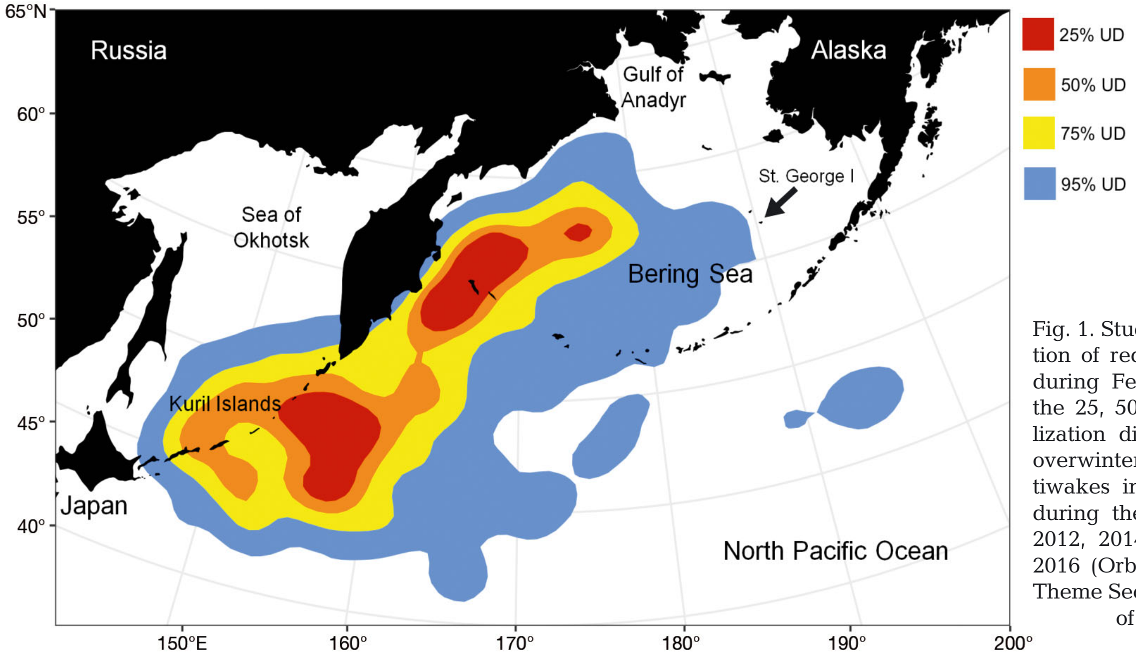

Fig. 1. Study site and distribution of red-legged kittiwakes during February. Shown are the 25, 50, 75, and 95% utilization distributions (UD) of overwintering red-legged kittiwakes in February tracked during the winters of 2011–2012, 2014–2015, and 2015–2016 (Orben et al. 2018, this Theme Section). Map courtesy of R. A. Orben

Feather sampling

To minimize the impact of our study on museum collections, we used only a small portion of a primary feather for our analyses, and whenever possible left the feather still attached to the museum skin. Specifically, we cut a 20 mm section, approx. 20 mm from the tip of the first primary along the proximal side of the vane to standardize feather samples across individuals (Harris et al. 2016). In the field, birds were captured using a noose pole, the first primary was clipped off at the base, and the same 20 mm section described above was later removed in the lab. For both museum and wild-caught birds, we plucked 3 head feathers between the upper nape and crown of the head (see Table S2 in the Supplement for samples by year).

Corticosterone analysis

We weighed and measured (head feathers only) feathers to the nearest 0.05 mg and 0.5 mm. We combined all 3 head feathers (measuring each separately but weighing them collectively) into a single sample for each individual (Lattin et al. 2011). We washed feather samples in isopropanol (HPLC grade, Sigma-Aldrich) by adding 1 ml of isopropanol to a vial containing the feather sample, vortexed for 5 s, and removed the isopropanol 50 s later. After the washing, we added 5 ml of methanol (HPLC grade, Fisher Scientific) to each sample. We proceeded with extraction and analysis procedures reported elsewhere (see Bortolotti et al. 2008, Will et al. 2015) with the exception that samples were filtered via solid phase extraction (Bond Elut C18 cartridges, Agilent Technologies). We added 2000 cpm (counts per minute) of radio-labeled corticosterone (PerkinElmer NET399) to each sample to account for losses of hormone during analysis. On average recoveries were 94.8%.

Feathers were analyzed in 5 radioimmunoassays (Wingfield & Farner 1975). Intra-assay CV was <1% (range: 0.72 to 0.97%) and inter-assay CV was 1.2%. We standardized concentrations to sample mass (ng g^{-1}) and feather length (pg mm^{-1}, head feathers only).

