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# Basin-scale oceanographic processes, zooplankton community structure, and diet and reproduction of a sentinel North Pacific seabird over a 22-year period

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## ABSTRACT

Climate-driven variation in the distribution, abundance and phenology of low trophic-level organisms can have cascading effects within marine food webs, and understanding these complex ecosystem dynamics is of vital importance in an age of dramatic environmental change. We tested the hypothesis that marine conditions associated with the state of the Pacific Decadal Oscillation (PDO) exert primary influence on the biogeographic affinities of the zooplankton community, and thus the composition of nestling diets and reproduction of a zooplanktivorous seabird, Cassin's Auklet (*Ptychoramphus aleuticus*). The 22-year study (1996–2017) took place on Triangle Island, British Columbia, Canada, located at the northern extreme of the California Current System (NCCS) and site of the world's largest breeding colony. Based on annual zooplankton tows in the vicinity of Triangle Island, the biomass of 'Subarctic' zooplankton species (copepods) was elevated in years in which the PDO was in its negative (cold-water) state. The biomass of 'Subarctic' zooplankton was unrelated to both the El Niño-Southern Oscillation (ENSO) and North Pacific Gyre Oscillation (NPGO) indices. Principal Components Analysis (PCA) showed that in those PDO-negative years, diets fed to nestling auklets included more copepod biomass and less euphausiid biomass. Virtually all ($>$ 99%) of the copepod biomass consisted of just one species, *Neocalanus cristatus,* one of the North Pacific Ocean's diagnostic 'Subarctic' copepods. PCA also identified a secondary effect of the El Niño-Southern Oscillation (ENSO) on diets, in that auklet parents delivered more larval fish and less copepods-plus-euphausiids to nestlings in years in which ENSO was in a strongly positive state (i.e., El Niño). The growth rates of nestling auklets, indexed by their mean mass at 25 days of age, was higher in years in which they received more copepods-plus-euphausiids rather than larval fish, and in years in which they received more copepods rather than euphausiids. A previous study in the Central California Current System found that ENSO (to the mid-1990s) and then the NPGO (since the mid-1990s) exerted primary influence on productivity in Cassin's Auklets. In combination, the two studies illustrate how basin-scale climatic processes can non-homogeneously influence productivity in a single species across oceanic domains. For Cassin's Auklet, the contrast can be attributed to latitudinal differences in the prey base (more copepod-based in the north, more euphausiid-based in the south), and linked to ocean transport, temperature, and phenology. This correlational study provides mechanistic insight into ecological functioning in the offshore waters of the NCCS, with application to marine systems elsewhere. We highlight the particular importance of the 'Subarctic' copepods to a zooplanktivorous predator in the NCCS, and the value of seabirds as indicators in this rich marine ecosystem.

## 1. Introduction

Research aimed at understanding the consequences of climate-driven variation in the structure and function of marine communities is immensely challenging, especially in an age in which environmental conditions globally are in extreme flux (Stenseth et al., 2004; Richardson, 2008). As found in marine systems in other parts of the world (Beaugrand et al., 2009; Chiba et al., 2009), the zooplankton community of the Northern California Current System (NCCS) responds both strongly and rapidly to variation in basin-scale oceanographic

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processes (Peterson and Keister, 2003; Mackas et al., 2004). The NCCS is a highly productive but variable upwelling-driven system (Ware and Thomson, 2005) spanning the west coast of North America from central Oregon to southern British Columbia. In this system, a subarctic zooplankton (copepod) community is dominant in the offshore waters when the Pacific Decadal Oscillation (PDO) is in its negative phase and a cold, productive water mass from the Gulf of Alaska is transported equatorward into the region (Bi et al., 2011; Keister et al., 2011; Liu et al., 2015). The movement of this subarctic water mass results from southward wind stress, created by an increase in the intensity of the North Pacific High and a decrease in the intensity of the Aleutian Low (Keister et al. 2011; Fisher et al., 2015). Conversely, when the PDO is in its positive phase, there is a poleward flow of warm, less productive water from the south, and an entrained community of southern zooplankton is transported into the NCCS (Batten and Walne, 2011; Keister et al., 2011).

