Final Project Report

PROJECT INFORMATION

Title	Climate Effects on Arctic Food Resources: Retrospective Analysis of Rate of Advancement of Invertebrate Phenology
Project ID	ALCC2011-08
Authors of report	Rebecca Shaftel Alaska Center for Conservation Science University of Alaska Anchorage rsshaftel@alaska.edu Daniel Rinella Anchorage Fish and Wildlife Conservation Office U.S. Fish and Wildlife Service daniel_rinella@fws.gov
Principal Investigators & Co-Principal Investigators	(Same as authors)
Project period	July 1, 2011 to April 30, 2017
Report submission date	April 30, 2017
Award number	CESU agreement #70181-7-K403 / USFWS F11AC00601
With support from	Arctic LCC and U.S. Fish and Wildlife Service
Key words	Arctic Shorebird Demographic Network, ASDN, invertebrate biomass, phenology, timing

Alaska Center for Conservation Science
University of Alaska Anchorage

Abstract

Temperatures are warming fastest at high latitudes and annual temperatures have increased by 2-3˚ C in the Arctic over the second half of the 20th century. Shorebirds respond to cues on their overwintering grounds to initiate long migrations to nesting sites throughout the Arctic. Climate-driven changes in snowmelt and temperature, which drive invertebrate emergence, may lead to a lack of synchrony between the timing of shorebird nesting and the availability of invertebrate prey essential for egg formation and subsequent chick survival. We modeled the biomass of invertebrates captured in modified Malaise traps as a function of accumulated temperature and weather variables for eight North American research camps in the Arctic Shorebird Demographic Network over the years 2010-2012. Models were based on data from the closest weather station and used to hindcast invertebrate biomass for the last ~60 years. From the hindcasted invertebrate data we calculated three measures of invertebrate phenology: the first day with invertebrate biomass above 10 mg; the number of days in May, June, and July with invertebrate biomass above 10 mg; and the date of peak invertebrate biomass. The 10-mg threshold was based on literature indicating it provided sufficient daily prey biomass to support normal shorebird chick growth. Additionally, a sensitivity analysis using 5, 15, and 20 mg showed that our results were robust to variation in this threshold. Each response was regressed against year to investigate changes over time. Changes in hindcasted invertebrate phenology were most conspicuous at the northernmost camps and were on the order of 1 to 3 days per decade. At Barrow, Ikpikpuk, and MacKenzie Delta, the timing of the first day with invertebrate biomass above 10 mg has advanced by 2 to 2.5 days per decade. At Barrow and Ikpikpuk, the number of days with invertebrate biomass above 10 mg has increased by 1.5 to 2 days per decade. The timing of peak invertebrate biomass has advanced at Ikpikpuk and Cape Krusenstern by 1 to 1.5 days per decade. Although our results suggest that seasonal prey availability for arctic shorebirds is advancing, the potential for trophic mismatch is most likely at the northernmost sites we evaluated, although it may be mitigated by similar advances in shorebird migration and nesting as reported from other Arctic sites.

Recommended Citation for this report:

Shaftel, R.S. and D.J. Rinella. 2017. Climate Effects on Arctic Food Resources: Retrospective Analysis of Rate of Advancement of Invertebrate Phenology. Arctic Landscape Conservation Cooperative Project ALCC2011-08 Final Technical Report, 22 pp.

Table of Contents

Abstract i
Introduction 1
Methods 2
Invertebrate sampling 2
Weather data 3
Statistical analysis 6
Results 8
Invertebrate biomass models 8
Comparison of local versus regional weather data for modeling invertebrate biomass 9
Sensitivity analysis of invertebrate biomass thresholds 10
Differences in invertebrate phenology between camps 12
Trends in invertebrate phenology 16
Discussion 18
Phenological Mismatch 18
Recommendations for Future Research 18
Management Applications 19
Products 20
References Cited 21

Tables

Table 1. Total number of invertebrate sample events for each year at each camp, by habitat type. 3

Table 2. Camp latitude and longitude and weather stations used to model invertebrate biomass for hindcasting. 4

Table 3. Weather variables used for hindcasting daily invertebrate biomass at each camp. 6

Table 4. Coefficient of determination (r^2) of observed versus fitted values for eight ASDN camps. 8

Table 5. Mean values and differences in phenology between six ASDN camps for 1992-2012. Significant differences are shown by letters ($p < 0.05$). 13

Table 6. Regression results for trends in invertebrate phenology. All regressions are based on models without wind and over longest time period available (1950 or later, see Table 2). Significant trends are bolded ($p < 0.05$)..... 17

Figures

Figure 1. Modified Malaise pitfall trap..... 2

Figure 2. Location of eight Arctic Shorebird Data Network camps and the closest weather stations. 5

Figure 3. Parameter estimates and 85% confidence intervals for six ASDN camps. Camps are ordered from east to west..... 10

Figure 4. Sensitivity of hindcasted first day with sufficient invertebrate biomass to support normal shorebird chick growth to four biomass thresholds. Significant trends are shown with solid lines ($p < 0.05$). 11

Figure 5. Sensitivity of hindcasted number of days with sufficient invertebrate biomass to support normal shorebird chick growth to four biomass thresholds. Significant trends are shown with solid lines ($p < 0.05$). 12

Figure 6. Timing of first day with hindcasted daily invertebrate biomass greater than 10 mg for six ASDN camps from 1950-2012. Significant trends are shown in blue ($p < 0.05$). 13

Figure 7. Annual number of days with hindcasted daily invertebrate biomass greater than 10 mg for six ASDN camps from 1950-2012. Significant trends are shown in blue ($p < 0.05$). 14

Figure 8. Timing of hindcasted peak daily biomass for six ASDN camps from 1950-2012. Significant trends are shown in blue ($p < 0.05$)..... 15

Appendix A. Final Confidence Sets used for Hindcasting Invertebrate Biomass at the Nome, Cape Krusenstern, Barrow, Ikpikpuk, Colville River, and MacKenzie Delta Camps.

Introduction

Temperatures are warming fastest at high latitudes and annual temperatures have increased by 2-3˚ C in the Arctic over the second half of the 20th century (ACIA 2004). Observed environmental changes resulting from increasing temperatures include earlier snowmelt and later freeze-up, decline in the water balance (precipitation – potential evapotranspiration), warmer lake and pond temperatures, increased shrubbiness, and thermokarsting (Hinzman et al. 2005). Animal responses to these alterations include changes in distribution, advancing phenology, and decreased fitness due to mismatches with food resources (Post et al. 2009).

The effects of climate change appear to be greatest for long-distance migrants that breed in seasonally productive habitats, like Arctic-nesting shorebirds (Both et al. 2009). Climate-driven changes in seasonality may lead to asynchrony between Arctic-nesting shorebirds and their invertebrate prey because the timing of shorebird arrival on the breeding grounds, which is constrained to match long-term average conditions, has not advanced along with warming trends (Meltofte et al. 2007, Grabowski et al. 2013). The breeding success of Arctic shorebirds is sensitive to any resulting mismatches with prey availability because most species rely on breeding-ground food resources for egg formation (i.e., they are income breeders; Morrison and Hobson 2004, Meltofte et al. 2007) and because the survival of chicks, which begin foraging on their own soon after hatching, is dependent upon adequate food during the short Arctic summer (McKinnon et al. 2012).

The phenology of invertebrates is largely driven by local weather conditions on the Arctic breeding grounds. Invertebrates become available upon seasonal emergence, the timing of which is determined by snowmelt and the attainment of temperature thresholds required for development (Danks and Oliver 1972, Høye and Forchhammer 2008a). The prey biomass available to Arctic-breeding birds varies across the breeding season according to the density and activity level of invertebrate prey species. Density is best described by variables representing seasonal development, such as date or accumulated temperature, while activity is best described by daily weather conditions (Tulp and Schekkerman 2008, Høye and Forchhammer 2008b, Bolduc et al. 2013). Temperature is the most important determinant of activity, although wind speeds, precipitation, humidity, and radiation can also play a role (Tulp and Schekkerman 2008, Bolduc et al. 2013).