Stable isotope analysis

Typically feathers are washed in a 2:1 chloroform: methanol solution to remove dirt and oils from the feather's surface prior to stable isotope analysis (Dobush et al. 1985). In this study, feathers were washed of dirt and surface oils during the isopropanol wash followed by sonication and overnight extraction in methanol at 50°C. Corticosterone is a cholesterol-based hormone, thus the 12 h methanol extraction process is targeted specifically at removing fats from within the feather matrix (Bortolotti et al. 2008). Therefore, after the methanol extraction, feathers had been effectively washed and were ready for stable isotope analysis (mean primary C:N ratio = 3.16, mean head C:N ratio = 3.06, pure protein ~3.5‰, Cherel et al. 2014). We weighed out 0.6 to 1.0 mg (carbon and nitrogen) or 2.3 to 3.2 mg (sulfur) of pulverized primary feather tissues, or a single intact head feather, and loaded the sample material into a tin boat. Stable isotope analyses for carbon and nitrogen were conducted at the Alaska Stable Isotope Facility (ASIF, Fairbanks AK), while analyses for sulfur was conducted at the Colorado Plateau Stable Isotope Laboratory (CPSIL, Flagstaff, AZ). All primary samples were analyzed for all 3 isotopes. There were no head feathers for sulfur analysis for 2005, and a subset of samples was analyzed for the years 2011, 2015, and 2017 (17 samples from 2011 were analyzed, 8 from 2015, and 8 from 2016). Briefly, samples were loaded into an auto-sampler, which dropped them into an elemental analyzer (EA Costech ECS 4010) interfaced with a Delta+XP Thermo Electron isotope ratio mass spectrometer.

We used delta notation to express stable isotope ratios, 'R', compared with PeeDee Belamnite (carbon), atmospheric nitrogen, and Canyon Diablo Triolite (sulfur; $\delta X = R_{\text{sample}}/R_{\text{standard}}$). At ASIL, peptone was used as an internal standard and analyses were completed in 4 separate runs. Inter-run standards were within ± 0.01‰ for both $\delta^{15}N$ and $\delta^{13}C$, and on average intra-run standards were within ± 0.1‰ for both $\delta^{15}N$ and $\delta^{13}C$. Head feathers from 2010 and 2011 were analyzed by Orben et al. (2015) at the University of California Santa Cruz (UCSC); UCSC internal standards ($\delta^{15}N$ mean = 5.38, SD = 0.09; $\delta^{13}C$ mean = −12.61, SD = 0.16; n = 16) were comparable ($\delta^{15}N$: $t_{26} = -0.72$, $p = 0.48$; $\delta^{13}C$: $t_{26} = 0.32$, $p = 0.75$) when run at ASIF ($\delta^{15}N$ mean = 5.39, SD = 0.07; $\delta^{13}C$ mean = −12.56, SD = 0.21; n = 12). Samples analyzed for sulfur stable isotope ratios were completed in 5 separate runs and were standardized against 6 International Atomic Energy Agency reference standards (IAEA standards and inter-run variation around the expected value S1 ± 0.45‰, S2 ± 0.72‰, S3 ± 0.13‰, S4 ± 1.07‰, SO6 ± 0.71‰, NBS 127 ± 0.21‰) and 8 internal standards.

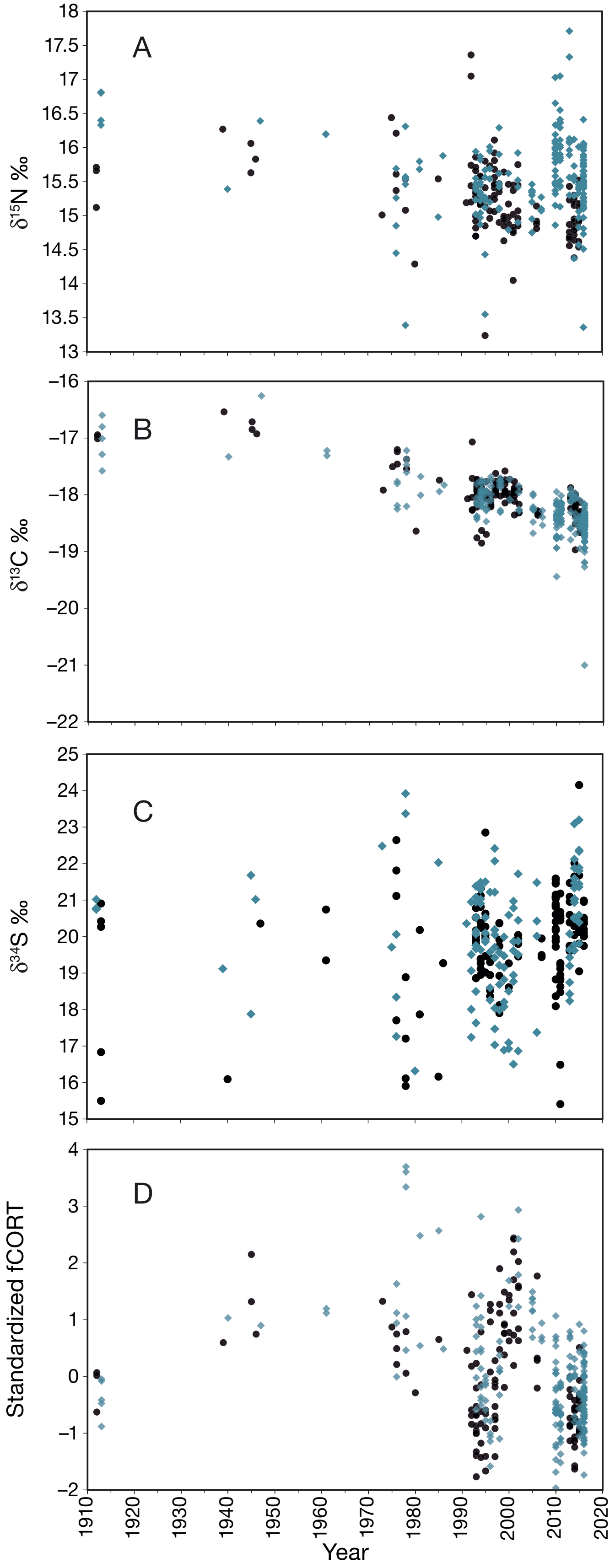

Fig. 2. Red-legged kittiwake stable isotope signatures and stress exposure from 1913 to 2016. (A) δ^{15}N values for head feathers (blue diamonds, n = 194 individuals) and first primary feathers (black circles, n = 122 individuals). (B) δ^{13}C values for head and first primary feathers. (C) δ^{34}S values for head and first primary feathers. (D) Standardized fCORT concentration for head and first primary feathers. Concentrations have been standardized ((concentration — mean concentration)/SD) to illustrate temporal trends and avoid comparing concentrations between feather types

