

Fine-Scale Temporal and Spatial Patterns of a High Arctic Marine Bird Community

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Abstract

Understanding the complex dynamics of environmental change in northern latitudes is particularly critical for arctic avian communities, which are integral components that maintain biological connections between the mid and northern latitudes. We report on studies done in 2010-2012 in northwest Greenland as part of a larger effort focused on understanding the population dynamics of high arctic marine bird communities. We use several data sources and analysis techniques, including diet data, stable isotopes, and Bayesian inference, to identify the potential relationships between ecological response of coastal marine birds and rapid environmental change such as increased freshwater runoff from glacier melt, inshore oceanographic change, and cascading trophic perturbations. Our preliminary results indicate that community-wide spatial and temporal dynamics of this high arctic marine bird

community are far greater during our study period than was evident in past decades. We also find that the magnitude of change is greater here in the high Arctic (e.g., 78°N) compared to low arctic coastal marine ecosystems (e.g., western Aleutian Islands, 53°N). In particular, we show that the ecological patterns observed within such widespread arctic species as Dovekie (*Alle alle*) and Black-legged Kittiwake (*Rissa tridactyla*) indicate diets are strongly perturbed from a decade earlier. Moreover, we find that the variance in environmental and ecological parameters is increasing over relatively small temporal and spatial scales. We hypothesize that these fine-scale changes are related to oceanographic and trophic-level responses to increased freshwater injection into coastal waters, in addition to larger-scale perturbations possibly related to a cascade of climate-related factors.

Introduction

It seems now indisputable that the Arctic is undergoing dramatic changes in climate, accompanied by a cascade of effects associated with warming temperatures and consequent environmental change (see Wassmann 2011 for an entry point into the literature). Coastal arctic ecosystems are particularly vulnerable given that they are at the interface of marine and terrestrial environments of the Arctic, and recent evidence suggests that change is accelerating in these regions compared to coastal systems outside of the Arctic (Carmack et al. 2006; McPhee et al. 2009; Wassmann 2006, 2011; Dunton et al. 2012). Coastal marine ecosystems are strongly influenced by fluxes of freshwater, nutrients, and organic matter from river inputs (Holmes et al. 2012), a factor particularly important in the Arctic. Overall, the Arctic Ocean receives about 10% of the global river discharge but only comprises about 1% of the global ocean volume. Consequently, arctic coastal ecosystems are strongly influenced by the terrestrial environment, which often imparts estuarine features at large and small scales (Aagaard and Carmack 1994; Serreze et al. 2003, 2006; McClelland et al. 2012).

Little is known about the effect of increased inputs of river and meltwater associated with arctic warming on adjacent coastal ecosystems, but it is clear that rapid changes are taking place in the fringing shelves of the Arctic Ocean (Carmack and Wassmann 2006, Wassmann 2011). Among the most complex of arctic shelves is the terrestrially dominated network outflow domain of the Canadian Arctic Archipelago and Nares Strait–North Water Polynya (Carmack and Wassmann 2006). Arctic Ocean surface waters flow southward through diverse channels and sounds, strongly mixed with freshwater flow from terrestrial sources like small rivers, glacial melt channels, and estuaries (Tremblay et al. 2006, McClelland et al. 2012). The juncture of northwest Greenland, Ellesmere Island (Canada), and the southern reaches of the

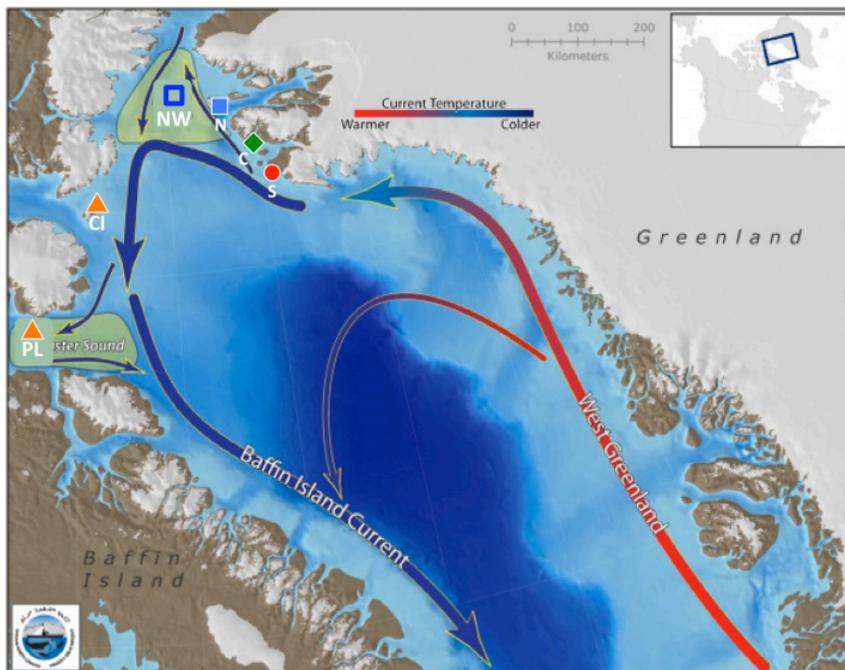


Figure 1. Northwest Greenland sampling localities. This study: N (blue square) = North. C (green diamond) = Central. S (red circle) = South). Previous studies: NW (open blue square) = North Water study. CI (orange triangle) = Cornwallis Island (Hobson 1993). PL (orange triangle) = Prince Leopold Island (Moody et al. 2012). Map courtesy of Oceans North Canada (<http://oceansnorth.org>). See text for details.