We examined patterns of invertebrate availability at nine sites extending from western Alaska to eastern Canada for a previous report, Climate Effects on Arctic Food Resources: Predictive Models for Surface-Available Invertebrate Biomass (Shaftel and Rinella 2017). These nine sites are part of the Arctic Shorebird Demographic Network (ASDN) wherein biologists used standardized methods to collect invertebrate samples throughout the 2010-2012 summers (Brown et al. 2010). Our modeling results confirmed the importance of both accumulated and daily temperatures as predictors of invertebrate availability, while also showing that wind negatively affected invertebrate availability at the majority of camps. In order to assess changes in invertebrate phenology over the last half century, we constructed new models of invertebrate biomass using data from the nearest weather station. In this report, we

address two questions: 1) how do models based on data from weather stations differ from our original models based on local weather data? and 2) how has invertebrate phenology changed over the last 60 years?

Methods

Invertebrate sampling

Invertebrate samples were collected from modified Malaise pitfall traps (Figure 1) during the summers of 2010 – 2012 at nine camps in the ASDN (Figure 2). The modified Malaise traps capture both crawling and low-flying invertebrates. Capture rates reflect the abundance and activity of invertebrates and provide a good proxy of shorebird prey availability (Tulp and Schekkerman 2008). Invertebrate biomass from pitfall traps has been linked to growth of several species of shorebird chicks: red knot (*Calidris canutus*), dunlin (*Calidris alpina*) and little stint (*Calidris minuta*) (Schekkerman et al. 2003, Meltofte et al. 2007, Tulp and Schekkerman 2008). A comparative study found that invertebrate composition and abundances were similar between pitfall traps and the modified Malaise traps used in this study (Tulp et al. 1998). Each camp permanently established two line transects of five modified Malaise pitfall traps spaced 15 meters apart. One transect was placed in a mesic habitat (pond edges and low-centered polygons) and one transect was placed in a dry habitat (frost boil tundra or dry lowland sites). Samples were generally collected every three days, preserved in 95% isopropyl alcohol or 70 to 100% ethanol, and shipped to the processing laboratory at the end of the field season. At each camp, sampling began at the day of snow out (end May to mid-June) and finished at the completion of shorebird hatching (early- to late-July).

Figure 1. Modified Malaise pitfall trap.

All insect samples were processed at Aquatic Biology Associates, Inc. in Corvallis, Oregon and identified by Robert Wisseman and James DeGiulio. Field samples were transferred to 95% ethanol upon receipt in the lab. All organisms were identified to order or family using a dissecting scope at 12X magnification. Length of invertebrates was measured with a stage micrometer gridded at 1 mm intervals to nearest 0.25 mm for individuals <2 mm long and to nearest 0.5 mm for individuals >2 mm long. Published length weight regressions were used to calculate biomass.

A total of 597 invertebrate samples were collected across the nine camps, three years, and two habitats (Table 1). Six camps had three years of data, two camps had two years of data, and Prudhoe Bay had one year. Generally, the Barrow, Nome, and Colville camps collected data over the longest portion of the summer season (≥ 13 samples each year). We did not include Prudhoe Bay in our hindcasting analysis because it only had one year of data and modeling results from our first report indicated high uncertainty in parameter estimates.

Table 1. Total number of invertebrate sample events for each year at each camp, by habitat type.

Camp	Dry Habitat			Mesic Habitat		
	2010	2011	2012	2010	2011	2012
Barrow	16	18	19	14	19	17
Canning River Delta	9	11	12	9	11	11
Cape Krusenstern	0	11	14	0	11	12
Colville	0	16	18	0	14	15
East Bay	13	11	13	13	11	10
Ikpikpuk	11	13	12	11	13	12
Mackenzie River Delta	8	12	10	8	12	10
Nome	13	19	19	13	17	18
Prudhoe Bay	9	0	0	9	0	0

We calculated the mean biomass per trap for each taxon, habitat, and sampling event (the number of traps collected varied from two to five per sampling event, although five traps were collected on 97% of all sample dates). We further divided the mean biomass per trap by the number of days between sampling events (the number of days varied from one to 12, although 93% of samples were collected every three days). For the first sample collected each year, we divided by three days. We summed the taxa biomasses to calculate the total daily invertebrate biomass per trap used for statistical modeling.

Weather data

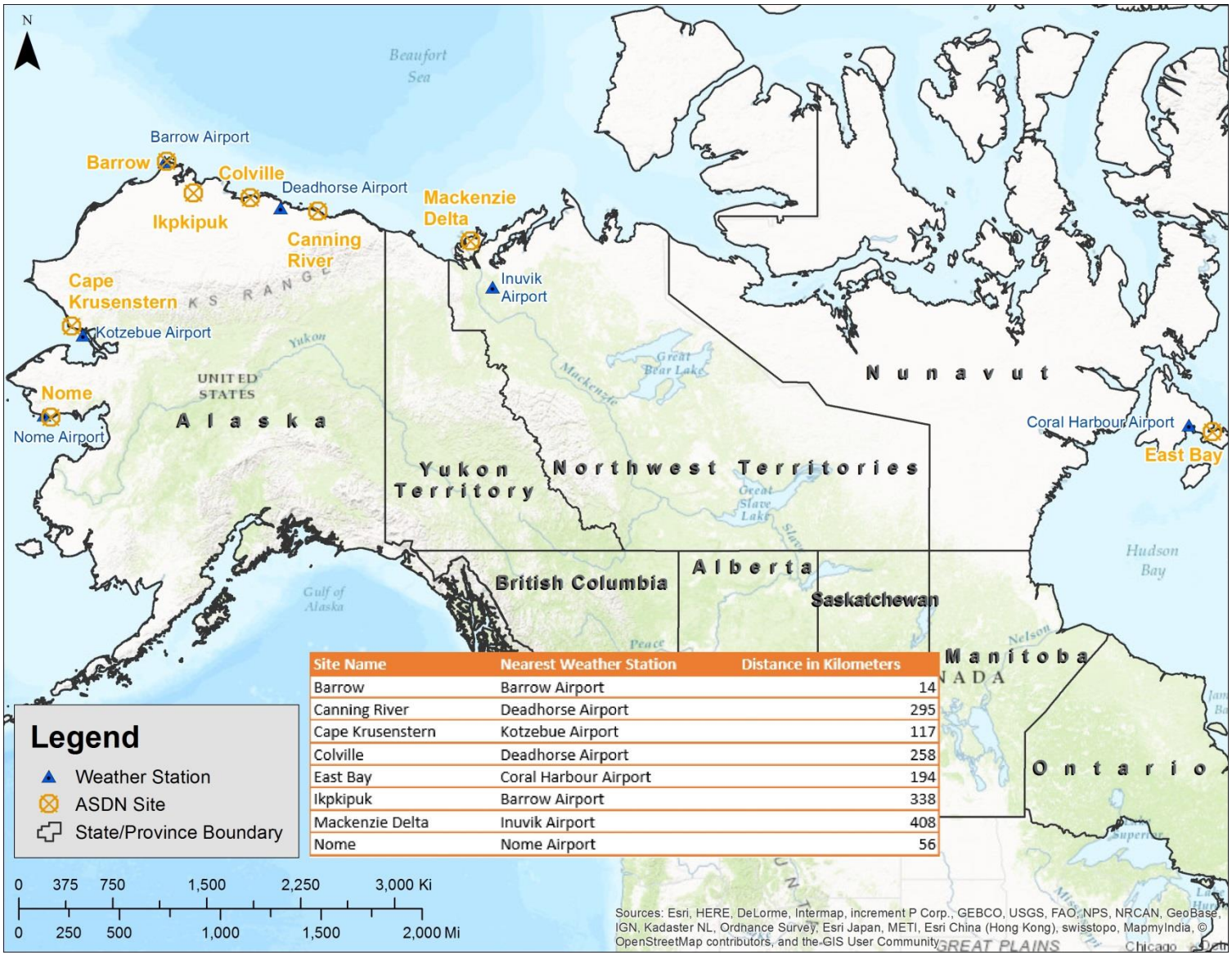
Weather data were downloaded from the closest weather station to each camp from Climate Data Online (https://www.ncdc.noaa.gov/cdo-web/, Figure 2). For each station, daily data for temperature, precipitation and wind speed were requested to 1950 or for the longest time period available. For Inuvik and Deadhorse, data from different weather stations were combined to generate the longest time series possible. The start and end dates and parameters available for each weather station are shown in Table 2. Wind data were not available at the Inuvik or Prudhoe Bay weather stations (1986-1999) so wind was not included in the models for the Mackenzie Delta, Canning River, or Colville River camps. Wind data were not collected prior to 1983 at *any* of the weather stations, which led us to construct models with and without wind to hindcast over two time periods (see Statistical Analysis). Precipitation was missing for >20 days for the May-June-July period in 1999-2001 at Deadhorse Airport/Prudhoe Bay, which led to missing predictions on some dates for those years.