Environmental variables

To detect course-grained patterns in the responses of red-legged kittiwake isotopic signatures and physiology (Fig. 2) to long-term environmental variability, we used regional climate indices that have been shown to be ecologically relevant and/or detect regime shifts. Environmental predictors (www.bering-climate.noaa.gov/data/index.php) were selected based on 2 criteria: (1) ecological relevance, and (2) a correlation between −0.5 and 0.5 with any of the other candidate variables. April sea-ice coverage was the one exception, which is correlated (−0.76) with the annual Pacific Decadal Oscillation (PDO) index (Mantua & Hare 2002). We retained April sea-ice coverage in our models due to the potential ecological impacts of ice cover on the return migration to the colony at the risk of affecting the explanatory power of the PDO in our models. Variables included in models of head feather parameters included Year, PDO, the Arctic Oscillation (AO), and February sea-ice coverage (IceFeb), and for primary feathers, Year, PDO, the AO, the Aleutian Low (ALow), and April sea-ice coverage (IceApr). Detailed descriptions follow.

We included Year in the model selection process to account for any trends over time not fully captured by the other parameters (Bond et al. 2003). In the case of carbon, Year accounted for the Suess effect (Revelle & Suess 1957).

The PDO has historically been the primary indicator of regime shifts in the Bering Sea (Rodionov & Overland 2005), and previously has been related to seabird physiology and diets on the Pribilof Islands (Satterthwaite et al. 2012). The PDO is derived from a principal component analysis of sea surface temperature anomalies across the North Pacific (above 20° N latitude). It is corrected for the global average temperature, so is independent of warming trends associated with climate change (Newman et al. 2016). Positive PDO values are associated with generally warmer conditions (e.g. low winter sea-ice extent and early spring retreat in the Bering Sea), while negative values are associated with generally colder conditions.

In the past few decades, the AO has manifested regime shifts more prominently than the PDO (Rodionov & Overland 2005). The AO is derived from an empirical orthogonal function of monthly mean sea-level pressures poleward of 20° N (Thompson & Wallace 1998). The formation, retention, and movement of sea ice are highly influenced by the AO (Rigor et al. 2002).

Another winter index that potentially predicts the productivity of the Bering Sea is the ALow (i.e. the winter North Pacific Index). The ALow is the mean area-weighted sea-level pressure in November to March, expressed as anomalies compared with the period 1961–2000. The position and strength of the ALow is hypothesized to affect the degree and depth to which the surface layers are mixed, which influences the nutrients available to organisms during spring and summer plankton production (Rodionov & Overland 2005, Rodionov et al. 2007).

Previous research has suggested that red-legged kittiwake migration might be influenced by sea ice (Orben et al. 2015), and indicates that sea ice during the month of April affects breeding season conditions and reproduction (Murphy et al. 2016). We used sea-ice coverage in February and April as explanatory variables in our head and primary feather models, respectively. We calculated ice coverage from maps produced by the National Atmospheric and Oceanic Administration (ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/, available from the National Snow and Ice Data Center). We converted images to grayscale in Adobe Photoshop then calculated the mean pixel intensity in Image J as a proxy for ice coverage. Based on recent records of red-legged kittiwake winter migration patterns, we estimated sea-ice coverage for an area including the Bering Sea, Sea of Okhotsk, and a small portion of the North Pacific (Orben et al. 2018).

Statistical analysis

We conducted all analyses in R version 3.2.3 (R Core Development Team 2015). Head feather corticosterone (fCORT) concentrations were calculated by feather length (pg mm^{-1}, detrended for the effect of sample mass, Will et al. 2014), and primary fCORT concentrations were calculated by feather sample mass (ng g^{-1}). All fCORT concentrations were log-transformed to meet assumptions of normality. We show standardized fCORT concentrations in all figures, calculated as the difference of the concentration from the mean divided by the standard deviation. Stable isotope signatures obtained from both head and primary feathers were normally distributed. We normalized and centered the Year and Ice Coverage explanatory variables so as not to overinflate the coefficient estimates.

We ran multiple general linear mixed-effects models using the 'lme4' package in R (Bates et al. 2015). Models included fCORT, $\delta^{15}N$, $\delta^{13}C$, or $\delta^{34}S$ as response variables, Year as a random intercept and the aforementioned environmental variables as fixed effects. We used Akaike's information criterion (AIC) model selection, based on corrected AIC (AIC$_c$) for small sample sizes, to address whether stable isotope signatures and nutritional stress changed in response to changes in the environment. We report the averaged model from the 95% model subset (the model set whose cumulative model weight is 0.95) and the summed variable model weights. The averaged model coefficients were calculated as $\bar{\beta} = \sum_{i=1}^{n} w_i \hat{\beta}$ where the model-averaged parameter estimate ($\bar{\beta}$) is the summation of the model weight (w_i) and estimated model coefficient ($\hat{\beta}$) for each model in the subset (n = total number of models) (Symonds & Moussalli 2011, refer to Tables S3 & S4 in the Supplement for complete model sets). We modeled response variables at 2 timescales to accommodate the temporal limitations of some of our explanatory variables and the sparse data points from early years: 1913–present (hereafter the 'all data' dataset), and 1979–present (the '40-yr' dataset). The all data were tested against the PDO, ALow (primaries only), ice cover, and Year while the 40-yr data were tested against the PDO, ALow (primaries only), Year, AO, and ice cover.