In the North Pacific Ocean, zooplankton species with southern biogeographic affinities tend to be small-bodied and lipid-poor relative to northern species, which require large body size and large lipid reserves to support spawning and overwintering in cold water (Lee et al., 2006). As a result, the quality of prey available near the base of the food webs of the NCCS tends to be lower when the PDO is in its positive (warm) phase, and this is expected to have demographic consequences for marine predators (Mackas et al., 2007; Keister et al., 2011). The negative consequences may be exacerbated by the fact that primary producers in general tend to produce fewer essential fatty acids in warmer water, further reducing prey quality at the base of the food web (Hixson and Arts, 2016). That link between basin-scale oceanographic processes and prey quality at low trophic levels of the NCCS is often invoked to explain temporal variation in recruitment of Pacific salmon *Oncorhynchus* spp., iconic predators of immense ecological, cultural and commercial value in this system (Mantua et al., 1997; Malick et al., 2015). However, it has proven difficult to elucidate the mechanistic, step-by-step processes involved in driving recruitment variation (Hertz et al., 2016, Kilduff et al., 2015).

Colonial seabirds are often employed as sentinel proxies to gauge the broader, ecosystem-wide consequences of variation in ocean climate (Aebischer et al., 1990; Thompson and Ollason, 2001). They can be effective in this important role, provided inference is made appropriately (Durant et al., 2009), because most species are relatively easy to observe and to capture, thus enabling researchers to measure a broad suite of morphological, behavioural, physiological and demographic traits (Cairns, 1987; Piatt et al., 2007). As central-place foragers (Orians and Pearson, 1979), colonial seabirds provide information about the environmental conditions they experience within a more-or-less defined area around breeding colonies.

Cassin's Auklet (*Ptychoramphus aleuticus*) is a small (~190 g), highly colonial, burrow-nesting, zooplanktivorous seabird, and one of a small number of seabirds that can be considered characteristic of the California Current System (CCS) (Ainley et al., 2011). Across the CCS, foraging environments for Cassin's Auklets range from seasonally variable, high-productivity environments in the north to aseasonal, low-productivity environments in the south, although basin-scale climatic processes tend to homogenize oceanographic conditions system-wide to some degree (Wolf et al., 2009). Reflecting their potential value as ecosystem indicators for the CCS (Hazen et al., 2019), the number of starved, post-fledging, juvenile and adult Cassin's Auklet carcasses recovered on beached bird surveys from California to southern British Columbia in the fall and winter over 15 years (2001–2015) correlated positively with the relative abundance of southern copepods taken in zooplankton tows off the northern Oregon coast, and correlated negatively with the relative abundance of northern copepods (Jones et al., 2018). Those observations suggest the existence of a consequential mechanistic link between prey quality and demographic processes in a zooplanktivorous predator in the CCS.

Long-term research at a Cassin's Auklet breeding colony on the Farallon Islands, off northern California in the Central CCS, showed that the El Niño-Southern Oscillation index (ENSO) was the dominant mode of climatic variation affecting the birds' productivity from 1971 to 1995; but that the North Pacific Gyre Oscillation index (NPGO) was more influential thereafter (Schmidt et al., 2014). At that southerly colony, the euphausiids *Thysanoessa spinifera* and *Euphausia pacifica* are the most important prey fed to nestlings (Ainley et al., 1996; Abraham and Sydeman, 2004). However, the majority (~70%) of the global population of Cassin's Auklet breeds further north, on several large colonies scattered along British Columbia's outer coast (Rodway and Lemon, 2011). Triangle Island, located at the northern extreme of the CCS and within the Transition Zone with the Alaska Current System (Cummins and Freeland, 2007), supports the world's largest colony of several hundred thousand pairs. There, Cassin's Auklets breed most successfully when the primary prey fed to nestlings is late-stage (C4 and C5) *Neocalanus cristatus* copepodites (Vermeer, 1985; Hedd et al., 2002). *N. cristatus* is one of the diagnostic copepods of the North Pacific Ocean's 'Subarctic' zooplankton community (Miller et al., 1984), which predomintes in the NCCS in cold-water, PDO-negative years (Keister et al., 2011; Liu et al., 2015). In addition, temperature-dependent rates of development and survival dictate that the period when late-stage *Neocalanus* copepodites are resident in near-surface waters is later and more prolonged in cold years (Mackas et al., 1998), and thus better aligned temporally with the period when Cassin's Auklets are provisioning offspring (Bertram et al., 2001; Hipfner, 2008). While provisioning, the auklets forage for *N. cristatus* in deep, cold, oceanic water along and seaward of the continental shelf break, typically 50–100 km to the west of Triangle Island (Bertram et al., 2017; Domalik et al., 2018).

