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**Latitudinal temperature-dependent variation in timing of prey availability can
impact Pacific seabird populations in Canada**

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Abstract

We modelled how nestling growth rates of Cassin's Auklet (*Ptychoramphus aleuticus* (Pallas, 1811)) varied with timing of peak copepod prey availability at two breeding colonies in British Columbia: on Triangle Island, in the California Current Ecosystem, and Frederick Island, in the Gulf of Alaska Ecosystem. We used time series of nestling growth rates and estimated the seasonal timing of peak biomass of copepods (*Neocalanus cristatus* (Kröyer, 1845)) using a temperature-dependent phenology equation. We developed a single model to examine intercolony differences in the effect of the timing of regional peak prey biomass on seabird nestling growth rates. This model indicated nestling growth rates on Triangle Island varied widely and were positively associated with timing of peak zooplankton biomass, such that higher growth rates were observed when the peak biomass occurred later in the breeding season. In contrast, nestling growth rates were consistently high at Frederick Island, where peak copepod biomass always occurred relatively late. If ocean climate warming results in a poleward shift of *Neocalanus* abundance and induces earlier and more narrow timing of availability, episodes of poor nestling growth will increase in frequency on Triangle Island, and could eventually affect auklets on more northerly colonies.

Keywords: Ocean climate variability, sea surface temperature, *Ptychoramphus aleuticus*, Cassin's Auklet populations, nestling growth, *Neocalanus*, zooplankton phenology

Introduction

In the Northeast Pacific, changes in reproduction of upper trophic level predators like seabirds have been linked to ocean climate variability through impacts on prey populations (Bertram et al. 2001; Jones et al. 2002; Sydeman et al. 2006; Hipfner 2008; Wolf et al. 2009). The world's largest population of Cassin's Auklet (*Ptychoramphus aleuticus* (Pallas, 1811)) on Triangle Island, in the California Current Ecosystem, exhibits pronounced breeding failures when spring is early and ocean temperatures are warm, such as in 1998 during the large El Niño Southern Oscillation (ENSO) event. In warm, early spring years, the timing of auklet breeding is mismatched with the timing of the availability of their key prey, the calanoid copepod *Neocalanus cristatus* ((Kröyer, 1845), Bertram et al. 2001; Hedd et al. 2002; Hipfner 2008; Hipfner et al. 2010). The phenology-related mismatches can lead to stunted nestling seabird growth and large-scale breeding failures due to starvation.

The seabird colonies in our study system are in oceanographically unique locations in the northeast Pacific Ocean because they straddle the location where two large marine ecosystems (Gulf of Alaska and California Current ecosystem, Peterson and Schwing 2003) are formed from the bifurcation of the North Pacific current. Frederick Island is part of the Gulf of Alaska Ecosystem, which is associated with the northward flowing Alaska current and coastal downwelling domain, while Triangle Island is in the California Current Ecosystem associated with the southward flow of the California current and the coastal upwelling domain (Fig. 1, adapted from Ware and McFarlane 1989). It is important to note that the open water in the "transition zone" between the two large marine ecosystems provides an obstacle to poleward transport of warm southern waters by disrupting the effectively continuous coastline that extends from central California to the northern tip of Vancouver Island (but see Zamon and Welch 2005). In El Niño years, the impacts of ocean warming on prey populations will have a greater influence in the California Current Ecosystem than in the Gulf of Alaska Ecosystem to the north in part because of the impediment to poleward flow imposed at the border between the northern and southern ecosystems (Fig. 1). In addition to interannual variation, it is recognized that ocean temperatures in these ecosystems also

fluctuate on multidecadal scales. The California Current (CC) and Gulf of Alaska (GOA) ecosystems alternate between anomalous warm and cool states, also known as regimes (Peterson and Schwing 2003), which are indexed by the Pacific Decadal Oscillation and linked to large-scale changes in the wind patterns, ocean temperatures, and biological productivity (Mantua et al. 1997). Mackas et al. (2007) reviewed time series data on the availability of zooplankton to upper trophic level predator populations, including seabirds from Triangle Island, and reported “warm” and “low productivity” years from 1992-1998, and 2003-2006, with “cool and “productive” years from 1999-2002. The timing of availability of *Neocalanus* copepods was earlier in the warm years which led to mismatches and lower production at upper trophic levels in those years (Mackas et al. 2007).