We also used linear regression analysis ('lm' function in R) to test whether nutritional stress and/or stable isotope values of an individual during one season were correlated with stress and stable isotope signatures in that same individual the following season. Using the 'rptR' package in R (repeatability analysis; Stoffel et al. 2017) we also tested for interseasonal individual consistency in stable isotope signatures and nutritional stress. Finally, we used population data reported by the United States Fish and Wildlife Service's Alaska Maritime National Wildlife Refuge to examine possible relationships between winter physiology or stable isotope signatures and population size. The red-legged kittiwake population on St. George Island experienced a strong decline in the years 1976 to 1989, and has since been increasing (up to the last reported count in 2014, Tappa & Romano

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Table 1. Head feather AIC model selection results. Averaged models for fCORT, $\delta^{13}C$, $\delta^{14}N$, and $\delta^{34}S$ are described for the full dataset ('All data', upper row) and the 40 yr dataset ('40 yr', lower row). The number of models in the 95% model subset is noted in the first column and also given are the summed model weights, Σw_i, where w_i is the probability of model i being the best model in the subset, and w_i is summed for each model containing the variable of interest (PDO [Pacific Decadal Oscillation]; Year; IceFeb [February sea-ice coverage]; AO [Arctic Oscillation]). For the full set of candidate models refer to the Supplement at www.int-res.com/articles/suppl/m593p261_supp.pdf

Models in subset	Averaged model head feathers Variable = $\beta_{intercept} + \beta_{PDO} + \beta_{Year} + \beta_{IceFeb} + \beta_{AO}$	Σw_i PDO	 Year	 IceFeb	 AO
fCORT					
3	$fCORT_{All\ data}$ = 0.35 – 0.012 (PDO) – 0.001 (Year)	0.53	0.69	–	–
9	$fCORT_{40\ yr}$ = 0.278 – 0.005 (PDO) – 0.001 (Year) + 0.005 (IceFeb) + 0.012 (AO)	0.51	0.62	0.45	0.32
$\delta^{13}C$					
2	$\delta^{13}C_{All\ data}$ = –18.31 – 0.04 (PDO) – 0.016 (Year)	0.61	1	–	–
4	$\delta^{13}C_{40\ yr}$ = –17.98 – 0.049 (PDO) – 0.02 (Year) – 0.002 (IceFeb) + 0.007 (AO)	0.36	0.78	0.2	0.18
$\delta^{15}N$					
3	$\delta^{15}N_{All\ data}$ = 15.65 – 0.08 (PDO) – 0.006 (Year)	0.59	0.88	–	–
7	$\delta^{15}N_{40\ yr}$ = 14.93 – 0.05 (PDO) + 0.002 (Year) + 0.002 (IceFeb) – 0.13 (AO)	0.56	0.23	0.16	*0.9*
$\delta^{34}S$					
2	$\delta^{34}S_{All\ data}$ = 18.94 + 0.018 (PDO) + 0.019 (Year)	0.25	0.95	–	–
5	$\delta^{34}S_{40\ yr}$ = 19.47 + 0.17 (PDO) + 0.045 (Year) + 0.011 (IceFeb) + 0.006 (AO)	0.69	0.97	0.27	0.12

2017, Fig. S1 in the Supplement). We used a non-parametric bootstrapping test for small sample sizes (Dwivedi et al. 2017) to compare the mean stable isotope values and fCORT concentrations in head feathers between the time periods 1976–1989 and 1990–2014.

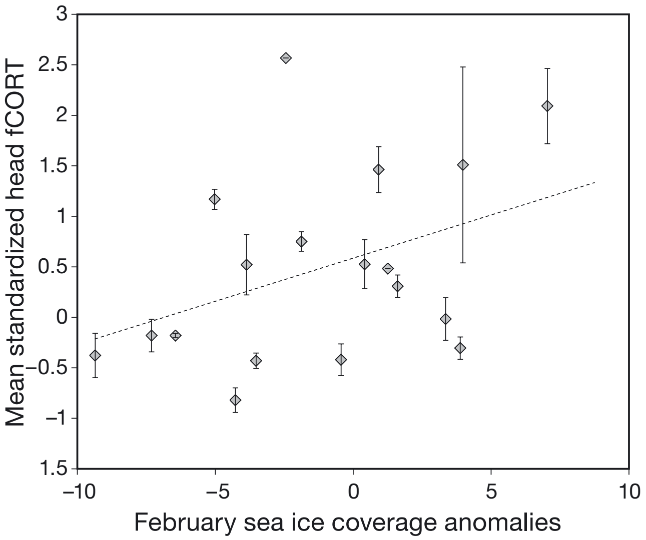

Fig. 3. Exposure of red-legged kittiwake to stress during the winter (as revealed by head fCORT concentrations) in response to February sea-ice coverage. The average of annual standardized head fCORT concentrations are shown ± SE, n = 18 yr; dashed line represents the slope of the linear regression ($r^2 = 0.19$, mixed effects model, with year as a random effect: $F_{1,13} = 4.36$, $p = 0.056$)

RESULTS

Temporal dynamics of late winter stable isotopes and nutritional stress as reflected in head feathers

Sea-ice coverage was positively correlated with fCORT concentrations (Table 1, Fig. 3). At the century scale, fCORT concentrations have generally declined over time and were lower in years when the PDO was positive (Table 1).