We considered two alternative weather stations for the Colville River camp. The Colville Village weather station is very close to the camp, but data collection began in 1996, which we decided was too short a time series for hindcasting. A weather station in Kuparuk was missing data for the majority of June and July in 2011, which limited our ability to model the observed invertebrate data. Therefore, we used the Deadhorse Airport/Prudhoe Bay station to model data from the Colville River camp.

Table 2. Camp latitude and longitude and weather stations used to model invertebrate biomass for hindcasting.

Camp	Latitude	Longitude	Weather Station(s)	Start Year[1]	Weather Data
Barrow	71.30	-156.76	Barrow Airport	1950	Temperature, wind, precipitation
Canning	70.11	-145.85	Deadhorse Airport/Prudhoe Bay	1986	Temperature, precipitation
Colville	70.44	-150.68	Deadhorse Airport/Prudhoe Bay	1986	Temperature, precipitation
East Bay	63.99	-81.70	Coral Harbor Airport	1950	Temperature, precipitation
Ikpikpuk	70.55	-154.73	Barrow Airport	1950	Temperature, wind, precipitation
Krusenstern	67.11	-163.50	Kotzebue Airport	1950	Temperature, wind, precipitation
Mackenzie	69.37	-134.89	Inuvik Airport/Inuvik Climate Station	1957	Temperature, precipitation
Nome	64.44	-164.96	Nome Airport	1950	Temperature, wind, precipitation

[1] Wind data collection began in 1983 at all weather stations where it was collected. Data were requested to 1950, but some stations were initiated later than 1950.



Site Name	Nearest Weather Station	Distance in Kilometers
Barrow	Barrow Airport	14
Canning River	Deadhorse Airport	295
Cape Krusenstern	Kotzebue Airport	117
Colville	Deadhorse Airport	258
East Bay	Coral Harbour Airport	194
Ikpkipuk	Barrow Airport	338
Mackenzie Delta	Inuvik Airport	408
Nome	Nome Airport	56

Figure 2. Location of eight Arctic Shorebird Data Network camps and the closest weather stations.

Statistical analysis

We modeled daily invertebrate biomass per trap for each camp as a function of temperature, wind, precipitation, and cumulative degree days (CDD, Table 3). We modeled invertebrate biomass from the dry habitats only because the results from our original models indicated no differences in daily invertebrate biomass between the two habitats at seven of the nine camps (Shaftel and Rinella 2017) and samples from the two habitat types were often collected on different days and therefore could not be combined. Daily weather data were adjusted for the number of days between sample events by averaging temperature and wind and by summing precipitation. Cumulative degree days were calculated by summing the positive daily temperatures since the first day of the first week of above freezing temperatures up to and including the day sampled. We chose the first week (continuous 7-day period) of above freezing temperatures rather than the first day above zero because this data more closely matched the observed day of snow out collected at the camps during the 2010 to 2012 field seasons (n = 12, mean absolute deviation = 6.4 for first day of first week above zero and mean absolute deviation = 15 for first day above zero).

Table 3. Weather variables used for hindcasting daily invertebrate biomass at each camp.

Variable	Units	Notes
Temperature	˚C	Mean over days between sample events
Wind	m/s	Mean over days between sample events
Precipitation	mm	Sum over days between sample events
Cumulative degree days	˚C	Sum since 1st week of temperatures above zero

We used linear mixed effects models with a random intercept for year because each camp was sampled over two or three years. For cumulative degree-days, we included a quadratic term to allow for a non-linear relationship with biomass. We centered all of the continuous predictor variables by subtracting their mean because it made the intercept interpretable as the estimated biomass in the middle of the season (mean cumulative degree-days) during average weather conditions and it decreased the correlation between cumulative degree-days and its quadratic term. We tested for collinearity in the weather variables using pairwise plots and variance inflation factors (VIF). The predictor with the highest VIF was removed in a stepwise procedure until all predictors had VIF < 5.

A suite of all possible models was built using four to five predictors at each camp (wind data were not always available); squared cumulative degree-days was only included in models that also had the linear term. Models were compared using Akaike's Information Criterion (AIC). We used all subsets modeling to match the statistical framework we used to evaluate important weather predictors in our original analysis. We defined our confidence set as all models with

ΔAIC $\leq$ 4 and removed models with uninformative parameters (Arnold 2010). Parameter estimates were averaged over all models in the confidence set by substituting zero when a parameter was missing from a model (Anderson 2008, Grueber et al. 2011).

We calculated confidence intervals (85%) for each parameter to determine how effect sizes and uncertainty changed when using data from weather stations versus local data. We also used the observed versus predicted coefficient of determination, r^2, to assess and compare model performance (Piñeiro et al. 2008).

Model assumptions were evaluated using a global model with all predictors and included normality of the residuals, normality of the random effects, homogeneity of variances (normalized residuals plotted against fitted values and each predictor), a check for outliers using Cook's distance, and a check of temporal autocorrelation using the autocorrelation function. All analyses were conducted in R using the nlme and MuMIn libraries (Pinheiro et al. 2014, R Core Team 2014, Barton 2016).

We originally hindcasted daily invertebrate biomass to 1983 so that we could include the wind predictor in our models and because we expected to find significant changes in invertebrate phenology over the last 30 years. However, we found no significant trends in any of the invertebrate responses so we decided to evaluate changes over a longer time period. Using model-averaged parameter estimates, we hindcasted invertebrate biomass for the months of May, June and July to 1950. Historic weather data used for hindcasting were smoothed over three-day intervals to match the resolution of the predictors used to build the models by averaging daily temperature and wind and summing daily precipitation. A table of the final confidence sets used for hindcasting invertebrate biomass from 1950 to 2012 is provided in Appendix A.

We calculated three measures of invertebrate phenology: the first day with invertebrate biomass above 10 mg; the number of days in May, June, and July with daily invertebrate biomass above 10 mg; and the date of peak invertebrate biomass. We calculated our responses for years with greater than 90% of days over the May, June, and July time period. We found limited information linking invertebrate biomass from modified Malaise or similar traps to shorebird chick growth rates, although red knot chicks in Siberia grew normally on days where 10 mg or more of invertebrates were captured in pitfall traps (Schekkerman et al. 2003). In order to address this uncertainty, we conducted a sensitivity analysis using four thresholds (5, 10, 15, and 20 mg) of invertebrate biomass for two responses: the first day above a threshold and the number of days above a threshold. We selected the date of peak invertebrate biomass from a seven-day moving average of hindcasted biomass to ensure that our response represented a biologically meaningful time period of high invertebrate activity rather than a single isolated emergence event. Each response was regressed against year to investigate changes in invertebrate availability over time. We were also interested in differences in phenology between sites and

used a recent 20-year period (1992 to 2012) for this comparison. Differences were assessed using ANOVA followed by Tukey's Honest Significant Differences.

Results

Invertebrate biomass models

Daily temperature and CDD were correlated to varying degrees at all the camps as both predictors increased over the sampling season, which ended in July. For Cape Krusenstern, we removed daily temperature to avoid problems with collinearity; at the remaining camps, correlation was not strong enough to justify removal. By keeping CDD and its squared term, we could still test for a non-linear seasonal component of invertebrate biomass and evaluate changes in peak biomass over time.

Observed versus fitted coefficient of determinations ranged from 0.28 to 0.77 (Table 4). The airport weather data used to model invertebrate biomass at the Canning River and East Bay camps resulted in poor model performance (r^2 of 0.34 and 0.28, respectively). These camps are excluded from the remainder of our analysis.

Table 4. Coefficient of determination (r^2) of observed versus fitted values for eight ASDN camps.

Camp	r^2 (weather station data)	r^2 (local data)[1]
Nome	0.56	0.68
Cape Krusenstern	0.58	0.64
Barrow	0.77	0.79
Ikpikpuk	0.58	0.72
Colville River	0.73	0.85
Canning River	0.34	0.55
Mackenzie Delta	0.52	0.75
East Bay	0.28	0.62

[1]These are based on the models from our previous report, Climate Effects on Arctic Food Resources: Predictive Models for Surface-Available Invertebrate Biomass (Shaftel and Rinella 2017).

The inclusion of the squared term for CDD indicates that invertebrate biomass increased to a maximum and then decreased over the sampling season at four of the camps: Nome, Cape Krusenstern, Ikpikpuk, and Barrow (Figure 3). At Colville River and Mackenzie Delta, by contrast, invertebrate biomass increased linearly over the summer season. Daily temperature correlated with higher invertebrate biomass at all of the camps except for Cape Krusenstern,

where it was removed due to collinearity. Invertebrate biomass was negatively correlated with precipitation at Nome, Barrow, and Ikpikpuk and with wind at Cape Krusenstern, Barrow, and Ikpikpuk.