Research on seabird nestling diet is consistent with the concept that the phenology of temperature-dependent copepod prey and Cassin’s Auklet predator populations can be mismatched on Triangle Island in the California Current Ecosystem but a similar mismatch has not been observed on Frederick Island, in the Gulf of Alaska Ecosystem (Bertram et al. 2009). In addition, local adult annual survival for Cassin’s Auklet is lower on Triangle Island, where the population has declined significantly (1989-2009, Rodway and Lemon 2011), than on Frederick Island (Bertram et al. 2005) where declines have not been reported. Variation in nestling growth rate and production contributes to the observed differences in local adult annual survival between the colonies. Seabird nestling growth rate is commonly measured and forms a key component of vital rate estimation because it is positively correlated with mass at fledging (Morbey and Ydenberg 1997), earlier nest departure (Morbey and Ydenberg 1997; Hipfner et al. 2010), and probability of recruitment into the breeding population (Morrison et al. 2009). Quantitative knowledge of the vital rates of births and deaths facilitates the partitioning of sources of variation that can cause populations to fluctuate. Despite having a small number of breeding colonies, Canada holds 80% of the global population of Cassin’s Auklet. Therefore, the decline on Triangle Island (Rodway and Lemon 2011) is of great conservation importance. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014) has designated the Cassin’s Auklet as Special Concern, in part

due to the effects of ocean climate warming on prey population, which in turn impacts breeding performance and survival of nestling and adult birds.

In western Canada, nestling growth as an index of production of Cassin's Auklet has been studied in detail on Triangle Island in the California Current Ecosystem but only limited historical data exist for Frederick Island (Vermeer 1987) in the Gulf of Alaska. Here we quantify the degree to which variation in ocean climate influences the production of nestlings from colonies through regional impacts on prey availability on colonies in the California Current and Gulf of Alaska ecosystems. Our analysis was facilitated by the use of a temperature-dependent phenology equation for *Neocalanus* copepods (Mackas et al. 2007) that permitted us to calculate the timing of peak biomass in ocean waters where copepods are accessible to diving planktivorous seabirds like Cassin's Auklet. Latitudinal differences in the timing of copepod prey biomass peaks are expected based on regional temperature differences in the northeast Pacific ecosystems. The phenology equation demonstrates that variability of *Neocalanus* life cycle timing is associated in a strong linear fashion with cumulative anomalies of upper-ocean temperature during the season when the copepods feed and grow in the near-surface layer (Mackas et al. 2007).

We contrast interannual variability in the nestling growth rates, and seek to develop a single statistical model that explains the observed variation in colony production on Triangle and Frederick islands. Such a model allows for the prediction of future impacts of ocean climate change on seabird populations on Canada's Pacific coast. It is useful to have a single model that can accommodate clear differences between the two seabird colonies in the California Current and Gulf of Alaska ecosystems in response to variation in prey availability, which results from the latitudinal temperature-dependent prey phenology.

Methods

Study sites

We studied the growth of Cassin's Auklet nestlings on two key seabird colonies located near the continental shelf break on the west coast of British Columbia, Canada (Fig. 1). Triangle Island (51°52'N; 129°05'W) is located near Cape Scott at the northern tip of Vancouver Island and experiences the northern end of the California Current Ecosystem. Frederick Island (53° 56'N, 133° 11'W) lies off the northwest coast of Haida Gwaii at the southern end of the Alaska Current Ecosystem. The colony on Triangle Island was estimated to have 548,000 pairs of birds in 1989 (Rodway 1991), but the number of burrows had declined 40% by 2009 (note that the methods used to detect trends did not measure burrow occupancy or colony size so an estimate of the number of pairs of birds in 2009 was not provided by Rodway and Lemon 2011). Frederick Island was last surveyed in 1980 and had an estimated 90,000 pairs of birds (Rodway et al. 1994) making it the largest colony Cassin's Auklet colony in Haida Gwaii.

