



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

Alexis P. Will*, Evgenia V. Kitaiskaia, Alexander S. Kitaysky

Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

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 ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$). 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 $\delta^{15}\text{N}$ 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

*Corresponding author: awill4@alaska.edu

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).

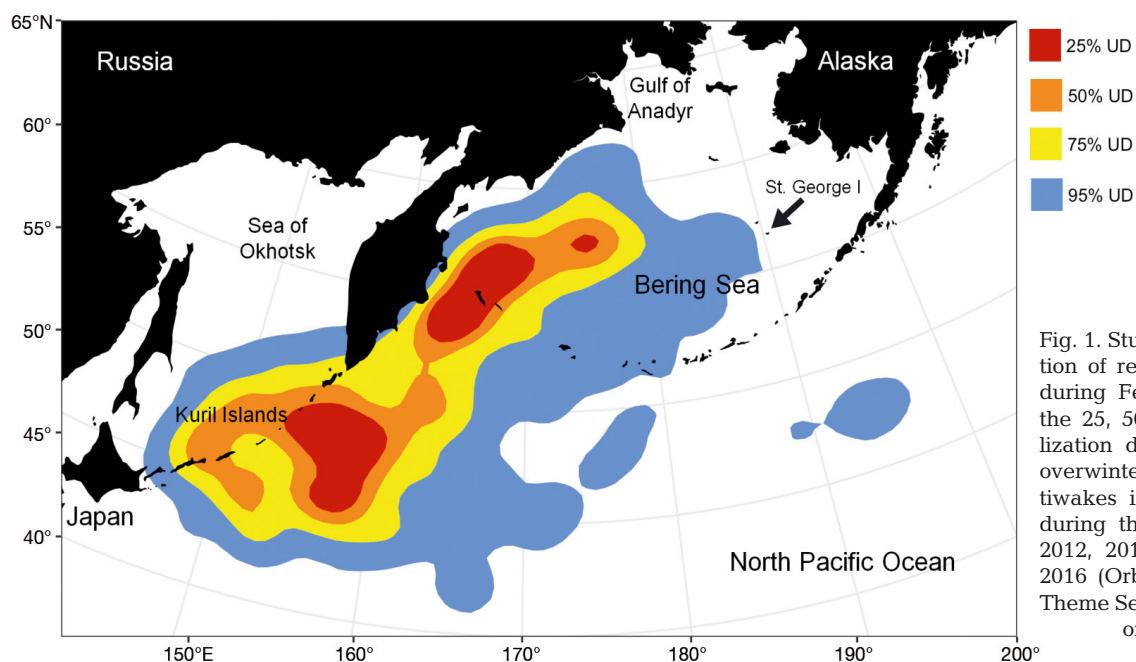


Fig. 1. Study site and distribution of red-legged kittiwakes during February. Shown are the 25, 50, 75, and 95% utilization distributions (UD) of overwintering red-legged kittiwakes in February tracked during the winters of 2011–2012, 2014–2015, and 2015–2016 (Orben et al. 2018, this Theme Section).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