In general, Year best predicted changes in wintertime $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ over the past century (Table 1). $\delta^{13}C$ values declined over time (Suess effect); however, $\delta^{34}S$ values increased over time and increased in years with positive PDO values (Table 1). The AO appeared most frequently in the 95% model subset for $\delta^{15}N$ values and $\delta^{15}N$ values decreased during positive phases of the AO (Table 1). In the past 40 yr, $\delta^{15}N$ values have generally increased; however, over the longer time period covered by all of the data, $\delta^{15}N$ values have decreased (Table 1).

Temporal dynamics of breeding season stable isotopes and nutritional stress as reflected in primary feathers

During the breeding season, fCORT concentrations decreased when the ALow and PDO were positive. $\delta^{13}C$ values decreased during positive phases of the

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Table 2. Primary feather AIC model selection results. Averaged models for fCORT, δ^{13}C, δ^{14}N, and δ^{34}S are described for the full dataset ('All data', upper row) and the 40 yr dataset ('40 yr', lower row). The number of models in the 95% model subset is noted in the first column and also given are the summed model weights, Σw_i, where w_i is the probability of model *i* being the best model in the subset and w_i is summed for each model containing the explanatory variables (ALow [Aleutian Low]; PDO [Pacific Decadal Oscillation]; Year; IceApr [April sea-ice coverage]; AO [Arctic Oscillation]). For the full set of candidate models refer to the Supplement

Models in subset	Averaged model primary feathers	Σw_i				
	Variable = $\beta_{\text{intercept}} + \beta_{\text{ALow}} + \beta_{\text{PDO}} + \beta_{\text{Year}} + \beta_{\text{IceApr}} + \beta_{\text{AO}}$	ALow	PDO	Year	IceApr	AO
fCORT						
2	$\text{fCORT}_{\text{All data}} = 2.79 - 0.127\ (\text{ALow}) - 0.16\ (\text{PDO}) - 6.9\text{E}{-}05\ (\text{Year})$	0.98	0.98	0.25	–	–
12	$\text{fCORT}_{40\ \text{yr}} = 0.96 - 0.116\ (\text{ALow}) - 0.151\ (\text{PDO}) - 0.001\ (\text{Year}) - 0.003\ (\text{IceApr}) - 0.005\ (\text{AO})$	0.85	0.96	0.33	0.27	0.35
δ^{13}C						
2	$\delta^{13}\text{C}_{\text{All data}} = -13.72 - 0.037\ (\text{ALow}) - 0.055\ (\text{PDO}) - 0.013\ (\text{Year})$	0.62	1	0.45	–	–
22	$\delta^{13}\text{C}_{40\ \text{yr}} = -16.95 - 0.03\ (\text{ALow}) - 0.041\ (\text{PDO}) - 0.008\ (\text{Year}) - 0.001\ (\text{IceApr}) + 0.002\ (\text{AO})$	0.39	0.49	0.75	0.28	0.24
δ^{15}N						
4	$\delta^{15}\text{N}_{\text{All data}} = -15.04 - 0.02\ (\text{ALow}) + 0.021\ (\text{PDO}) - 0.01\ (\text{Year})$	0.3	0.31	0.99	–	–
20	$\delta^{15}\text{N}_{40\ \text{yr}} = -14.77 - 0.05\ (\text{ALow}) - 0.008\ (\text{PDO}) - 0.02\ (\text{Year}) - 0.03\ (\text{IceApr}) + 0.02\ (\text{AO})$	0.42	0.27	0.88	0.8	0.29
δ^{34}S						
6	$\delta^{34}\text{S}_{\text{All data}} = 18.66 + 0.108\ (\text{ALow}) + 0.283\ (\text{PDO}) - 0.003\ (\text{Year})$	0.37	0.56	0.37	–	–
17	$\delta^{34}\text{S}_{40\ \text{yr}} = 18.5 + 0.57\ (\text{ALow}) + 0.66\ (\text{PDO}) - 0.018\ (\text{Year}) - 0.009\ (\text{IceApr}) - 0.031\ (\text{AO})$	0.8	0.87	0.53	0.17	0.26

PDO, whereas δ^{15}N and δ^{34}S values increased when the PDO was positive (Table 2).

In the past 40 yr, δ^{13}C and δ^{15}N decreased over time (Table 2). The PDO was most often included in the top models that described recent changes in δ^{34}S values (Table 2). During warm conditions (positive PDO), fCORT concentrations decreased (Fig. 4), and δ^{34}S values increased (Table 2). When April sea-ice coverage was low, δ^{15}N values increased (Table 2).

The relationship between δ^{15}N and the PDO reversed between the 2 model sets. In the past 40 yr, δ^{15}N values decreased during warm conditions (positive PDO) compared with having increased during warm conditions when all of the data were considered (Table 2).