Nestling growth rates

We used our data and published records (Vermeer 1987; Bertram et al. 2001) to calculate average annual chick growth rates from Triangle Island (1978, 1981, 1994-2000, 2005) and Frederick Island (1980, 1981, 1994-1998, 2000, 2005). Early in the season, nesting burrows were visited every 3-5 days to look for hatchlings so that age could be estimated using a wing length versus age relationship developed from the sample of known aged nestlings (Bertram et al. 2001). This relationship was developed independently for each colony. We recorded mass (g), wing length (mm), and estimated the age (d) for each nestling.

Growth rate (y_i) for an individual chick i was defined as the difference in mass for a 5-day old chick (m_{5i}) and its mass at 25 days (m_{25i}) divided by 20 days or $y_i = (m_{25i} - m_{5i})/20$, in accordance with standard methods developed from detailed examinations of intraspecific variability in nestling growth of Cassin's auklets at Triangle Island, British Columbia (Morbey 1995; Morbey and Ydenberg 1997). The simple linear model is a commonly applied tool for growth rate estimation in the early – mid chick rearing period (Harfenist 1995; Bertram et al. 2001; Hedd et al. 2002) prior to the attainment of peak

mass and mass loss until fledging. The individual growth rates were averaged to produce annual growth rates for each colony/year, and estimated standard errors were calculated. Confidence intervals for the 1978 estimate from Triangle Island (from Vermeer 1987) could not be constructed because the raw data were not available.

In 2005 Frederick Island was visited on a single day (11 June) and a sample of 14 nestlings was measured for wing length (mm) and mass (g). Note that Bertram et al. (2002) demonstrated that measures of mass in relation to wing length collected from small samples on a single day clearly revealed patterns of interyear and intercolony variation in nestling growth and development. In this study, the units for our estimate of nestling growth were grams per day. Therefore, to convert the sample from Frederick in 2005 to comparable units we used wing length to estimate age of the nestlings and then regressed age on mass, and interpreted the slope of this line as the estimate of nestling growth rate in that year (Appendix 1). The effect of small sample sizes was accounted for by weighting the growth rate estimates from each colony by the sample size in each year (see *Model development and selection* below).

Estimation of peak timing of zooplankton prey

There is a significant negative correlation between the timing of peak *Neocalanus* biomass and sea surface temperature (SST) in the Northeast Pacific (Mackas et al. 2007), so we used SST data from nearby light houses to estimate prey timing around the seabird colonies. Monthly SST from Pine Island (50°35'N, 127°26'W) was used to estimate timing of prey biomass at Triangle Island, and SST data from Langara Island (54°09'N, 133°02'W) light station was used for Frederick Island. Pine Island light station SST data have been used previously (Bertram et al. 2001, 2009) and provide a valid index of SST within foraging ranges (Boyd et al. 2008) of breeding seabirds on Triangle Island (see also Borstad et al. 2011; McKinnell et al. 2014)). Sea surface temperature values from light stations were obtained from Fisheries and Oceans Canada (FOC 2014) and converted to degree-days for the months of March, April, and May. During the *Neocalanus* growing season the cumulative warmth of the upper ocean as degree-days