Comparison of local versus regional weather data for modeling invertebrate biomass

The models used for hindcasting in this report differ from the models in our first report in three ways: weather conditions recorded at regional weather stations are different from those experienced at the camps due to large distances between them, the regional weather stations did not record relative humidity or wind for the time period of interest, and we had to redefine our calculation of CDD because observed or remotely-sensed date-of-snowmelt datasets were not available. At two of the camps (East Bay and Canning River), the models constructed using data from distant weather stations resulted in poor fit and were subsequently dropped from the analysis. These same sites also had the worst model fit based on local weather data (Table 4). At four of the camps, the decreases in model fit, based on the coefficient of determination between observed versus fitted values, were small to moderate (-0.06 to -0.14): Cape Krusenstern, Nome, Colville, and Ikpikpuk. The MacKenzie Delta camp suffered a larger decrease in model fit when using regional weather data (-0.23). The change in model fit for the Barrow camp was negligible (-0.02) as the same data were used for both models; the difference reflects the removal of the relative humidity predictor and the change in the calculation of CDD.

The use of weather station data also resulted in simplified models at some of the camps. At Colville and MacKenzie Delta, the squared term for CDD was no longer included in the final model set. Both wind and precipitation were absent from the final model set for Colville. At the Nome camp, the effect of CDD on invertebrate biomass changed from a negative linear fit to a non-linear fit (resulting in an additional parameter) and there was no wind effect in the hindcasting model. At the Barrow camp, daily temperature was included in the hindcasting model, where it had not been in the original model. The exclusion of relative humidity in the hindcasting models may have increased the variation explained by temperature, as they are often inversely related. The model parameters at the Ikpikpuk and Cape Krusenstern camps did not change, although temperature was replaced with CDD at Cape Krusenstern to address collinearity.

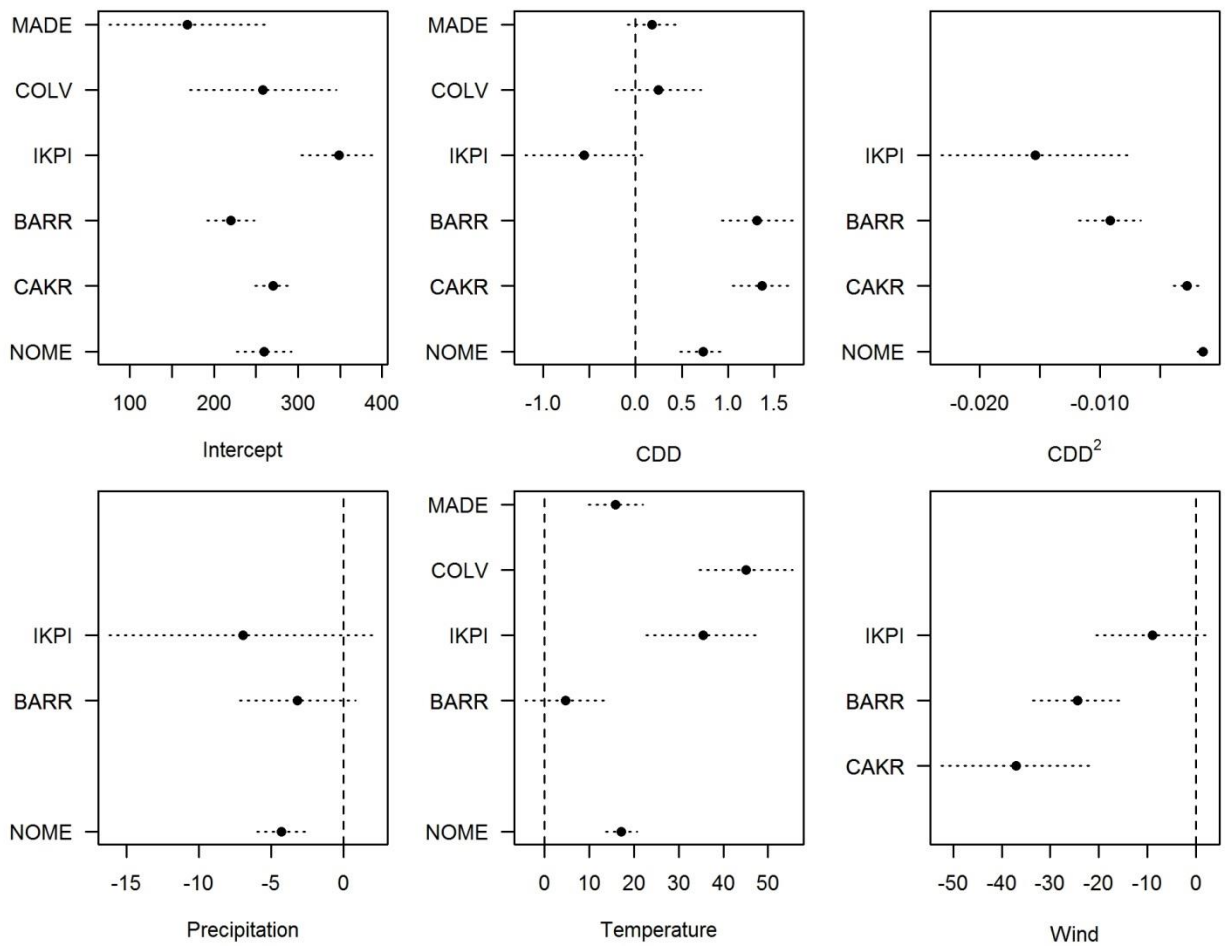


Figure 3. Parameter estimates and 85% confidence intervals for six ASDN camps. Camps are ordered from east to west.

Sensitivity analysis of invertebrate biomass thresholds

The hindcasted first day and number of days with sufficient invertebrate biomass for normal shorebird chick growth had limited sensitivity to variation in biomass thresholds. Significant trends in invertebrate phenology remained the same across camps for both responses and all thresholds, with one exception (Figure 4 and Figure 5). At MacKenzie Delta, there was no change in the timing of the first day above 20 mg, although the first days above 5, 10, and 15 mg occurred from 2 to 4 days earlier per decade. At both the MacKenzie Delta and the Barrow camps, there were several years when daily invertebrate biomass per trap never reached 20 mg (15 and 12 years, respectively), suggesting that this threshold may not be biologically meaningful, especially for the northernmost camps.