Inter-seasonal relationships

Elevated stress levels in primary feathers (n = 69), grown during the breeding season, corresponded to elevated stress levels in head feathers, grown during the winter ($F_{1,67} = 17.26$, $p < 0.0001$, Fig. 5). δ^{13}C values were positively correlated between the breeding and wintering seasons ($F_{1,67} = 43.12$, $p < 0.0001$, Fig. 5). There was no correlation in δ^{15}N or δ^{34}S signatures between the breeding season and the following winter (δ^{15}N, $F_{1,67} = 1.675$, $p = 0.2$; δ^{34}S, $F_{1,62} = 0.3451$, $p = 0.56$). There was low consistency among the stable isotope signatures and nutritional stress of individuals (δ^{15}N, repeatability estimate $R = 0.122$; δ^{13}C, $R = 0.077$; δ^{34}S, $R = 0.019$; fCORT, $R = 0$) but high consistency within a given year (δ^{15}N, $R = 0.412$; δ^{13}C, $R = 0.686$; δ^{34}S, $R = 0.433$; fCORT, $R = 0.436$).

Seven of the museum specimens collected late in the breeding season had already grown new first primary feathers, enabling us to test whether head feather stress and stable isotope values were correlated between the winter period and the following summer period. Nutritional stress, δ^{15}N and δ^{13}C val-

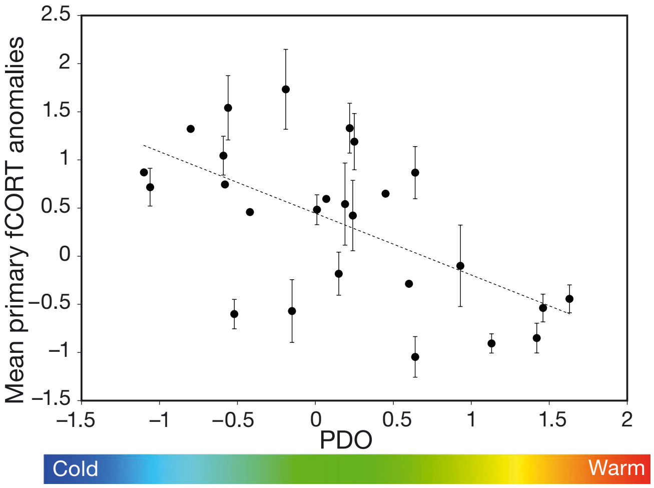

Fig. 4. Summer stress in red-legged kittiwakes (as reflected in primary fCORT concentrations) was inversely related to PDO. Annual primary fCORT standardized means ± SE, n = 27 yr; line represents the slope of the linear regression ($r^2 = 0.36$, mixed effects model with year as a random factor: $F_{1,23} = 12.08$, $p = 0.002$)

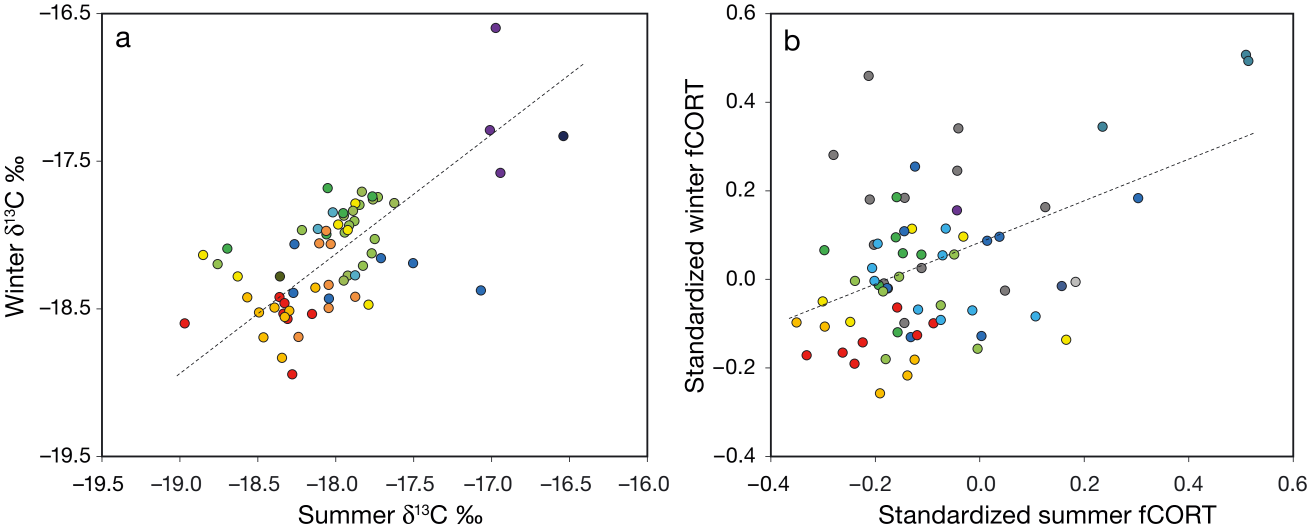

Fig. 5. Individual red-legged kittiwake summer and winter $\delta^{13}C$ values (a) and stress levels (b). $\delta^{13}C$ values and head and primary fCORT concentrations for feathers from 69 individuals from 15 different years between 1913 and 2016 (colored by year for illustrative purposes); dashed line represents the slope of the linear regression (fCORT: $r^2 = 0.20$, $F_{1,67} = 17.26$, $p < 0.0001$; $\delta^{13}C$: $r^2 = 0.41$, $F_{1,67} = 43.12$, $p < 0.0001$)

ues during the pre-nuptial molt did not correlate with nutritional stress, $\delta^{15}N$ and $\delta^{13}C$ values during the breeding season ($F_{1,6} < 0.733$, $p > 0.425$ for simple linear regressions on $\delta^{15}N$, $\delta^{13}C$, and fCORT, with values for head feathers as the predictor and values for primaries as the response). Head feather $\delta^{34}S$ values tended to be inversely correlated with $\delta^{34}S$ values in primary feathers ($F_{1,6} = 4.018$, $p = 0.092$).