Nares Strait in Northern Baffin Bay bounds the region of the North Water Polynya (Fig. 1). Here, physical forcing facilitates mixing of surface waters from the Arctic Ocean and terrestrial sources, and result in a highly productive, spatially stochastic ecosystem. Primary productivity here is highest in the Arctic Ocean, and through stratification and other processes, biogenic production remains pelagic, with little contribution to the benthos (Carmack and Wassmann 2006).

Recent evidence indicates that warming temperatures are accelerating in the Greenland Arctic. In 2012, air temperature anomalies for midsummer in northwest Greenland were about +1.0°C (Fig. 2a), and for winter 2012-2013, about +2.0°C (Fig. 2b). In general, western Greenland (Baffin Bay) was warmer than eastern Greenland (Atlantic), and southern regions warmer than northern regions, but the patterns were not

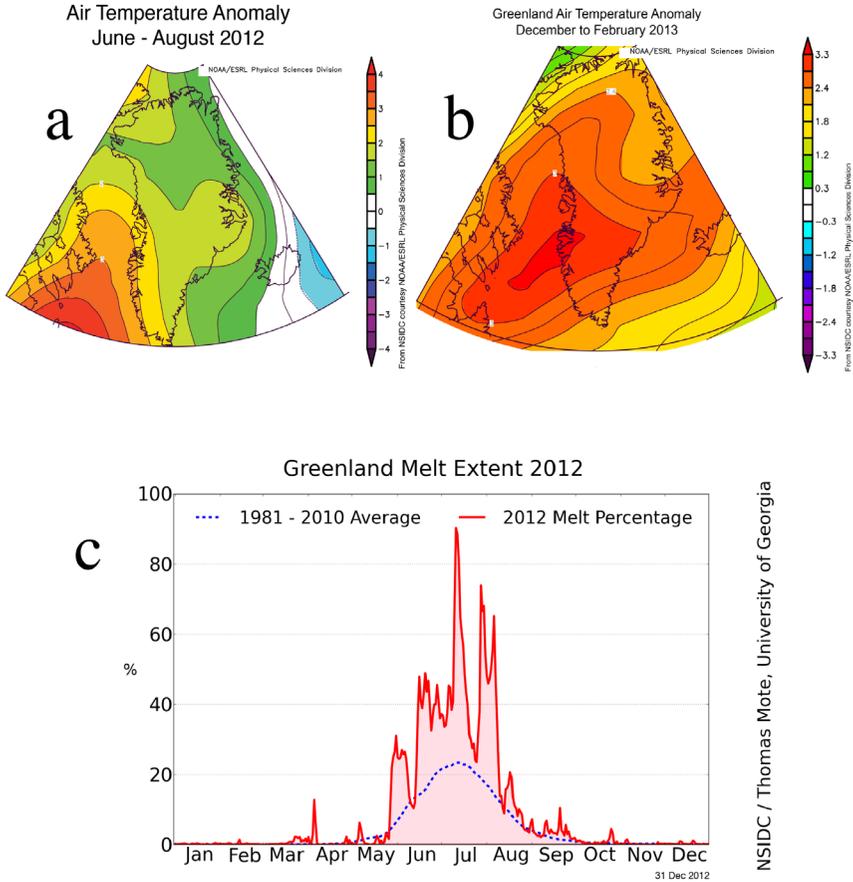


Figure 2. 2012 Greenland air temperature and ice melt anomalies. (a) Air temperature anomaly June–August 2012. (b) Air temperature anomaly, December 2012–February 2013. (c) Ice sheet melt anomaly, 2012 compared to 1981–2010 average. Images courtesy of NOAA ESRL National Snow and Ice Data Center (<http://nsidc.org/greenland-today/>). See text for references.

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uniform. Unsurprisingly, these warmer temperatures were associated with a much higher than normal extent of melting of the Greenland ice sheet (Fig. 2c). At peak, the extent of melting in July 2012 was about four times that expected from values averaged over three decades (Mote 2013). Melt patterns over 2012 were highly variable, with several distinct peaks distributed over at least six months.

Similar patterns were observed during the same time period on much smaller spatial scales. Daily discharge flows measured at the mouth of the Fox River, located near Thule in our study area, show that water outflow from glacier melt in summer increased from 2010 to 2012 (Fig. 3a). Average daily flows in 2012 more than doubled since monitoring began in 2011, and the variability in peak flows and timing increased during the same time period (Fig. 3b). Peak flow was greater in 2012, with most daily values far exceeding those obtained on the same day in previous years. Variability also appeared to be greater in 2012 than in 2010 or 2011 (Fig. 3b). The best fit of the daily discharge data (e.g., by second order nonlinear models) showed similar patterns for 2010 and 2011. Peak flow for these years was early in summer and decreased rapidly by the end of July, and model fit was robust and highly significant (2010: $r^2 = 0.499$, $P < 0.01$; 2011, $r^2 = 0.671$, $P < 0.001$). By contrast, the best fit of the data observed in 2013 was not significant, reflecting the highly variable nature of the observations (2012: $r^2 = 0.262$, $P > 0.05$) (J.M. Welker unpublished).