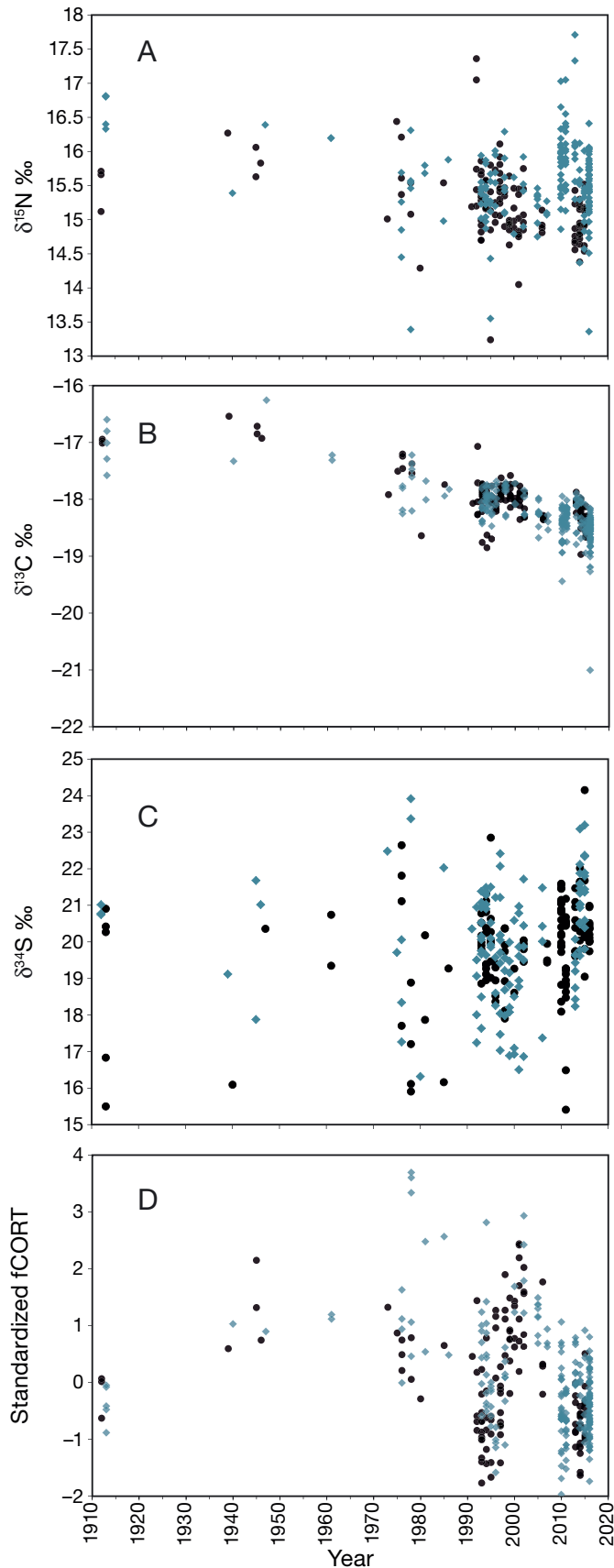
Feathers were analyzed in 5 radioimmunoassays (Wingfield & Farnier 1975). Intra-assay CV was <1% (range: 0.72 to 0.97%) and inter-assay CV was 1.2%. We standardized concentrations to sample mass (ng g^{-1}) and feather length (pg mm^{-1} , head feathers only).

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 $\pm 0.01\%$ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and on average intra-run standards were within $\pm 0.1\%$ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Head feathers from 2010 and 2011 were analyzed by Orben et al. (2015) at the University of California Santa Cruz (UCSC); UCSC internal standards ($\delta^{15}\text{N}$ mean = 5.38, SD = 0.09; $\delta^{13}\text{C}$ mean = -12.61, SD = 0.16; n = 16) were comparable ($\delta^{15}\text{N}$: $t_{26} = -0.72$, p = 0.48; $\delta^{13}\text{C}$: $t_{26} = 0.32$, p = 0.75) when run at ASIF ($\delta^{15}\text{N}$ mean = 5.39, SD = 0.07; $\delta^{13}\text{C}$ 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 $\pm 0.45\%$, S2 $\pm 0.72\%$, S3 $\pm 0.13\%$, S4 $\pm 1.07\%$, SO6 $\pm 0.71\%$, NBS 127 $\pm 0.21\%$) and 8 internal standards.