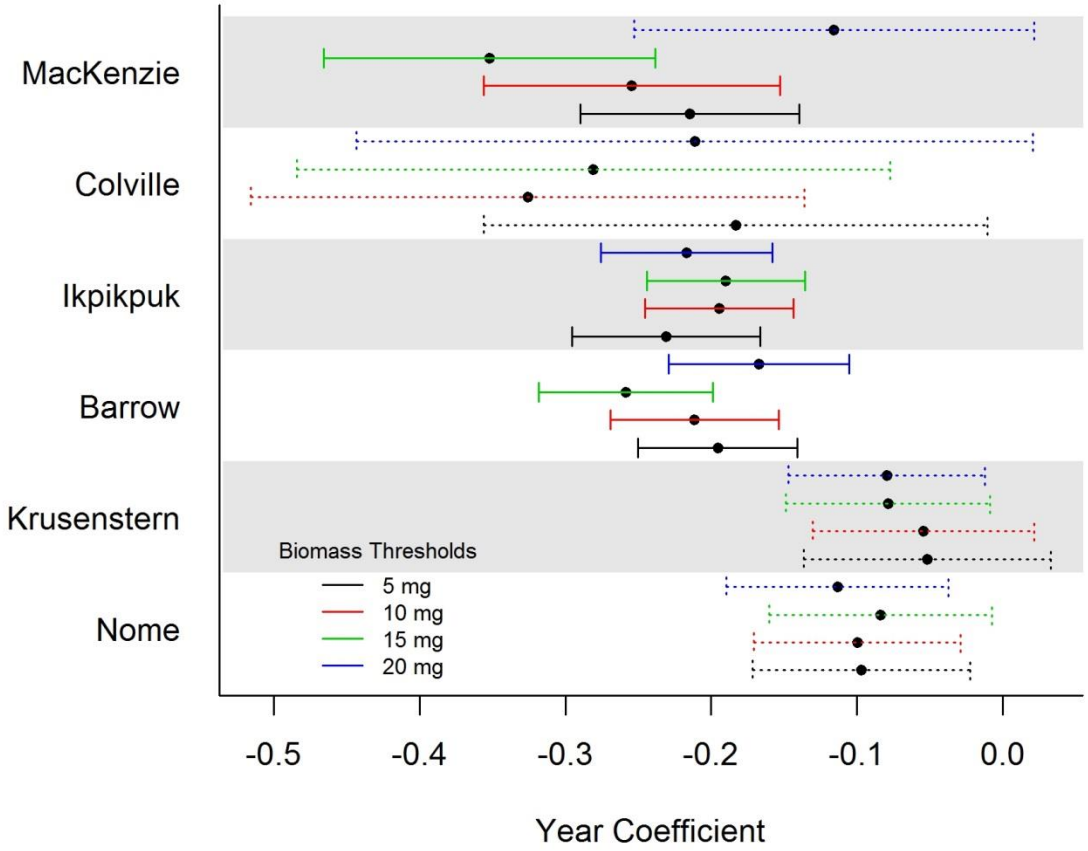


Figure 4. Sensitivity of trends in hindcasted first day with sufficient invertebrate biomass to support normal shorebird chick growth to four biomass thresholds. Parameter estimates for year ±1 standard error, significant results are shown with solid lines ($p < 0.05$).

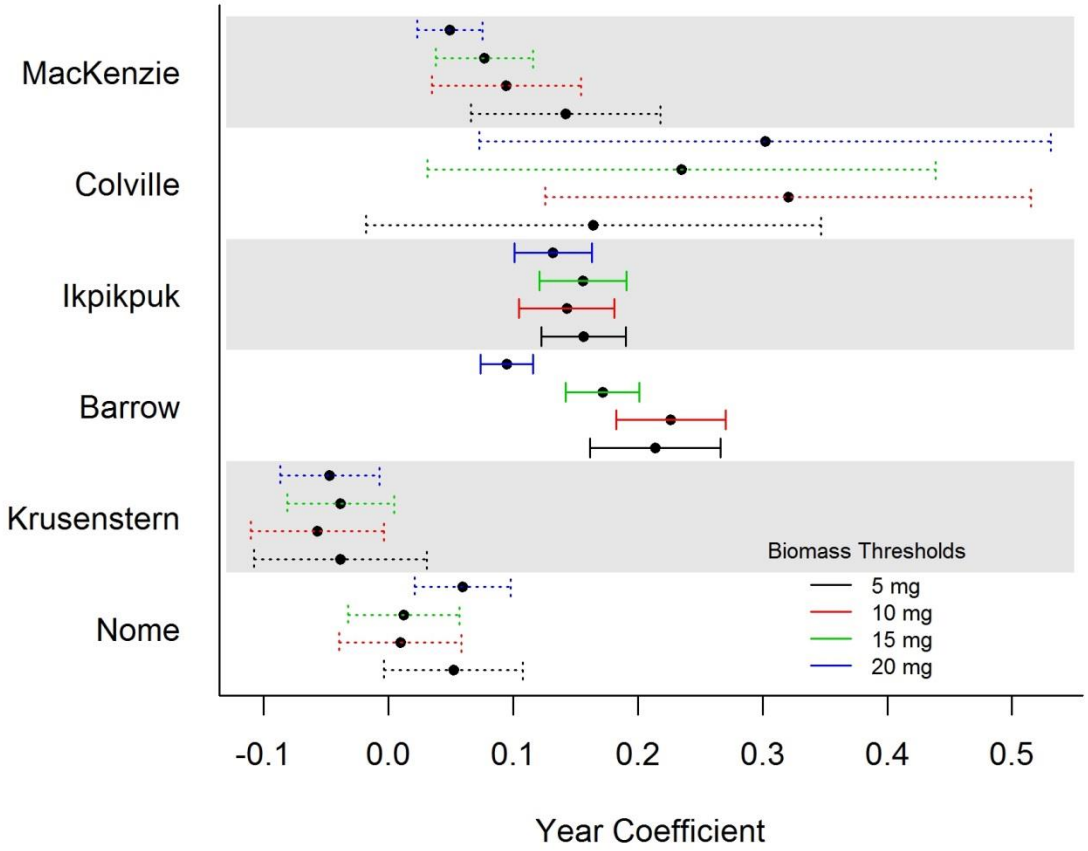


Figure 5. Sensitivity of trends in hindcasted number of days with sufficient invertebrate biomass to support normal shorebird chick growth to four biomass thresholds. Parameter estimates for year ±1 standard error, significant results are shown with solid lines ($p < 0.05$).

Differences in invertebrate phenology between camps

Across all camps, the first day with hindcasted daily invertebrate biomass greater than 10 mg ("first day") ranged from May 11 to July 27 over the entire time period (Figure 6). At the Nome and Cape Krusenstern camps, the first day often occurred in May, while at camps further north, the first day most often occurred in June. At the Barrow camp, the first day never occurred earlier than June 19. A comparison of the first day across camps for a recent 20-year period (1992 – 2012) indicated that Barrow was significantly later than all of the other camps (Table 5). The first day was significantly earlier at the Nome and Cape Krusenstern camps and the Colville, Ikpikpuk, and MacKenzie Delta camps all fell somewhere in between, although the difference between the Ikpikpuk and Cape Krusenstern camps was not significant.

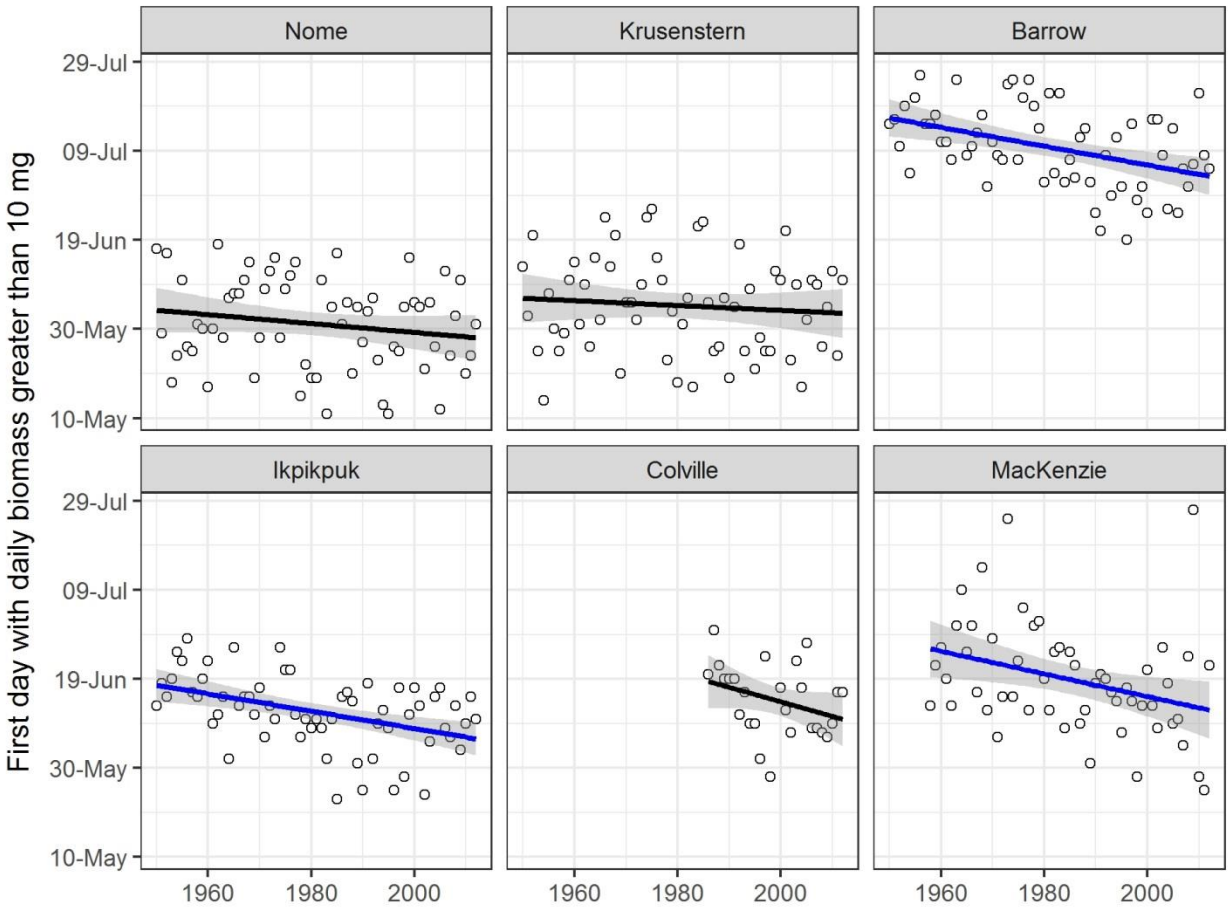


Figure 6. Timing of first day with hindcasted daily invertebrate biomass greater than 10 mg for six ASDN camps from 1950-2012. Significant trends are shown in blue ($p < 0.05$).