Marine food webs are strongly influenced by physical oceanographic factors as described above, and it is well known that primary and secondary productivity in arctic shelves are often controlled by these changes, with consequent cascading effects upward into upper trophic levels (Fredrickson et al. 2006, Tremblay et al. 2006, Wassmann 2006). In order to better understand arctic food web dynamics on fine temporal and spatial scales, we are utilizing the foraging ecology of breeding seabirds as an indicator of oceanographic conditions and local prey availability in coastal northwest Greenland. Here, we focus on two species: Black-legged Kittiwakes (*Rissa tridactyla*)—piscivorous and distributed in the pan-Arctic, and Dovekies (*Alle alle*)—planktivorous and found in Atlantic arctic waters. Seabirds serve well as indicators of food web dynamics because they are accessible during breeding season and their diets span many trophic levels (Abraham and Sydeman 2006, Arimitsu et al. 2012, Drew et al. 2013). Different prey species, especially plankton, are adapted to different oceanographic conditions (Scott et al. 2000, Beaugrand et al. 2002, Harding et al. 2008), and the strong link between distribution/abundance and hydrography can help inform us on the complexity of food web dynamics (Karnovsky et al. 2012). We will utilize changes in the proportion of stable isotopes of carbon $\delta^{13}\text{C}$ and nitrogen $\delta^{15}\text{N}$ as proxy indicators of diet (see Hobson 1993, Quillfeldt et al. 2005, for an entry into the literature). We are particularly interested in

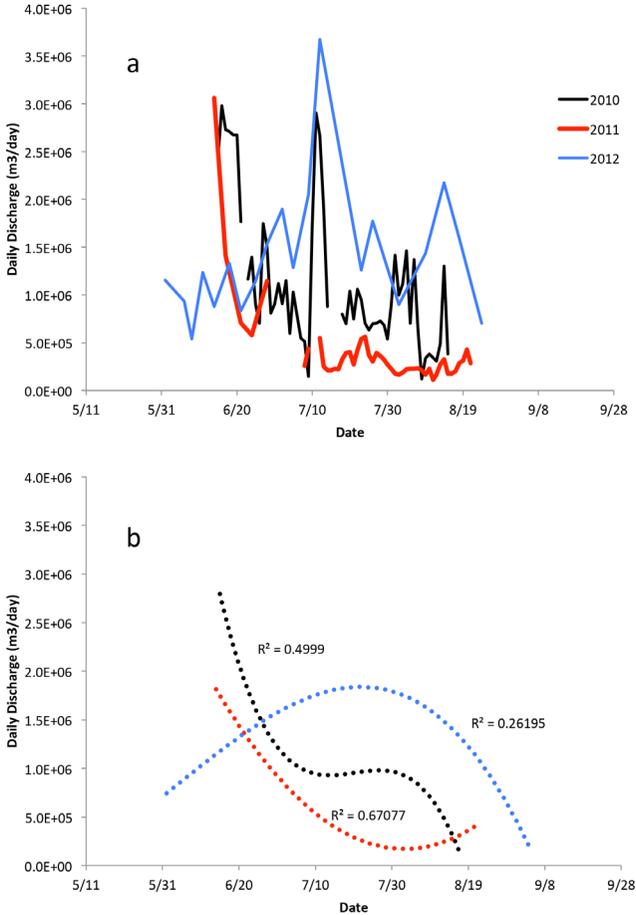


Figure 3. Daily discharge flow of Fox River (Thule, Greenland). (a) Data represent total flow (10^6 m³ per day) measured at river mouth. (b) Best fit models of data shown in (a). Data courtesy of J.M. Welker.

understanding how stochasticity and variability in climate through hydrography may affect food web stability and dynamics.

Methods

Collecting localities in northwest Greenland (N = north region, C = central region, S = south region) are shown in Fig. 1, along with localities associated with previous studies in the region (e.g., CI = Cornwallis Island, Canada [Hobson 1993]; NW = North Water Polynya [Hobson et

al. 2012]; PL = Prince Leopold Island, Canada [Moody 2012]. We report results primarily from the central region, which encompasses islands and coastal waters (75°N–76.5°N); and the north region (76.5°N–78°N) including closely adjacent Hakluyt and Northumberland Islands (77.4°N 72.7°W). Adults were captured on their nest during incubation and chick rearing (July–August) in 2010 and 2011. All birds continued incubation immediately after they were returned to the nest. Blood samples (25 μ L) were taken from the brachial vein from each adult, as were several upper wing covert and breast feathers, and the birds were released after banding. Blood samples were air dried, and all samples were transported at 10°C to the laboratory.