In this paper, we combine results of systematic annual zooplankton tows with annual studies of nestling diet and growth on Triangle Island over a 22-year period (1996–2017) to test the hypothesis that variation in the biogeographic affinity of the local zooplankton community, driven by variation in oceanographic conditions associated with the state of the PDO, exerts primary influence on Cassin's Auklet diet and productivity. To facilitate comparison with results from the Farallon Islands, we also examine variation in the auklets' diet and productivity on Triangle Island in relation to the ENSO (Multivariate ENSO Index, MEI) and NPGO indices. Responses of the zooplankton community of the NCCS to MEI are generally similar to the responses to the PDO, i.e., the community is more northerly when MEI is in its negative, cold-water phase (La Niña) than its positive, warm-water phase (El Niño) (Hooff and Peterson, 2006). But the MEI varies at higher frequency than the PDO and its biological effects are less consistent (Fisher et al., 2015). The ENSO and PDO indices also tend to correlate positively, although El Niño events can occur even when PDO is in its negative phase (Verdon and Franks, 2006). As for the NPGO, when this climatic mode is in its positive phase, there is an earlier onset of upwelling in the CCS and the planktonic ecosystem is more productive through the spring and summer as a result (Di Lorenzo et al., 2008; Chenillat et al., 2012).

## 2. Methods and materials

### 2.1. Zooplankton surveys

The sampling and analytical methods used to characterize inter-annual variation in the biomass anomalies of the zooplankton community are the same as those employed by Mackas et al. (1998) and Mackas et al (2001). The Northern Vancouver Island (NVI) lines provide the best representation of the preyscape available to Cassin's Auklets breeding on Triangle Island (Fig. 1). Time-series sampling along these lines began in 1990, and spanned the entire 22-year period (1996–2017) of the study. The NVI lines were run twice per year, but the dates varied from year to year: the first run occurred between late April and early June, the second in August or early September. On all