relative to a 6 degree baseline was calculated as $(SST^{\circ}C - 6^{\circ}C) * 31d$ for March and May or $(SST^{\circ}C - 6^{\circ}C) * 30d$ for April (Mackas et al. 2007). The sum of the degree days for these three months (x) was then used in a temperature-dependent phenology equation to obtain point estimates for the timing of peak biomass of *N. plumchrus* ((Marukawa, 1921)) near Triangle Island and Frederick Island (date of peak biomass = $169 - 0.16x$; Mackas et al. 2007). The peak biomass timing estimates are assumed to be known values for modelling purposes. Within the *Neocalanus* species there is a consistent pattern of earlier peaks in response to warmer surface waters (Mackas et al. 2012). In the Northwest Pacific, *N. cristatus* timing in the Oyashio region has a similar shift to ‘earlier in warm years’ as *N. plumchrus* in the eastern Pacific ocean (Mackas et al 2012). In the absence of a regional equation for *N. cristatus*, we use the *N. plumchrus* temperature dependent model (above) as an index for the timing for *N. cristatus* in response to interannual variation in SST near the seabird colonies. Note that *N. cristatus* represented > 99% of the copepod biomass in the nestling diet of Cassin’s Auklet on Triangle and Frederick islands during the time frame of this study (Bertram et al. 2009). Note, too, that Batten and Mackas (2009) demonstrated a shortened duration of the annual *N. plumchrus* biomass peak in the Northeast Pacific in response to ocean climate warming, in addition to earlier peak biomass timing. Given the strong temperature-dependent nature of the *Neocalanus* life cycle in surface waters (Mackas et al. 2012), we expect that *N. cristatus* will also respond to warmer ocean surface temperatures with earlier peaks of shortened duration. Importantly, Hipfner (2008) demonstrated that it was the timing of prey availability, rather than prey abundance, which was the key factor determining the seasonal prevalence of *N. cristatus* in the nestling diet and concluded that seasonal timing mismatches could have significant demographic consequences for the Cassin’s Auklet population on Triangle Island.

Variation in Average Nestling Growth Rates

We used two statistics to assess the variability of average colony nestling rates: the weighted coefficient of variation (CV) and Heath’s population variation (PV; Heath 2006). The PV statistic improves on CV for small sample sizes and non-Gaussian

distributions (Heath 2006). For reference we also computed CV, the more widely familiar measure of variability in ecology studies. We bootstrapped the observed values of growth rate averages on Triangle ($n=10$) and Frederick ($n=9$) islands to estimate a sampling distribution for weighted CV and PV ($n=10,000$ bootstrap replicates). We sought to visually test for non-overlapping confidence intervals (CIs) in order to approximate $\alpha=0.05$ tests of between-island differences. However, as explained in Payton et al. (2003), the use of 95% CIs results in overly conservative type I error rates. Corrected confidence levels in the range of 84% and 90% are suggested depending on the ratio of standard errors between the two samples being compared (the exact relation is derived in Schenker and Gentleman 2001). In our cases (weighted CV and PV) the bootstrapped sampling distributions appeared normal, and their ratio of standard errors was 2.8 and 2.4, respectively (estimated from the data), thus we used confidence levels of 89% and 90% for CV and PV, respectively, each of which yields a non-overlapping test at a 95% confidence level.

Model development and selection

To account for differences in the variability in the average growth rates from Triangle and Frederick islands we used a weighted least squares regression model (Montgomery et al. 2012), weighting each island by its estimated variance of the reciprocals of sample size of nestlings in each year. This approach allowed us to use all available data to identify a single model that would best explain differences and variation between colonies, and yielded greater statistical power than treating data from each colony separately.

We assume for simplicity that the effect of peak biomass timing on nestling growth rates is either linear or quadratic. We examined the effect of regional timing of peak zooplankton biomass and colony identity on average nestling growth rate through all-regressions selection. The global model was:

$$E(y_i) = \beta_0 + \beta_1 c_i + \beta_2 b_i + \beta_3 (cb)_i + \beta_4 b_i^2 + \beta_5 (cb^2)_i$$

Where $c_i \in \{0,1\}$ is an indicator variable for Triangle Island, and b_i is the value of peak biomass date corresponding to the i^{th} observation. We performed an “all-regressions” selection by testing all subsets of explanatory variables. The all-regressions approach is both parsimonious and has good explanatory power, and is recommended for small sets of covariates, as in our case (Montgomery et al. 2012). We used adjusted R-squared as our ranking criterion for variable selection. All analyses were done using R software (R Core Team, 2016).