Stable isotope analysis was performed on blood and feather samples after lyophilization and cryogenic homogenization (CryoMill) under liquid nitrogen. Lipids were not removed from prey samples; instead a correction to raw δ isotope values was utilized based on previous results (D. Causey unpublished). Relative abundances of stable isotopes of carbon and nitrogen in blood and feathers were determined using continuous flow isotope ratio mass spectrometers (Delta Plus and Delta V Advantage, Thermo Finnigan, Waltham, MA). Results are presented in the usual δ notation relative to VPDB (belemnite) and atmospheric nitrogen for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively. We used analysis of variance (ANOVA) followed by post-hoc range tests (Tukey multiple comparison test for unequal sample sizes, Zar 1996; $P < 0.005$) to compare values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between sites and across times. Unless otherwise indicated, values reported are means \pm 1SE and statistical significance was assumed at $P < 0.05$.

Tissue fractionation of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in birds has been well studied, and times of integration differ among tissues, molt sequence, and species (see Hobson 2008 for review). Further, isotopic concentrations of various biochemical components of food fractionate differently among tissues (Hobson 1993, Bearhop 2004). We used average values of integration time and discrimination (fractionation) derived from experimental and observational studies (Caut et al. 2009, Hobson and Bond 2012) on Dovekies and Black-legged Kittiwakes. Thus, we considered that stable isotope values for red blood cells reflected incorporation over the preceding 2–3 weeks, and stable isotopes values obtained from wing coverts and breast feathers were incorporated previous to collection 4–6 weeks and 8–12 weeks respectively. We used stable isotope values from the literature to serve as proxy values for potential diet items and trophic position (Hobson et al. 2012, D. Causey unpublished), and these in turn were used to derive a mixing model of diet preferences.

We used SIBER 4.0 (Jackson et al. 2011) to quantify and compare isotopic niche widths of samples in a Bayesian framework, and SIAR 4.0 (Parnell et al. 2010; R development Core Team 2009) to estimate the

percent contribution of each potential food source to inferred diet from stable isotope analysis of blood and feathers. The stable isotope values associated with different tissues and different times can be used as an estimate for diet composition, changes in diet, and foraging ecology (Hobson 2008). For each data class of tissue, locality, and time a convex hull can indicate the isotopic limits of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Layman et al. 2012). The convex hull indicates the range of $\delta^{15}\text{N}$ values that estimate trophic depth and the range of $\delta^{13}\text{C}$ values that estimate the diversity of food resources, or feeding locality, or both. The total area of the convex hull has been used to indicate niche width (Layman et al. 2012), but we use here the standard ellipse of the data (Jackson et al. 2011). The standard ellipse is analogous to the SD of univariate data and is determined by the associated covariance Matrix M , defined by:

$$M = \begin{bmatrix} \delta_x^2 & \text{cov}(x, y) \\ \text{cov}(y, x) & \delta_y^2 \end{bmatrix} \quad (1)$$

which defines its shape and size, and the means of the x and y values that define its location. The eigenvalues (λ) and the eigenvectors (v) of M then give the lengths of the semi-major axis with $a = \lambda_1^{-1}$ and the semi-minor axis with $b = \lambda_2^{-1}$, with the angle of a with the x axis $\theta = \sin^{-1}(v_{12})$. Computation of the area of the resulting ellipse (SEA, standard ellipse area) is given by $SEA = \pi ab$; overlaps in area are tested for significance using Bayesian estimation. See Jackson et al. (2011) for greater detail and explanation.

Results

Black-legged Kittiwakes

Stable isotope values from whole blood and feathers collected from Black-legged Kittiwakes in the central region in 2010 are shown in Fig. 4. The convex hulls (Layman et al. 2012) shown by dotted lines indicate the isotopic limits of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each data class. The standard ellipses indicate that there is significant separation in stable isotope values between time periods, except between mid-breeding (C_M : 7/24/2010) and late-breeding (C_L : 8/1/2010) periods, and between values obtained from feathers (C_S : April 2010, C_W : February 2010). The position of the standard ellipses shows a strong pattern of depletion in $\delta^{13}\text{C}$ values through time, but $\delta^{15}\text{N}$ values do not appear to differ significantly. Differences in standard ellipse areas (SEA) indicate as well that data variance significantly increases in spring (e.g., C_S) and late breeding (C_L). Data from 2011 indicate similar patterns but $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are