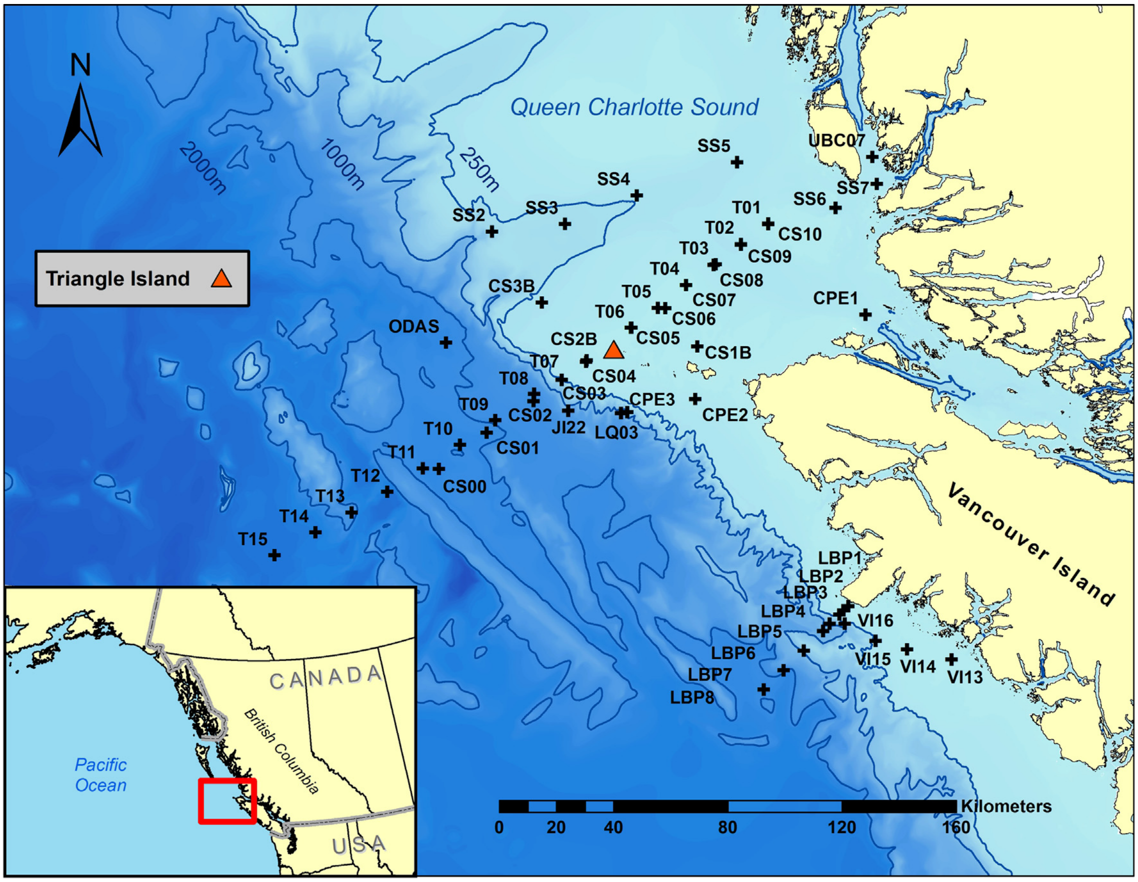

**Fig. 1.** Map of the southern British Columbia coast showing the locations of the zooplankton sampling stations along the Northern Vancouver Island transect line. The location of Triangle Island, site of the world's largest Cassin's Auklet breeding colony of several hundred thousand pairs, is indicated by the red star. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

surveys, vertically-integrated zooplankton biomass and abundance were estimated from the catch of flow-metered bongo nets of 0.56 m diameter fitted with 0.23 mm mesh. Most ($>$ 90%) of the samples were vertical net hauls, from 250 to 0 m where bottom depth exceeded 250 m, and near-bottom-to-sea-surface elsewhere. The samples were classified by depth and cross-shore location into "offshore" (bottom depth $>$ 200 m) and "shelf" (bottom depth $<$ 200 m) subregions. Because provisioning auklets forage mainly seaward of the shelf break, over deep, cold water (Domalik et al., 2018), we used results from the "offshore" stations along the NVI lines to correlate against climate indices and Cassin's Auklet diets.

Zooplankton samples collected on the surveys, preserved in 10% buffered formalin in seawater, were returned to shore for identification and enumeration to species and size or developmental stage (down to the retention level of the net mesh). All zooplankton enumeration was done at the Institute of Ocean Sciences, Sidney, B.C., by M. Galbraith. Abundance and biomass were estimated for more than 50 zooplankton species in the NVI tows. Seasonal variation is intense and somewhat repeatable across years; because sampling dates varied from year to year, simple annual averages confound seasonal with interannual differences. We dealt with this by estimating a multi-year average seasonal cycle (= "climatology"), and used the climatology as a baseline against which to compare monthly conditions during any single year. To describe interannual variability, a $\log_{10}$-scale biomass anomaly (in g m$^{-3}$ of seawater) for each species and for each month sampled was calculated within each year, and then the monthly anomalies were averaged to give an annual anomaly (Mackas et al., 2001). Because the anomalies are $\log_{10}$ scale they are multiplicative on a linear scale: an anomaly of $+1$ for a given taxon means that taxon had 10x higher biomass than in the climatology; an anomaly of $-1$ means the biomass was 1/10th the climatology. Following Mackas et al. (2001), the log-scale anomaly estimates for euphausiids were corrected for differences in catch ratios in day (lower) vs. night (higher) zooplankton tows using the formula $-d'\log10c$, where $c$ is the day:night catch ratio for a given euphausiid taxon, and $d'$ is the difference in fraction of daylight samples between the observation period and the corresponding climatology. In previous studies, the raw and corrected values for euphausiids correlated very strongly ($r = 0.91$), and total ranges, interannual patterns, and environmental correlations were very similar (Mackas et al., 2001; Mackas et al., 2004).