Results

Variation in Average Nestling Growth Rates

Both of the variability estimates, Heath’s Population Variation (PV) and weighted Coefficient of Variation (CV), demonstrated that Triangle Island experienced higher variability in nestling growth rate means than did Frederick Island during our study. The confidence intervals of 89% and 90% for CV and PV, respectively, did not overlap between colonies at in tests at the 95% confidence level (Fig. 2).

Identification of the best model

The best model using adjusted R-squared as our ranking criterion was:

$$E(\text{average growth}_i) = \beta_0 + \beta_1 \text{island}_i + \beta_3 (\text{island} \times \text{peak biomass date})_i$$

This model indicated a positive relationship between the timing of peak zooplankton biomass and nestling growth rates on Triangle Island, but not on Frederick Island (Fig. 3, Table 1 shows parameter estimates, Appendix 2 show the full list of tested models and R^2 values for these models). F-tests comparing the best model with the null models of island effect only, and of no effects whatsoever, yielded $p=0.007$ and $p=0.010$, respectively, which demonstrates that the effect of prey timing was significant on Triangle Island nestling growth rates.

Discussion

Our results showed greater variability in nestling growth rates on Triangle Island than on Frederick Island. Further, our model demonstrated colony differences in the range of regional peak biomass dates, which occurred earlier during the breeding season at Triangle Island than at Frederick Island, and those early years were associated with reduced nesting growth rates and breeding failures. As expected, there was a strong relationship between the timing of peak prey biomass and nestling production on Triangle Island in the California Current Ecosystem (Bertram et al. 2001; Hipfner 2008). The model is consistent with the concept of 'bottom-up' control of nestling production on Triangle Island related to the timing of availability of *Neocalanus* prey. Note, too, that a reported positive correlation between the timing of spring *phytoplankton* bloom and Cassin's Auklet growth rates from Triangle Island (1994-1999, see Ware and McQueen 2006) is also consistent with bottom-up control on marine bird reproduction through the influences of the timing of the phytoplankton peak on the energetic value and timing of peak availability of zooplankton prey for seabirds in the region of the colony. In contrast, on the Frederick Island colony, there was no impact of variation in the timing of peak zooplankton availability on nestling growth performance, and production was consistently high at this more northern colony. The timing of peak prey availability started later and extended further into the breeding season, but the range was shorter (17 d) on Frederick Island than the range (23 d) on Triangle Island. Importantly, no peak prey date values lower than day 129 (9 May) were observed on Frederick Island. Low nestling growth rates occurred on Triangle Island when peak biomass fell before date values of 129, when spring was early and warm, such as during the 1998 ENSO event when the peak biomass was the earliest peak on record. Even though the timing of peak biomass in 1998 was also the earliest observed for Frederick Island, the date was 11 d later than on Triangle Island and breeding performance was strong, as usual, on Frederick Island. It is noteworthy that another upper trophic level predator, coho salmon (*Onchorynchus kisutch*), also showed similar differential production in relation to oceanographic domain, with very poor juvenile growth and survival in 1998 and 2005 on the west coast of Vancouver Island but normal growth rates and survival in northern British Columbia / Southeast Alaska in those years (Trudel et al. 2007, 2008).