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

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

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 fig-

ures, 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, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, or $\delta^{34}\text{S}$ 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 $\bar{\beta} = \sum_{i=1}^n w_i \hat{\beta}_i$ where the model-averaged parameter estimate ($\bar{\beta}$) is the summation of the model weight (w_i) and estimated model coefficient ($\hat{\beta}_i$) 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

Table 1. Head feather AIC model selection results. Averaged models for fCORT, $\delta^{13}\text{C}$, $\delta^{14}\text{N}$, and $\delta^{34}\text{S}$ 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 = $\beta_{\text{intercept}} + \beta_{\text{PDO}} + \beta_{\text{Year}} + \beta_{\text{IceFeb}} + \beta_{\text{AO}}$	Σw_i			
		PDO	Year	IceFeb	AO
fCORT					
3	$\text{fCORT}_{\text{All data}} = 0.35 - 0.012 (\text{PDO}) - 0.001 (\text{Year})$	0.53	0.69	–	–
9	$\text{fCORT}_{40 \text{ yr}} = 0.278 - 0.005 (\text{PDO}) - 0.001 (\text{Year}) + 0.005 (\text{IceFeb}) + 0.012 (\text{AO})$	0.51	0.62	0.45	0.32
$\delta^{13}\text{C}$					
2	$\delta^{13}\text{C}_{\text{All data}} = -18.31 - 0.04 (\text{PDO}) - 0.016 (\text{Year})$	0.61	1	–	–
4	$\delta^{13}\text{C}_{40 \text{ yr}} = -17.98 - 0.049 (\text{PDO}) - 0.02 (\text{Year}) - 0.002 (\text{IceFeb}) + 0.007 (\text{AO})$	0.36	0.78	0.2	0.18
$\delta^{15}\text{N}$					
3	$\delta^{15}\text{N}_{\text{All data}} = 15.65 - 0.08 (\text{PDO}) - 0.006 (\text{Year})$	0.59	0.88	–	–
7	$\delta^{15}\text{N}_{40 \text{ yr}} = 14.93 - 0.05 (\text{PDO}) + 0.002 (\text{Year}) + 0.002 (\text{IceFeb}) - 0.13 (\text{AO})$	0.56	0.23	0.16	0.9
$\delta^{34}\text{S}$					
2	$\delta^{34}\text{S}_{\text{All data}} = 18.94 + 0.018 (\text{PDO}) + 0.019 (\text{Year})$	0.25	0.95	–	–
5	$\delta^{34}\text{S}_{40 \text{ yr}} = 19.47 + 0.17 (\text{PDO}) + 0.045 (\text{Year}) + 0.011 (\text{IceFeb}) + 0.006 (\text{AO})$	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.

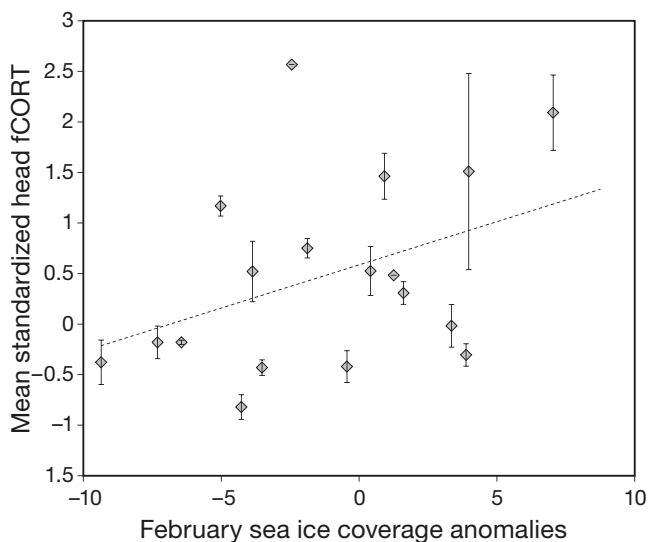


Fig. 3. Exposure of red-legged kittiwake to stress during the winter (as revealed by head fCORT concentrations) in response to February sea-ice coverage. The average of annual standardized head fCORT concentrations are shown \pm SE, $n = 18$ yr; dashed line represents the slope of the linear regression ($r^2 = 0.19$, 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 winter-time $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{34}\text{S}$ over the past century (Table 1). $\delta^{13}\text{C}$ values declined over time (Suess effect); however, $\delta^{34}\text{S}$ 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 $\delta^{15}\text{N}$ values and $\delta^{15}\text{N}$ values decreased during positive phases of the AO (Table 1). In the past 40 yr, $\delta^{15}\text{N}$ values have generally increased; however, over the longer time period covered by all of the data, $\delta^{15}\text{N}$ 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. $\delta^{13}\text{C}$ values decreased during positive phases of the