Because time series anomalies of zooplankton species with similar zoogeographic ranges and ecological niches tend to be very similar, the interannual variability of multiple species are also averaged within species groups to characterize the relative abundance of zooplankton with different biogeographic affinities present in each year. Thus 'Southern copepods' is a composite of *Paracalanus parvus*, *Mesocalanus tenuicornis*, *Clausocalanus* spp., *Calocalanus* spp. and *Ctenocalanus vanus*, species that are most abundant in the Southern CCS and/or further offshore in the North Pacific Central Gyre; 'Boreal shelf copepods' is a composite of the copepods *Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis*, which are normally most abundant on the continental shelf from central Oregon to the Bering Sea; and 'Subarctic oceanic copepods' is a composite of *Neocalanus cristatus, N. plumchrus*, and *Eucalanus bungii*, species that are most abundant seaward of the continental shelf throughout the subarctic Pacific Ocean (Mackas et al., 2004).

### 2.2. Seabird parameters

We quantified Cassin's Auklets nestling diets and breeding parameters in West Bay on Triangle Island, British Columbia, Canada (50°52′N, 129°05′ W), in each year from 1996 to 2017 (Fig. 1). In a typical year, most auklets breeding on Triangle Island lay their single-egg clutch in the first half of April, the peak of hatching occurs in mid-May, and most pairs complete breeding (i.e., fledge their chick) by the end of June or early July. After the breeding season, the auklets disperse widely across the northeastern Pacific Ocean, and in the winter individuals that breed on large colonies in British Columbia (Triangle, Frederick islands) can be found from Baja California to the Gulf of Alaska (Studholme et al., 2019). The majority spend winter within the CCS, however, and all have returned back to the vicinity of the colony by March.

Methods used to study interannual variation in growth rates of nestling Cassin's Auklets through the entire period of this study, gauged by the annual mean mass at 25 days old, were the same as those employed by Jones et al. (2018). Note that mean egg mass, thus initial chick mass, varies little from year to year (Hipfner et al., 2010). In 1996–2009, the mass of chicks of known age ($n = 14$–$88$ chicks per year) was measured directly when they were 25 days post-hatching. In 2010–2017, when burrows were not monitored from the start of egg-laying, the sample was made up of chicks of unknown age ($n = 15$–$38$ chicks per year) that had their mass and wing length measured in the middle of the chick-rearing period in early June. To derive an estimate of mean mass at 25 days, which approximates the end of the linear phase of mass gain (Hedd et al., 2002), mass (y) was regressed on wing length (x) for all chicks measured in each year, and the linear formula relating those measures used to calculate mass for a wing length of 77 mm, the average for a 25-day old nestling on Triangle from a previous study (Hedd et al., 2002). Because growth of the wings is a developmental priority for nestling auks (Øyan and Anker-Nilssen, 1996; Morrison et al., 2009), wing length at a given age is much less sensitive to variation in food intake than is mass at a given age, and the regression technique has proven to be robust (Gaston et al., 1983; Bertram et al., 2002).

Methods used to quantify interannual variation in the diets fed to Cassin's Auklet nestlings were the same as employed previously (Bertram et al., 2001; Hipfner, 2008). Adult auklets returning to the colony to deliver food to nestlings were captured soon after the onset of darkness (most between 2310 and 0030 h), either in pheasant nets erected between 2 large poles, or by hand on the ground. Provisioning auklets carry their zooplankton prey in a sublingual pouch, and upon capture, we gently massaged the pouch to induce the bird to regurgitate a sample of its food load through a funnel into a small, preweighed, screw-top plastic bottle (n = 931 samples in total, 14–50 samples per year). When possible, the birds were then released to deliver any remaining food to their nestlings, otherwise they were released seaward. Back at the research station, the bottle-plus-contents was re-weighed and then filled with 10% buffered formalin in seawater. Diet sampling in each year spanned 4–6 weeks, from mid-May to late June, the period when most Cassin's Auklets are provisioning nestlings on Triangle Island.

In the laboratory, regurgitated samples were transferred to stacked sieves and rinsed repeatedly with water to remove preservative. Individual items present in subsamples were identified to the lowest possible taxonomic level (usually species, especially for common items), enumerated, blotted dry, and weighed on an electronic balance. As with the zooplankton tows, prey species in Cassin's Auklet diets were enumerated by M. Galbraith in the lab at IOS.

### 2.3. Statistical analyses

We first examined how the three basin-scale oceanographic variables (PDO, MEI, and NPGO) influenced the annual biomass anomalies of the 'Subarctic', 'Boreal' and 'Southern' zooplankton (copepod) communities captured at offshore stations between 1996 and 2017 using three multiple regression models. We report the variation explained by the three indices combined, the significance of the full model, and the significance of each index.