Physiology and population trends

Head fCORT concentrations were higher (0.55 pg mm^{-1} ± 0.06) during the period of red-legged kittiwake population decline compared with the period of population increase (0.28 pg mm^{-1} ± 0.01; $t_{123} = 4.51$, $p < 0.0001$). $\delta^{13}C$ values in head feathers from 1976 to 1989 (mean ± SE: −17.80‰ ± 0.09) were higher than those from 1990 to 2014 (−18.23‰ ± 0.03; $t_{123} = 4.62$, $p < 0.0001$), while $\delta^{34}S$ values were lower (18.44‰ ± 0.68) in the period 1976–1989 compared with 1990–2014 (19.95‰ ± 0.11; $t_{113} = -2.19$, $p = 0.018$). There was a tendency for $\delta^{15}N$ to be higher after 1989 (15.30‰ ± 0.21 compared with 15.62‰ ± 0.05; $t_{123} = -1.53$, $p = 0.08$).

DISCUSSION

In long-lived species, such as red-legged kittiwakes, examining the response of individuals to environmental variability may reveal more clearly how changes in climate influences the habitat use and nutritional status of a species. Connections can then be made from the individual to parameters that affect individual fitness and population processes (Satterthwaite et al. 2012), such as adult quality, survival, and breeding attempts. We found that red-legged kittiwakes experienced food shortages during cold winters when sea ice-coverage was high and that both stress and stable isotope data indicate that the changes red-legged kittiwakes have experienced in previous decades were gradual and associated with changes in ocean temperature (the PDO). We also present preliminary evidence that these responses may correspond to the population trajectory of red-legged kittiwakes.

During the breeding season, red-legged kittiwakes rely on myctophids, primarily *Stenobrachius leucopserus* (Byrd & Williams 1993), the most abundant myctophid species in the Bering Sea (Beamish et al. 1999). Myctophids are mesopelagic fish that follow their prey in a diel vertical migration, rising to the upper water column at night (Beamish et al. 1999), where they become available to nocturnally foraging red-legged kittiwakes (Storer 1987). We found that, during positive phases of the PDO, red-legged kittiwake stable isotope signatures appear to consist of more oceanic prey species (lower $\delta^{13}C$, and increased $\delta^{34}S$). Concurrently, birds had lower levels of nutritional stress, as evidenced by low fCORT concentrations, suggesting that food may have been abundant during these periods. Specific mechanisms of how warm conditions might enhance myctophid abundance and/or availability, which would translate into low nutritional stress incurred by birds, are not known. One possibility is that the upper mixed layer is shallower in these years due to lighter winds (a weak ALow), and myctophids are easier to catch. Another possibility is that red-legged kittiwakes make use of the eddy field (Paredes et al. 2014, Yamamoto et al. 2016) located to the south of the Pribilof Islands (Napp et al. 2000). Eddy strength is positively correlated with the PDO (Panteleev et al. 2012). Further investigation into what drives myctophid abundance and makes them available to kittiwakes (especially during the day) is needed to clarify how warm conditions might reduce nutritional stress in breeding red-legged kittiwakes.

In contrast to the breeding period, it is unknown what red-legged kittiwakes eat during the winter. This makes it difficult to interpret the patterns we observed during the non-breeding period. Winters with high sea-ice coverage were associated with higher fCORT concentrations and higher δ^{15}N values. This suggests that birds were food limited and may have had to rely more heavily on endogenous reserves to meet their energy demands (Cherel et al. 2005). The mechanistic relationship between red-legged kittiwakes and winter sea ice, however, is unclear. Orben et al. (2015) suggested that the foraging of red-legged kittiwakes may be ice associated in a single-year study, but then found no consistent pattern of ice-habitat use in subsequent multi-year investigations (Orben et al. 2018). It is possible that red-legged kittiwakes may consume hyperid amphipods such as *Themisto* spp. (Byrd & Williams 1993) during the winter. Hyperids are predatory amphipods that are associated with the cold waters of the northern Bering Sea (Pinchuk et al. 2013) and have high δ^{15}N values relative to other zooplankton (Gorbatenko et al. 2014). However, fCORT concentrations suggest that too much ice may not be ideal; a signal that holds when head fCORT values, including those prior to 1979, were compared with reconstructed winter sea-ice coverage for the entire Arctic (Fig. S2 in the Supplement). Sea ice may directly interfere with the ability of red-legged kittiwakes to find enough food by acting as a physical barrier, or may dampen the strength of upwelling or eddy features. Alternatively, heavy sea ice in the Bering Sea may be a by-product of strong winds (Wang et al. 2009), which may increase flight (e.g. Amélineau et al. 2014) and/or thermoregulatory (Chappell et al. 1989) costs of overwintering red-legged kittiwakes. We found some evidence for a positive correlation between average continuous wind speed in February and head fCORT concentrations (Fig. S3 in the Supplement). This observation, however, warrants further investigation as the relationship depicted is parabolic and is based on a small sample size (n = 7 yr).