Table 5. Mean values and differences in phenology between six ASDN camps for 1992-2012. Significant differences are shown by letters ($p < 0.05$).

Site	First day[1]		Number of days		Peak date[1]	
Nome	148	d	52	d	181	d
Krusenstern	154	c, d	49	d	182	c, d
Barrow	186	a	22	a	200	a
Ikpikpuk	159	b, c	43	c	190	b, c
Colville	163	b	37	b	199	a, b
MacKenzie	165	b	17	a	189	c, d

[1] June 1st is Julian day 152 and July 1st is Julian day 182.

Across all camps and years, the number of days with hindcasted daily invertebrate biomass greater than 10 mg ("number of days") ranged from 0 at Barrow to 74 at Cape Krusenstern (Figure 7). The number of days was significantly lower at the MacKenzie and Barrow camps with means for 1992–2012 of 17 and 22 days, respectively (Table 5). The Nome and Cape Krusenstern camps had significantly more days each year with invertebrate biomass greater than 10 mg than the other camps (means of 52 and 49, respectively). The Ikpikpuk and Colville camps fell somewhere in the middle and were significantly different from one another and the other camps.

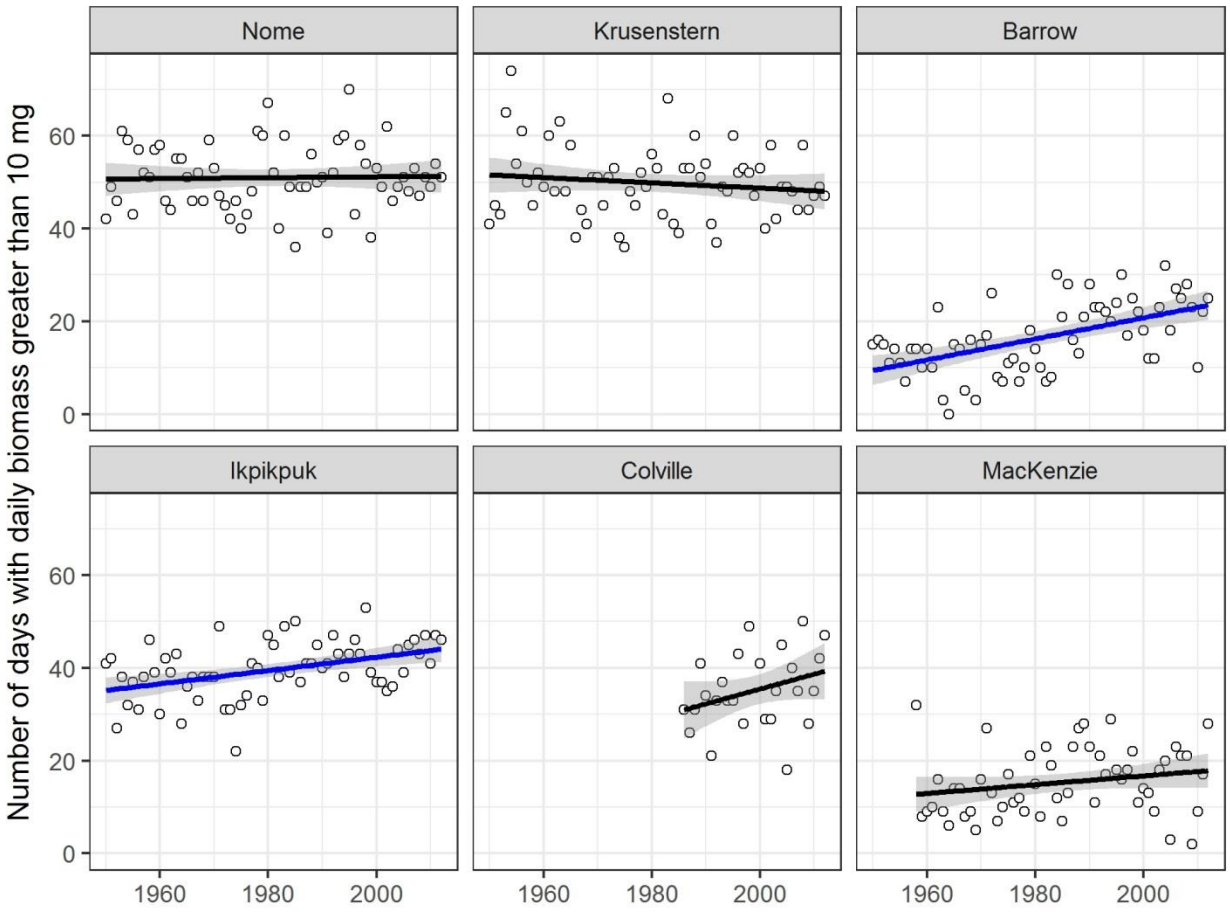


Figure 7. Annual number of days with hindcasted daily invertebrate biomass greater than 10 mg for six ASDN camps from 1950-2012. Significant trends are shown in blue ($p < 0.05$).

Across all camps, the date of peak hindcasted biomass ranged from June 2 (Nome) to July 29 (Barrow, Colville, and Ikpikpuk, Figure 8). The MacKenzie and Nome camps had high variability in the timing of peak biomass, with differences between the earliest and the latest peak date of 49 days or more from 1950 to 2012. Variability in the timing of peak biomass was closer to one month at the Barrow, Colville, and Cape Krusenstern camps. The Barrow and Colville camps had significantly later timing of peak invertebrate biomass for the 1992 to 2012 period than most of the other camps (July 18-19, Table 5). Barrow was significantly later than all of the other camps, while Colville was significantly later than all of the other camps but Ikpikpuk. The mean timing of peak invertebrate biomass was over two weeks earlier at the Nome and Cape Krusenstern camps (June 30 and July 1, respectively).