Table 2. Primary feather AIC model selection results. Averaged models for fCORT, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ 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 Variable = $\beta_{\text{intercept}} + \beta_{\text{ALow}} + \beta_{\text{PDO}} + \beta_{\text{Year}} + \beta_{\text{IceApr}} + \beta_{\text{AO}}$	Σw_i				
		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
$\delta^{13}\text{C}$						
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
$\delta^{15}\text{N}$						
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
$\delta^{34}\text{S}$						
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 $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values increased when the PDO was positive (Table 2).

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

The relationship between $\delta^{15}\text{N}$ and the PDO reversed between the 2 model sets. In the past 40 yr, $\delta^{15}\text{N}$ 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). $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ or $\delta^{34}\text{S}$ signatures between the breeding season and the following winter ($\delta^{15}\text{N}$, $F_{1,67} = 1.675$, $p = 0.2$; $\delta^{34}\text{S}$, $F_{1,62} = 0.3451$, $p = 0.56$). There was low consistency among the stable isotope signatures and nutritional stress of individuals ($\delta^{15}\text{N}$, repeatability estimate $R = 0.122$;

$\delta^{13}\text{C}$, $R = 0.077$; $\delta^{34}\text{S}$, $R = 0.019$; fCORT, $R = 0$) but high consistency within a given year ($\delta^{15}\text{N}$, $R = 0.412$; $\delta^{13}\text{C}$, $R = 0.686$; $\delta^{34}\text{S}$, $R = 0.433$; 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, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ val-

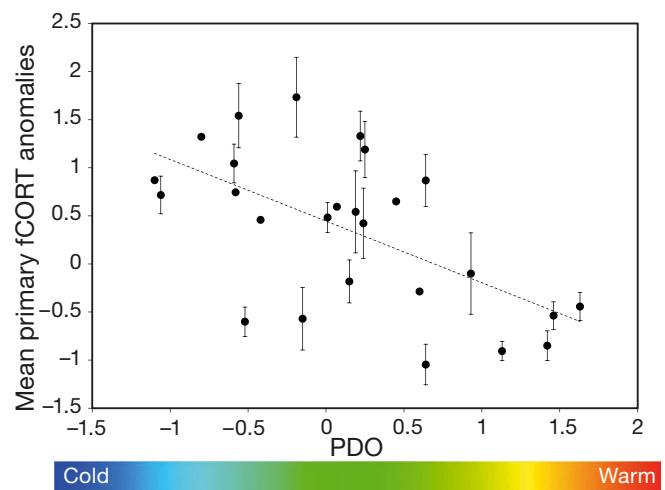


Fig. 4. Summer stress in red-legged kittiwakes (as reflected in primary fCORT concentrations) was inversely related to PDO. Annual primary fCORT standardized means \pm SE, $n = 27$ yr; line represents the slope of the linear regression ($r^2 = 0.36$, mixed effects model with year as a random factor: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