Environmental conditions during the breeding and non-breeding periods, when kittiwakes are in the eastern and western Bering Sea, respectively, appear to be correlated. The response of individuals within a year are similar between the 2 seasons; individuals with high primary (summer) fCORT concentrations had high head (winter) fCORT concentrations (Fig. 5). Circulating levels of corticosterone and the ability of birds to mount a response to prolonged stress change in response to both environmental stressors and the demands of different life stages (Sapolsky et al. 2000). The adrenocortical function in kittiwakes is responsive to environmental variability regardless of life stage and can change rapidly, responding to new stress within a matter of days and recovering from natural food shortages within several weeks (Shultz & Kitaysky 2008, Kitaysky et al. 2010). In red-legged kittiwakes, 7 mo separate the growth of the first primary feather and new head feathers. Thus, we suggest that the correlation of summer and winter stress is a reflection of environmental conditions that persist throughout the year rather than a carry-over effect. This is supported by high intra-annual consistency, and a positive correlation between δ^{13}C values in feathers (which have been shown to be unaffected by fasting, Hertz et al. 2015) grown during the breeding and wintering periods (Fig. 5), suggesting that primary production at the breeding and wintering locations is affected by similar processes within a given year.

Long-term changes in stable isotope values may reflect changes in primary production (e.g. δ^{13}C, Schell 2000) or food web structure (e.g. δ^{15}N, Grecian et al. 2016). While δ^{15}N values in both head and primary feathers decreased across our entire dataset, the decline was slight (~1‰). This is unlikely to indicate changes in trophic organization of the Bering Sea food web since ~3.4‰ generally separates a full trophic level (Minagawa & Wada 1984). More plausible explanations for this decline are long-term changes in baseline δ^{15}N ratios (Cabana & Rasmussen 1994) or a decline in prey quality over time (Oelbermann & Scheu 2002). A temporal decline in δ^{13}C values in head and primary feathers was much more apparent, but is mostly accounted for when corrected for the Seuss effect (Eide et al. 2017). Since correction factors for the Suess effect vary globally (Gruber et al. 1999), we also analyzed samples for δ^{34}S values to evaluate whether some of the decline in $\delta^{13}C$ may be attributed to a decline in the carrying capacity of the Bering Sea (Schell 2000, 2001). The temporal increase in $\delta^{34}S$ values in head feathers and the increase in $\delta^{34}S$ values in primary feathers with PDO suggest that changes in primary production have been relatively minor (~2‰, less than the 5‰ difference in experimental studies, Connolly et al. 2004). Fur seal *Callorhinus ursinus* teeth from St. Paul Island (60 km north of St. George Island) also show no evidence for major changes in primary production in the same region between 1948 and 2000 (Newsome et al. 2007). Thus, higher $\delta^{34}S$ values may alternatively be interpreted as increased consumption of prey that obtains more nutrients from deep ocean water (Peterson & Fry 1987).

We did find that the relationship between the food web and climate indices has changed. $\delta^{15}N$ values in primary feathers were negatively correlated with the PDO values when considering just the recent 40 yr dataset. However, over the entire dataset, the relationship is positive. The relationship between $\delta^{15}N$ values in head feathers and year also changed between the models for these 2 time periods. Schmidt et al. (2015) found that, starting in 2007–2008, Brandt's cormorants breeding in California broke with a previously established 40 yr pattern where El Niño and sea surface temperatures predicted survival and reproduction. It is possible that red-legged kittiwakes reflect recent (within the last 4 decades) changes in ecosystem responses to oceanographic conditions, which result in changes in the relationship between climate indices, stable isotope signatures, and nutritional stress. Our results suggest that this may have occurred in the past, and it may be expected to occur again in response to climate regime shifts.

Our study provides some support for the hypothesis that conditions during the winter may negatively affect red-legged kittiwakes. We provide evidence that, in the years covered by this study, colder conditions and higher sea-ice coverage during the winter may correspond to increased levels of stress incurred by birds. These conditions likely led to food shortages (Sorenson et al. 2017), a conclusion supported by a concurrent increase in $\delta^{15}N$. We acknowledge that it is possible that parasite (Raouf et al. 2006) or contaminant loads (Strong et al. 2015) may also contribute to higher stress during adverse winter conditions; however, little is known with respect to how these stressors might contribute to adult physiology and behavior during the non-breeding period. The mechanistic link between corticosterone and fitness has proven complex (e.g. Goutte et al. 2010, Madliger & Love 2016), but in black-legged kittiwakes *Rissa tridactyla*, higher nutritional stress incurred during reproduction has been shown to correlate with an increased probability of mortality (Satterthwaite et al. 2010). Elevated levels of nutritional stress and more on-shelf foraging in food webs with less benthic water inputs characterized red-legged kittiwake's overwinter experience during a period of population decrease (1976–1989). These findings are preliminary and are based on a very small sample size. However, for black-legged kittiwakes, time spent on the wintering grounds was correlated with the ability of individuals to recover from molecular damage that occurred during the breeding season (Schultner et al. 2014). This suggests that the overwinter period plays an important role in repair and maintenance at the cellular level. To substantiate this hypothesized link between red-legged kittiwake physiological status during winter molt and survival to the next life stage or skipping reproduction (as both affect adult annual return rates), the relationship between fCORT concentrations and red-legged kittiwake survival needs to be investigated on an individual basis (e.g. as done for black-legged kittiwakes, Satterthwaite et al. 2010). Furthermore, to understand the response of red-legged kittiwakes to future changes in the Bering Sea climate, we must improve our understanding of the migratory patterns of this species, their diets during the non-breeding season, and myctophid ecology to understand how changes in the region's environment affects food availability for this species.

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