The timing of avian breeding is largely entrained by an invariant photoperiod (Dawson 2008), but the actual laying date of an individual female is secondarily determined by nutritional factors (Stevenson and Bryant 2000). Over a highly variable five-year period on Triangle Island, the first Cassin's Auklet eggs of the season were laid within a narrow temporal window, and very early in the spring - in the last few days of March or the first few days of April – but median laying dates varied by up to three weeks (Hipfner et al. 2010). However, it was in the warm-water years, not the cold-water years, that breeding synchrony broke down, and more females laid later. The net effect of this flexibility in laying date was therefore to exacerbate, rather than mitigate, the consequences of temporal mismatching with their primary prey in those warm years (Hipfner 2008). This counterintuitive result likely reflects that the timing of laying by Cassin's Auklets is physiologically constrained by the need to accumulate sufficient reserves beforehand (Sorenson et al. 2009), and that the capacity to do so is limited by unfavourable environmental conditions, such as warm sea-surface temperatures, in the preceding winter (Schroeder et al. 2009). Previous studies indicate that carry-over effects from late winter and spring feeding conditions can affect the timing of laying in other species of seabirds (Guinet et al. 1998; Daunt et al. 2006; Durant et al. 2006).

Neocalanus are subarctic copepods and the ocean off British Columbia is near the southern end of the range for the genus. If future ocean climate warming continues to push the centre of zooplankton abundance poleward (Mackas et al. 2007) and to induce earlier and more narrow timing of *Neocalanus* availability (Batten and Mackas 2009), we expect that episodes of poor nestling growth will increase in frequency on Triangle Island and could eventually affect auklets on more northerly colonies like Frederick Island. We argue that the seabird colonies on Triangle and Frederick islands, because they reflect variation in distinct large marine ecosystems at different latitudes, represent key locations to gauge reproduction and survival that are needed to identify the causes of population trends for upper trophic level predators in the Northeast Pacific (see also Bertram et al. 2005, 2009).

Simultaneous research and monitoring on Triangle and Frederick islands (and replicate seabird colonies if possible) will provide unique insights into variation in the California Current and Gulf of Alaska ecosystems and will allow for the temperature dependent seabird production model presented here to be evaluated and tested.

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Table 1. Cassin's Auklet (*Ptychoramphus aleuticus*) nestling growth rate model. Maximum likelihood parameter estimates and estimated standard errors (SE) for the best model $E(y_i) = \beta_0 + \beta_1 c_i + \beta_3 (cb)_i$ chosen by adjusted R^2 . Note that the intercept for Triangle is $\beta_0 + \beta_1$.

Interpretation	Parameter	Estimate	SE
Frederick intercept	β_0	5.45	0.11
Difference in intercept between Frederick and Triangle	β_1	-9.92	2.99
Triangle slope	β_3	0.07	0.02

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Figure captions

Fig. 1. Location of Cassin's Auklet (*Ptychoramphus aleuticus*) colonies on Triangle Island and Frederick Island in relation to major currents, and oceanographic domains (adapted from Ware and McFarlane 1989). The Gulf of Alaska ecosystem is related to the coastal downwelling domain (1) driven by the Alaska Current. The California Current Ecosystem is related to the upwelling domain (3) of the California Current. The transition zone (2) separates the two large marine ecosystems and can vary in space because the north-south location of the bifurcation of the North Pacific Current can vary between years (see Freeland and Cummins 2005 and also Batten and Freeland 2007). The 2000m isobath and locations of Langara Island and Pine Island light stations are also shown in the inset.

Fig. 2. Inter colony variation in average nestling growth rate of Cassin's Auklet (*Ptychoramphus aleuticus*) estimated with Heath's population variability index (PV; Heath 2006) and weighted CV with 89% and 90% confidence intervals, respectively.

Fig. 3. Predicted values of expected growth rates for Cassin's Auklet (*Ptychoramphus aleuticus*), from the best model, $E(y_i) = \beta_0 + \beta_1 c_i + \beta_3 (cb)_i$, overlaid on the observed annual average nestling growth rates ($n=19$). The black solid line indicates model predicted values for Triangle Island and the grey line indicates those for Frederick Island. Vertical bars extend two standard errors from each of the observed growth rates, except for Triangle Island in 1978 and Frederick Island in 2005 (for which error estimates were unavailable). The estimates of timing of peak biomass for *Neocalanus* copepods were calculated using the temperature-dependent phenology relationship of Mackas et al. 2007 (see methods).

Fig.1.

Fig. 2

Fig. 3