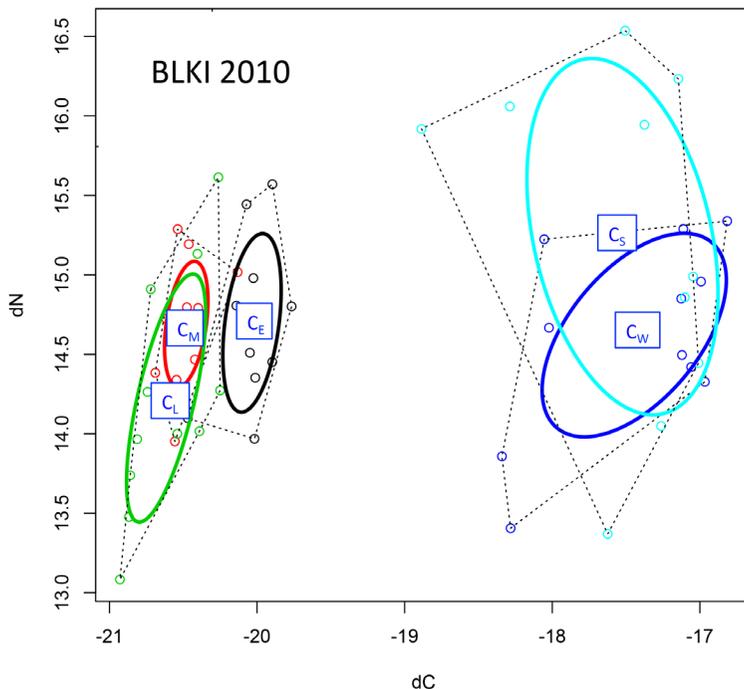


Figure 4. Stable isotope (δN , δC) values of Black-legged Kittiwake tissues in 2010. All data were obtained from tissue collected from birds in the central study area (see Fig. 1, text). C_W = central winter (dark blue), C_S = central spring (light blue), C_E = central early summer (black), C_M = central middle summer (red), C_L = central late summer (green). Open circles = paired δN and δC values; ellipses = Bayesian standard ellipses generated from data (Jackson et al. 2012); dotted lines = limits of convex hulls (Layman et al. 2012); squares = data centroids.

more depleted and with greater variance (not shown here). Centroid values for all data classes measured in 2010 and 2011 are shown in Fig. 5, along with approximate time periods for each transition. Centroid values obtained from blood samples (e.g., C_E , C_M , C_L) are more depleted in 2011 than in 2010, and the data from this 2011 show greater variance than from 2010 (MANOVA across years and data classes, $P < 0.05$). Stable isotope values from feathers collected in 2011 that will reflect incorporation in C_S and C_W time periods are in progress.

Stable isotope values from Black-legged Kittiwake blood samples in 2010 and 2011 (Fig. 6a and b, respectively) are plotted with values for

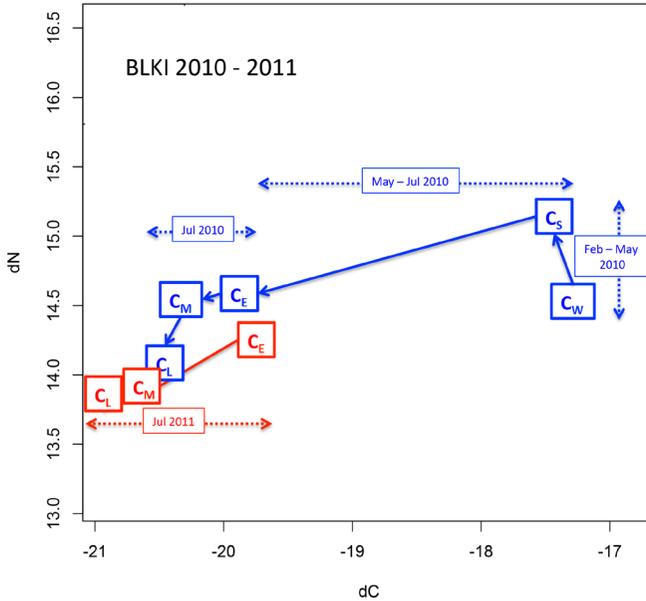


Figure 5. Comparative chronology of stable isotope (δN , δC) values of Black-legged Kittiwake tissues in 2010 and 2011. Blue = 2010, red = 2011. Abbreviations as in Fig. 4.

proxy diet items obtained from the literature (see Tremblay et al. 2006). Again, the values from the 2011 breeding season are more depleted and have greater variance for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and appear more close in range to prey items at lower trophic levels (e.g., herbivorous plankton, juvenile cod). These patterns are shown in greater detail by the use of Bayesian mixing models that predict the proportion of prey classes in diet (Fig. 7). The figure panels show the 50%, 75%, and 90% probability distributions for each category of potential diet items; an asterisk marks distributions that significantly differ (Bayesian posterior probability, $P < 0.05$) from other modeled organisms. For both years, in the early part of the breeding season (C_E), upper trophic level fish like adult arctic cod (e.g., *Boreogadus saida* “B_sai_ad”) likely predominated in kittiwake diets. Mid-breeding season (C_M), more freshwater-tolerant organisms like the predatory copepod *Euchaeta glacialis* (e.g., “E_gla”) were added to the diet; this pattern was more strongly pronounced in 2011 than in 2010. In late breeding season (C_L), freshwater-tolerant organisms predominated in both years. Moreover, Bayesian models predicted that the observed stable isotope values for kittiwake blood in 2011 was significantly