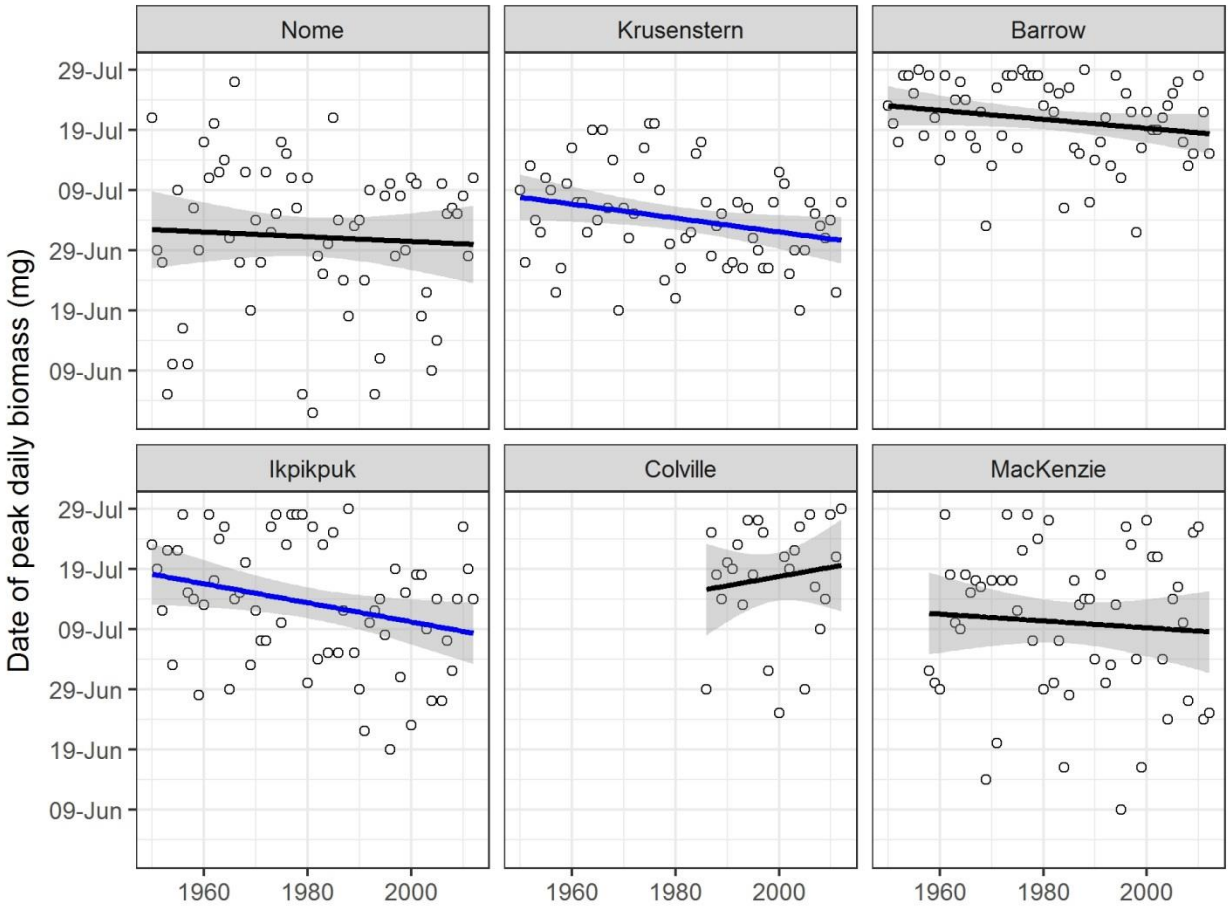


Figure 8. Timing of hindcasted peak daily biomass for six ASDN camps from 1950-2012. Significant trends are shown in blue ($p < 0.05$).

Trends in invertebrate phenology

We evaluated changes in invertebrate phenology (first day above 10 mg, number of days above 10 mg, and peak date) from 1950 to 2012. Changes in the first day above 10 mg occurred at three camps: Barrow, Ikpikpuk, and MacKenzie Delta (Figure 6). The advancement of the first day was two days per decade at the Barrow and Ikpikpuk camps and two and a half days per decade at the MacKenzie Delta camp (Table 6). The number of days above 10 mg increased significantly at the Barrow and Ikpikpuk camps at a rate of two and one and a half days per decade, respectively (Figure 7, Table 6). The date of peak biomass advanced approximately one and a half days per decade at Ikpikpuk and one day per decade at Cape Krusenstern (Figure 8, Table 6).

Significant differences in invertebrate phenology across the six camps mostly followed patterns of latitude. The southernmost camps, Nome and Cape Krusenstern, had the earliest timing in both the first day above 10 mg and peak biomass, in addition to having the highest number of days with sufficient food resources for shorebirds. Barrow, the northernmost camp, consistently had later timing of invertebrate biomass and fewer days with adequate food resources for shorebirds. Significant changes in invertebrate phenology occurred at the northernmost camps with the longest time series, with one exception. Ikpikpuk was the only camp with significant changes in all three aspects of invertebrate phenology, while the Barrow camp had significant changes in the timing of the first day above 10 mg and the annual number of days above 10 mg. There were no changes in invertebrate phenology at the Nome or Colville camps, although the Colville camp had a much shorter time series (to 1986) and none of the camps showed significant trends when invertebrate phenology was hindcasted to 1983. The only significant change in phenology at either of the more southern camps was the timing of peak biomass at Cape Krusenstern. The final model set for this camp was highly simplified with terms for CDD and its squared term only. The lack of any weather variables in the model, which dramatically increase the variability in daily invertebrate biomass, may have improved our ability to measure phenological change at this site.

Table 6. Regression results for trends in invertebrate phenology. All regressions are based on models without wind and over longest time period available (1950 or later, see Table 2). Significant trends are bolded ($p < 0.05$).

Site	Response[1]	Intercept[2]	Year coefficient	Year SE	Year *p-value*
Nome	first day	151	-0.100	0.071	0.164
Krusenstern	first day	155	-0.054	0.076	0.478
Barrow	**first day**	**191**	**-0.211**	**0.058**	**0.001**
Ikpikpuk	**first day**	**163**	**-0.195**	**0.051**	**0.000**
Colville	first day	171	-0.326	0.190	0.099
MacKenzie	**first day**	**171**	**-0.254**	**0.102**	**0.015**
Nome	number of days	51	0.010	0.049	0.848
Krusenstern	number of days	50	-0.057	0.053	0.290
Barrow	**number of days**	**16**	**0.226**	**0.044**	**0.000**
Ikpikpuk	**number of days**	**39**	**0.143**	**0.038**	**0.000**
Colville	number of days	29	0.321	0.195	0.113
MacKenzie	number of days	15	0.095	0.060	0.120
Nome	peak date	182	-0.039	0.089	0.661
Krusenstern	**peak date**	**185**	**-0.116**	**0.053**	**0.033**
Barrow	peak date	202	-0.075	0.046	0.106
Ikpikpuk	**peak date**	**194**	**-0.158**	**0.071**	**0.029**
Colville	peak date	196	0.154	0.243	0.532
MacKenzie	peak date	191	-0.057	0.108	0.602

[1] First day = Julian date of first hindcasted daily invertebrate biomass greater than 10 mg. Number of days = number of days in May, June, and July with hindcasted daily invertebrate biomass greater than 10 mg. Peak date = Julian date of peak hindcasted daily invertebrate biomass.

[2] Year was centered on 1980 for all regressions so the intercept indicates the hindcasted response for 1980.

Discussion

Phenological Mismatch

We found that changes in invertebrate phenology are not progressing as rapidly as reported from sites elsewhere in the Arctic (Høye et al. 2007, Tulp and Schekkerman 2008), as no significant changes in phenology were evident over the last 30 years (1983-2012). Hindcasting over the last 60 years indicated that phenology is not changing equally across the six sites we examined from the Alaskan and Canadian Arctic. Ikpikpuk, on the north coast, was the only site to show significant changes across all three aspects of invertebrate phenology. Nome, the southernmost site, had no measurable changes in phenology over the last 62 years. The hindcasted changes in timing of invertebrate biomass at Barrow, Ikpikpuk, MacKenzie Delta, and Cape Krusenstern are similar to changes in peak biomass estimated for a site in northern Siberia (2 days per decade, Tulp and Schekkerman 2008). These rates also match measured advancements in the timing of spring snowmelt across Alaska (Stone et al. 2002). In eastern Greenland, both snowmelt and emergence timing are advancing at much faster rates, on the order of 10 to 30 days per decade (Høye et al. 2007).

Observations of Arctic-breeding shorebirds indicate that the timing of migration and nesting is advancing at some sites, but not all. Shorebirds migrating to the Colville Delta are arriving one to one and a half days per decade earlier (Ward et al. 2016), while shorebirds migrating to Iceland are arriving from 4 to 8 days per decade earlier (Gunnarsson and Tómasson 2011). No changes in arrival dates were observed for 17 shorebird species on the Yukon-Kuskokwim Delta from 1977 to 2003 (Meltofte et al. 2007). Advancements in shorebird clutch initiation dates have been recorded at rates of 4 to 8 days per decade at Prudhoe Bay (Liebezeit et al. 2014) and 3 to 5 days per decade in the Canadian Arctic (Grabowski et al. 2013). Migration timing is inherently less flexible than egg laying as shorebirds are relying on distant cues to initiate migration, while they can time their egg laying to respond to snowmelt and food availability once they arrive on the breeding grounds (Liebezeit et al. 2014). Although our results suggest that seasonal prey availability for arctic shorebirds is advancing, the potential for trophic mismatch is most likely at the northernmost sites we evaluated, although it may be mitigated by changes in shorebird migration and nesting as reported from other Arctic sites.

Recommendations for Future Research

The ASDN camps collected two separate but complementary invertebrate datasets: (1) the modified Malaise trap data analyzed in this report that represent prey availability in the terrestrial environment and (2) sweep net samples from tundra pond margins that track the emergence phenology of aquatic insects. These datasets have great value due to their broad spatial scale and because they capture seasonal and inter-annual temporal variability. Next steps for these data should include modeling of individual taxonomic groups to better understand patterns of availability and emergence timing (Bolduc et al. 2013). Individual taxonomic groups could likely

be modeled with higher accuracy than models of total invertebrate abundance or biomass due to more synchronous responses to seasonal and weather conditions. Continuous water temperature data collected from the same ponds as the aquatic samples could be used for modeling the emergence timing of aquatic invertebrate groups (e.g. Chironomidae, Tipulidae, and Trichoptera). Understanding availability and emergence at a finer taxonomic resolution would facilitate inquiries into ecological processes performed by individual invertebrate groups, such as effects of pollinators or herbivores on their plant hosts (Hodkinson et al. 1998, Tiusanen et al. 2016), effects of parasites on mammals or birds (Post et al. 2009), and mismatch of preferred food resources with avian predators (Skagen and Oman 1996).