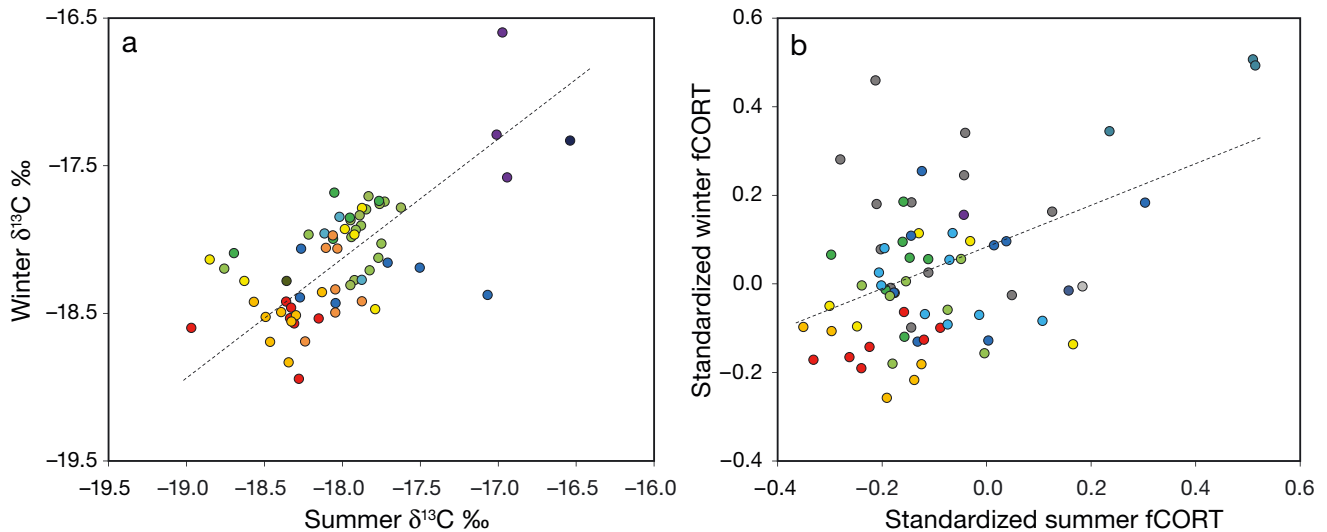


Fig. 5. Individual red-legged kittiwake summer and winter $\delta^{13}\text{C}$ values (a) and stress levels (b). $\delta^{13}\text{C}$ values and head and primary fCORT concentrations for feathers from 69 individuals from 15 different years between 1913 and 2016 (colored by year for illustrative purposes);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

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

Physiology and population trends

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

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 $\delta^{13}\text{C}$, and increased $\delta^{34}\text{S}$). 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 abun-

dance 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 $\delta^{15}\text{N}$ 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 hyperiid 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 $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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. $\delta^{13}\text{C}$, Schell 2000) or food web structure (e.g. $\delta^{15}\text{N}$, Grecian et al. 2016). While $\delta^{15}\text{N}$ values in both head and primary feathers decreased across our entire dataset, the decline was slight ($\sim 1\%$). This is unlikely to indicate changes in trophic organization of the Bering Sea food web since $\sim 3.4\%$ generally separates a full trophic level (Minagawa & Wada 1984). More plausible explanations for this decline are long-term changes in baseline $\delta^{15}\text{N}$ ratios (Cabana & Rasmussen 1994) or a decline in prey quality over time (Oelbermann & Scheu 2002). A temporal decline in $\delta^{13}\text{C}$ values in head and primary feathers was much more apparent, but is mostly accounted for when corrected for the Suess effect (Eide et al. 2017). Since correction factors for the Suess effect vary globally (Gruber et al. 1999), we also analyzed samples for $\delta^{34}\text{S}$ values to evaluate whether some of the decline

in $\delta^{13}\text{C}$ may be attributed to a decline in the carrying capacity of the Bering Sea (Schell 2000, 2001). The temporal increase in $\delta^{34}\text{S}$ values in head feathers and the increase in $\delta^{34}\text{S}$ 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 $\delta^{34}\text{S}$ 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. $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$. 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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*Editorial responsibility: Kyle Elliott,
Sainte-Anne-de-Bellevue, Québec, Canada*

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