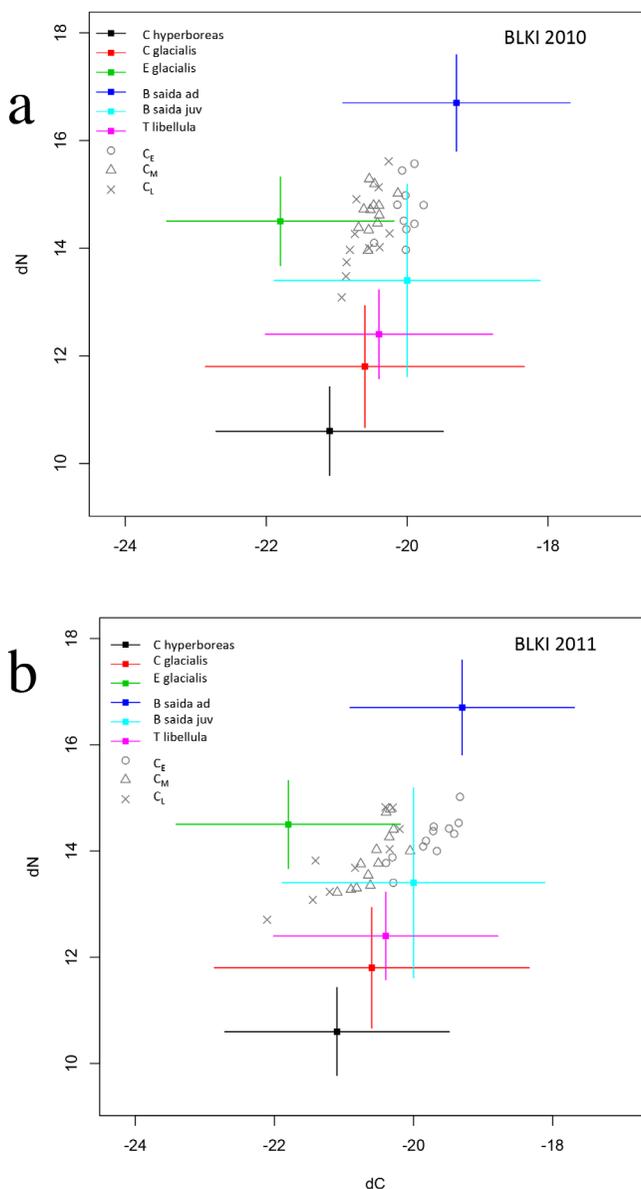


Figure 6. Stable isotope (δN , δC) values of Black-legged Kittiwakes and prey. Mean stable isotope values of reference prey are squares; horizontal and vertical lines are standard errors of the mean. C hyperboreas = *Calanus hyperboreas*, C glacialis = *C. glacialis*, E glacialis = *Eucalanus glacialis*, B saida = *Boreogadus saida*, T libellula = *Themisto libellula*; ad = adult, juv = juvenile; C_E = central early summer, C_M = central middle summer, C_L = central late summer.

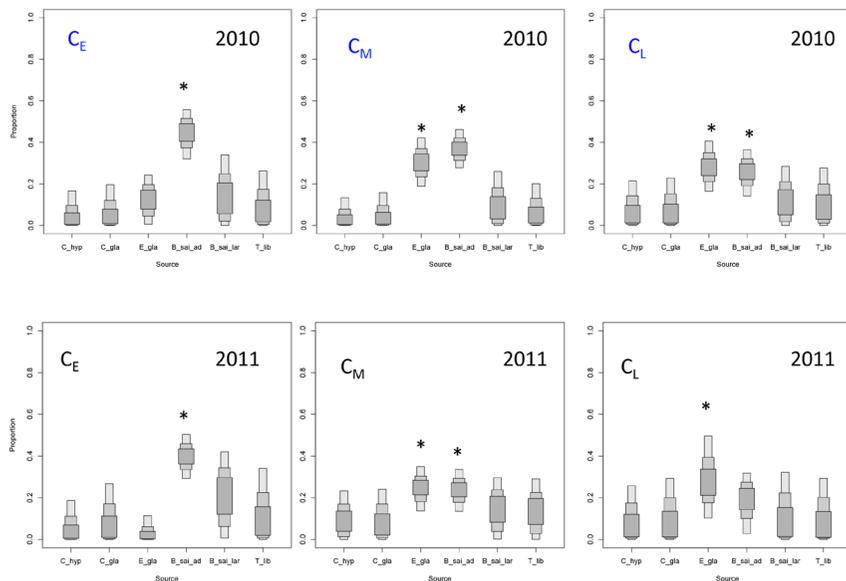


Figure 7. Bayesian mixing models of Black-legged Kittiwake diet. Plots represent predicted Bayesian proportions of prey items during sample periods. Shaded boxes are 50%, 75%, and 95% credible intervals from light to dark gray. Asterisk shows prey proportions that differ significantly ($P < 0.05$) from others in same sample period. C_{hyp} = *Calanus hyperboreas*, C_{gla} = *Calanus glacialis*, E_{gla} = *Eucalanus glacialis*, B_{sai_ad} = *Boreogadus saida* adult, B_{sai_juv} = *B. saida* juvenile, T_{lib} = *Themisto libellula*. C_E = central early summer, C_M = central middle summer, C_L = central late summer.

explained by a diet of primarily freshwater tolerant prey over typical upper trophic level marine fish.