The ASDN modified Malaise trap samples are currently being identified to a finer taxonomic resolution for several orders or groups by different investigators (e.g. Ephemeroptera, Plectoptera, Trichoptera, Diptera, spiders and Dytiscid beetles, Lanctot et al. 2015). These data should be integrated into a comprehensive baseline so that effects of climate change can be investigated using long-term datasets. Arctic invertebrates may be especially good indicators of climate change because they integrate the complex physical effects of their environment over time and because current conditions are limiting for many taxa (Danks 1992). Indicators of climate-driven changes on invertebrate taxa include changes in faunal composition (Oswood 1989), northward expansion of distributions (Post et al. 2009), and changes in generation times (Danks 1992). Additional sampling at the same ASDN sites in the future would enable investigation into these kinds of changes.

Future invertebrate sampling should consider options for collecting local weather data and extending the sampling season. Although collection of weather data requires additional investments of time and resources, local data improved our models at all sites and allowed a better understanding of wind and precipitation effects, which are spatially variable and not easily captured using regional weather stations. Terrestrial invertebrates continue to emerge into mid-August (Tulp and Schekkerman 2008, Bolduc et al. 2013) and collection of additional samples later in the season would improve models of invertebrate activity. In the data we analyzed, daily temperature and CDD were often strongly correlated from May through July ($r > 0.7$ at 7 of 9 camps), which made it difficult to include predictors of both density (CDD) and activity (daily temperature) in our models. Sampling into August would also capture invertebrate activity when shorebird chicks are feeding, which would provide valuable observations for testing the phenological mismatch hypothesis.

Management Applications

The phenological changes we modeled for arctic invertebrates may be applied by managers in several ways. Rates of change may be compared to other reported phenological changes in the Arctic, such as shorebird migrations, egg laying, snowmelt, flowering, or caribou migrations.

The mean dates and duration of invertebrate activity that we summarized for the most recent 20 year period may be used to infer potential mismatch with datasets from similar sites. The modeled daily invertebrate biomass may be used by ASDN researchers to test hypotheses about climate change effects on shorebird phenology, such as growth rates and nest timing.

Products

a. Publications, conference papers, and presentations: The results from our two reports will be combined into one publication.
b. Education and outreach: None at this time.
c. Other products:
    a. Access database

References Cited

Anderson, D. R. 2008. Model Based Inference in the life Sciences: A Primer on Evidence. First edition. Springer-Verlag, New York.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bolduc, E., N. Casajus, P. Legagneux, L. McKinnon, H. G. Gilchrist, M. Leung, R. I. G. Morrison, D. Reid, P. a. Smith, C. M. Buddle, and J. Bêty. 2013. Terrestrial arthropod abundance and phenology in the Canadian Arctic: modelling resource availability for Arctic-nesting insectivorous birds. The Canadian Entomologist 145:155–170.

Brown, S., R. Lanctot, and B. Sandercock. 2010. Arctic Shorebird Demographic Network Breeding Camp Protocol Version 1 - May 2010.

Danks, H. V. 1992. Arctic insects as indicators of environmental change. Arctic 45:159–166.

Grabowski, M. M., F. I. Doyle, D. G. Reid, D. Mossop, and D. Talarico. 2013. Do Arctic-nesting birds respond to earlier snowmelt? A multi-species study in north Yukon, Canada. Polar Biology 36:1097–1105.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of evolutionary biology 24:699–711.

Gunnarsson, T. G., and G. Tómasson. 2011. Flexibility in spring arrival of migratory birds at northern latitudes under rapid temperature changes. Bird Study 58:1–12.

Hodkinson, I. D., N. R. Webb, J. S. Bale, W. Block, S. J. Coulson, and a T. Strathdee. 1998. Global Change and Arctic Ecosystems: Conclusions and Predictions from Experiments with Terrestrial Invertebrates on Spitsbergen. Arctic and Alpine Research 30:306–313.

Høye, T. T., E. Post, H. Meltofte, N. M. Schmidt, and M. C. Forchhammer. 2007. Rapid advancement of spring in the High Arctic. Current Biology 17:449–451.

Lanctot, R. B., E. Weiser, B. K. Sandercock, and S. Brown. 2015. 2010-2014 progress report: Using a Network of Sites to Evaluate How Climate-mediated Changes in the Arctic Ecosystem are Affecting Shorebird Distribution, Ecology and Demography. U.S. Fish and Wildlife Service, Anchorage, AK.

Liebezeit, J. R., K. E. B. Gurney, M. Budde, S. Zack, and D. Ward. 2014. Phenological advancement in arctic bird species: Relative importance of snow melt and ecological factors. Polar Biology 37:1309–1320.

Meltofte, H., H. Meltofte, T. Piersma, T. Piersma, H. Boyd, H. Boyd, B. J. Mccaffery, B. J. Mccaffery, I. Tulp, and I. Tulp. 2007. Effects of climate variation on the breeding ecology of Arctic shorebirds. Meddelelser Om Gronland Bioscience 59:1–48.

Oswood, M. W. 1989. Community structure of benthic invertebrates in interior Alaskan (USA) streams and rivers. Hydrobiologia 172:97–110.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. Callaghan, T. Christensen, B. Elberling, A. Fox, and O. Gilg. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358.

Schekkerman, H., I. Tulp, T. Piersma, and G. H. Visser. 2003. Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. Oecologia 134:332–342.

Shaftel, R., and D. Rinella. 2017. Climate Effects on Arctic Food Resources: Predictive Models for Surface-Available Invertebrate Biomass. Anchorage, AK.

Skagen, S. K., and H. D. Oman. 1996. Dietary Flexibility of Shorebirds in the Western Hemisphere. Canadian Field-Naturalist 110:419–432.

Stone, R. S., E. G. Dutton, J. M. Harris, and D. Longenecker. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research: 107:1–13.

Tiusanen, M., P. D. N. Hebert, N. M. Schmidt, and T. Roslin. 2016. One fly to rule them all — muscid flies are the key pollinators in the Arctic. Proceeding of the Royal Society B 283.

Tulp, I., and H. Schekkerman. 2008. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. Arctic 61:48–60.

Tulp, I., H. Schekkerman, T. Piersma, J. Jukema, P. De Goeij, and J. Van de Kam. 1998. Breeding waders at Cape Sterlegova, Northern Taimyr, in 1994.

Ward, D. H., J. Helmericks, J. W. Hupp, L. Mcmanus, M. Budde, D. C. Douglas, and K. D. Tape. 2016. Multi-decadal trends in spring arrival of avian migrants to the central Arctic coast of Alaska: Effects of environmental and ecological factors. Journal of Avian Biology 47:197–207.

Appendix A. Final Confidence Sets used for Hindcasting Invertebrate Biomass from 1950 to 2012 at the Nome, Cape Krusenstern, Barrow, Ikpikpuk, Colville River, and MacKenzie Delta Camps.

Site	Intercept	CDD	CDD^2	Precipitation	Temperature	AICc	Δ AICc	Model Weight
Nome	3.564	0.0010	-0.000016	-0.037	0.201	118.31	0.00	0.72
Nome	3.579	0.0002	-0.000017	NA	0.221	120.23	1.91	0.28
Cape Krusenstern	3.813	0.0068	-0.000034	NA	NA	74.42	0.00	0.88
Cape Krusenstern	3.335	0.0051	NA	NA	NA	78.40	3.98	0.12
Barrow	2.187	0.0144	-0.000091	-0.047	0.142	140.90	0.00	0.48
Barrow	2.163	0.0134	-0.000087	NA	0.156	141.19	0.29	0.41
Barrow	2.233	0.0198	-0.000099	-0.055	NA	143.90	2.71	0.11
Ikpikpuk	3.319	0.0051	-0.000135	NA	0.346	86.34	0.00	0.55
Ikpikpuk	3.069	NA	NA	NA	0.356	86.73	0.38	0.45
Colville River	2.387	NA	NA	NA	0.514	121.13	0.00	1.00
MacKenzie Delta	1.765	NA	NA	NA	0.198	86.37	0.00	1.00