Dovekies

Dovekies are exclusively planktivorous, and stable isotope values of whole blood collected during the same time periods in 2010 and 2011 showed similar patterns of $\delta^{13}\text{C}$ depletion over seasons, as seen in Black-legged Kittiwakes, but not years (results not shown). Also similar to kittiwakes, Dovekies showed no significant differences in $\delta^{15}\text{N}$ values over season, time, or collecting locality as measured by percentage overlap in area of standard ellipse (Fig. 8). Instead, in 2011, there appeared to be a fine-scale geographic gradient in $\delta^{13}\text{C}$ values from northernmost collecting localities (N₁₁: Northumberland Island; H₁₁:

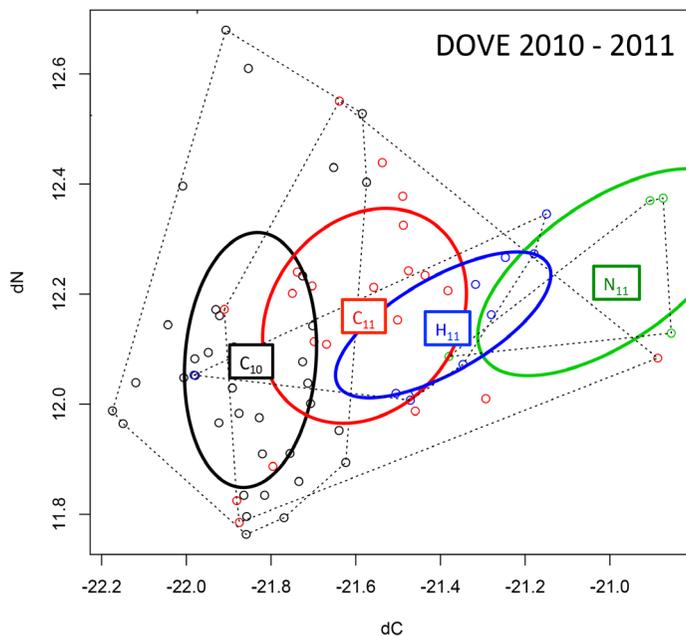


Figure 8. Stable isotope (δN , δC) values of Dovekie tissues in 2010 and 2011. C_{10} = central study region 2010 (black); C_{11} = central study region 2011 (red); H_{11} = Hakluyt Island 2011 (blue); N_{11} = Northumberland Island 2011 (green). Symbols and patterns as in Fig. 4.

Hakluyt Island) to regions to the south (C_{11} : Central), within a two-week period (7/22–8/3/2011). The range of $\delta^{13}\text{C}$ values observed in Dovekies during a 2011 over a 40 km distance was similar in magnitude to that observed in Black-legged Kittiwakes over their entire breeding period. Coincident biplot of $\delta^{13}\text{C}/\delta^{15}\text{N}$ values for Dovekies and potential food items (Fig. 9) indicated as expected that planktivory remained constant, but freshwater tolerant species (depleted in $\delta^{13}\text{C}$) were more likely constituents of the diet in the southern collecting region (e.g., compare C_{11} “triangle” with H_{11} “x”).

Discussion

Climate change is affecting the high Arctic, not only by increasing temperatures and consequent melt of snow and ice, but also by accelerating instability as measured by variance in environmental conditions. The nearshore coastal regions of northwest Greenland are strongly influenced by changes in terrestrial outflow from fluvial sources that

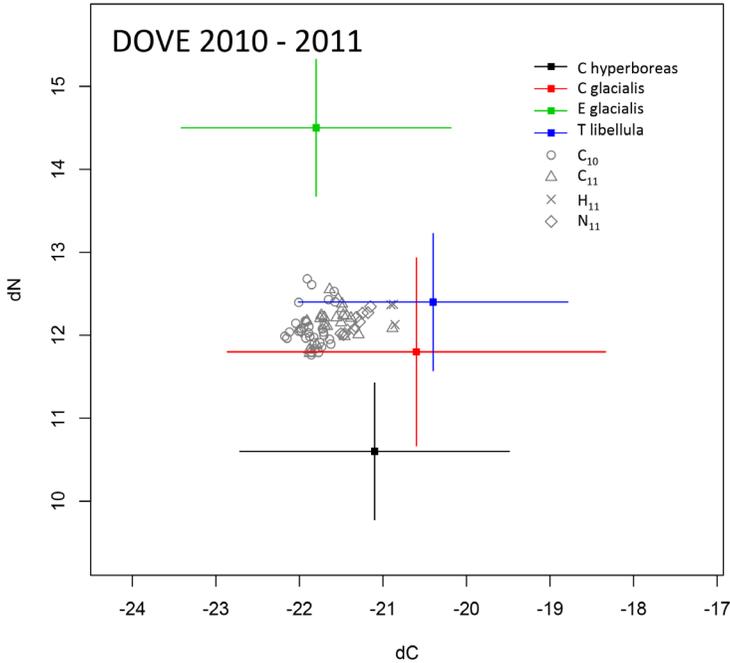


Figure 9. Stable isotope (δN , δC) values of Dovekie blood in 2010 and 2011. Mean stable isotope values of reference prey are squares; horizontal and vertical lines are standard errors of the mean. Abbreviations as in Figs. 6 and 8.

have the potential to inject increased nutrients and to lower salinity in marine ecosystems. While it is difficult to predict what effects these changes may have on fine-scale productivity, we can examine the effects on food web dynamics by focusing on foraging ecology and dietary changes in upper trophic level predators like seabirds. We focused here on two common, widely distributed species: Black-legged Kittiwakes (piscivore) and Dovekies (planktivore), and used stable isotope analysis of blood and feathers as an indicator of diet.

We found that stable isotope values for both species varied through seasons on fine-scale (weeks) and larger-scales (months), but the magnitude of change differed greatly between species. For example, while Dovekies did show gradient of values over a small geographic scale in $\delta^{13}C$ values, the change in $\delta^{15}N$ values was negligible. Furthermore, these changes were less than those found for Dovekies studied in Svalbard, at approximately the same latitudes but in a different region of the Arctic

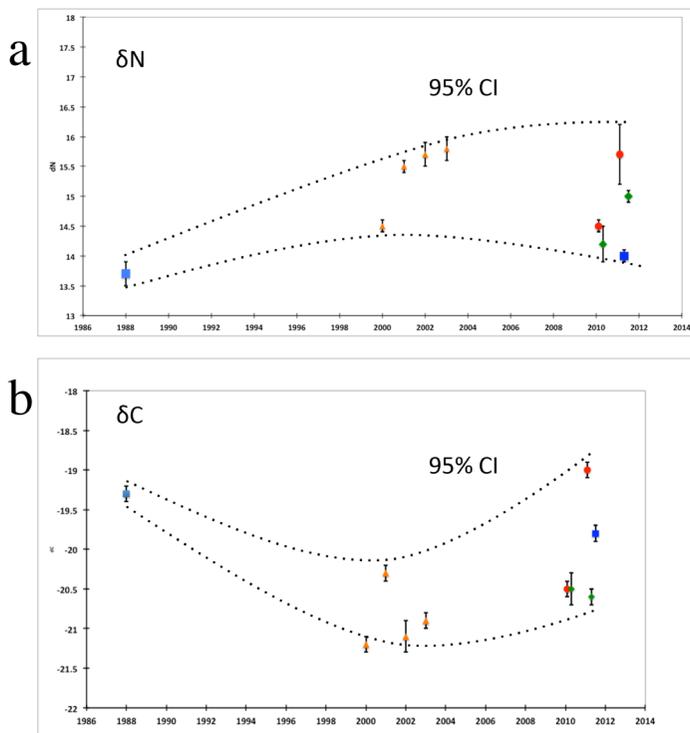


Figure 10. Chronology of stable isotope values of Black-legged Kittiwake tissues. Symbols and colors represent localities in Fig. 1; data from Hobson 1993 (blue square, 1988), Moody et al. 2012 (orange triangles, 2000-2003), and this study (2010-2011). Mean and standard errors are shown as symbols and vertical lines respectively. Dotted lines represent estimated 95% confidence intervals of data used in the analysis.

(Harding et al. 2008). The range of stable isotope values differed considerably between regions (e.g., Svalbard: $\delta^{13}\text{C}$ -23.0 to -19.0, $\delta^{15}\text{N}$ 10.0 to 11.0; this study, $\delta^{13}\text{C}$ -22.0 to -21.0, $\delta^{15}\text{N}$ 11.8 to 12.6) and suggests that the northwest Greenland plankton prey base is more depleted in carbon and enriched in nitrogen. These findings could be interpreted as being caused by longer connections between trophic levels and greater freshwater input in Greenland waters (e.g., Harding et al. 2008, Hobson and Bond 2012). Comparison of stable isotope values with reference planktonic prey items was not helpful, and Bayesian mixing models did not suggest that there was significant change in diet among diet

classes. Thus, there may be other factors at play that we are unable to determine at this point.

By contrast, the changes observed in Black-legged Kittiwakes were substantial and differed between fine and coarse time scales. Furthermore, variability in stable isotope values increased over years in both range of values and in variance. Furthermore, mixing models based on reference fish and plankton stable isotope values showed that Black-legged Kittiwakes apparently were shifting diets to more freshwater-tolerant food items. Compared to previous studies (reviewed in Hobson 1993, Hobson and Bond 2012), current values differ in magnitude and range for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 10). We attribute these patterns as indicative of instability in food webs, in selection of prey items, in stable isotopic composition of prey, or some combination of these factors.

Our study region, the coastal waters adjacent to the North Water Polynya, has been relatively unstudied compared to the rich record of work that exists for the pelagic environment to the east (see Tremblay et al. 2006). Conditions now are changing far faster than has been recorded earlier, and it is particularly important to understand the magnitude and dynamics of change in the high Arctic. We plan to continue study of the coastal marine ecosystem of northwest Greenland in coming years to better quantify the nature of change.

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