We characterized the food loads delivered to nestlings by grouping prey items into six categories: copepods, euphausids, amphipods, decapods, larval fish and other, calculating the proportion of each based on the wet biomass of the prey items. We then used a Principal Components Analysis to describe the variation in the prey composition of individual food loads. Each individual food load was treated as an independent and equal sample, regardless of its mass or completeness. We used average principal component scores to describe annual variation in the diets of nestlings (see van Donk et al. (2017) and Stalwick and Wiebe (2019) for use of this statistical approach for quantifying diets in birds). We then used a series of multiple regression models to examine (1) how the three basin-scale oceanographic variables (PDO, MEI, and NPGO) influenced annual variation in the prey composition of food loads (average PC1 and PC2 scores), and (2) how annual variation in the diet of nestlings influenced mean nestling mass when 25 days of age. In these multiple regression models we again report the variation explained by the full model containing either the three indices or the two principal component scores, the significance of the full model, and the significance of each variable in the model.

We used residual and autocorrelation function plots to assess the potential for temporal autocorrelation in annual biomass anomalies ('Subarctic', Boreal' and 'Southern' zooplankton), diet (PC1 and PC2) and nestling mass. Residual plots showed no temporal pattern and partial autocorrelation values with lags of 1–20 years were all low and non-significant. We therefore did not account for temporal autocorrelation in these regression models.

We retrieved data on the NPGO from http://www.o3d.org/npgo/, and on the PDO and MEI from https://www.esrl.noaa.gov/psd/data/climateindices/list/. We used these data to calculate the average PDO, MEI and NPGO for 1 October to 31 March. Those 6 months roughly span the period from the end of fall migration to the start of egg-laying for Cassin's Auklets breeding on colonies in British Columbia (Studholme et al., 2019). That 6-month window also accommodates lags of up to 8 months that are typical between climatic indices and zooplankton responses in the NCCS (Hooff and Peterson, 2006; Fisher et al., 2015; Liu et al, 2015).

## 3. Results

### 3.1. Oceanographic influences on the zooplankton community

Over the 22-year study period (1996–2017), the biomass of each of the 'Southern', 'Boreal' and 'Subarctic' zooplankton (copepod) communities captured at offshore stations in tows along the Northern Vancouver Island lines varied by almost an order of magnitude, i.e., 1.0 units of biomass anomaly (Fig. 2). The three basin-scale oceanographic variables (PDO, MEI and NPGO over the preceding 1 October to 31 March period), combined, explained 40% of the variation in biomass anomalies of the "Subarctic" group of copepods in the tows ($R^2 = 0.40$, $F_{3,18} = 4.06$, $p = 0.02$). Biomass anomalies of the 'Subarctic' group were negatively related to the PDO ($F_{1,18} = 7.73$, $p = 0.01$) (Fig. 3), but unrelated to the MEI ($F_{1,18} = 0.40$, $p = 0.53$) and NPGO ($F_{1,18} = 0.74$, $p = 0.40$). That same pattern exhibited by the 'Subarctic' copepod group held for *N. cristatus* alone ($R^2 = 0.58$, $F_{3,18} = 8.14$, $p = 0.001$; for PDO, $F_{1,18} = 9.50$, $p = 0.006$, for MEI, $F_{1,18} = 0.76$, $p = 0.39$; and for NPGO, $F_{1,18} = 2.78$, $p = 0.11$).

In contrast, the three basin-scale oceanographic variables explained little of the variation in biomass anomalies of the 'Boreal' group of copepods ($R^2 = 0.16$, $F_{3,18} = 1.18$, $p = 0.37$; for PDO, $F_{1,18} = 2.75$, $p = 0.11$, for MEI, $F_{1,18} = 0.47$, $p = 0.50$; and for NPGO, $F_{1,18} = 0.43$, $p = 0.52$). However, the three basin-scale oceanographic variables explained 81% of the variation in biomass anomalies of the 'Southern' group of copepods ($R^2 = 0.81$, $F_{3,18} = 24.79$, $p < 0.001$). Biomass anomalies of the "Southern" group were negatively related to the PDO

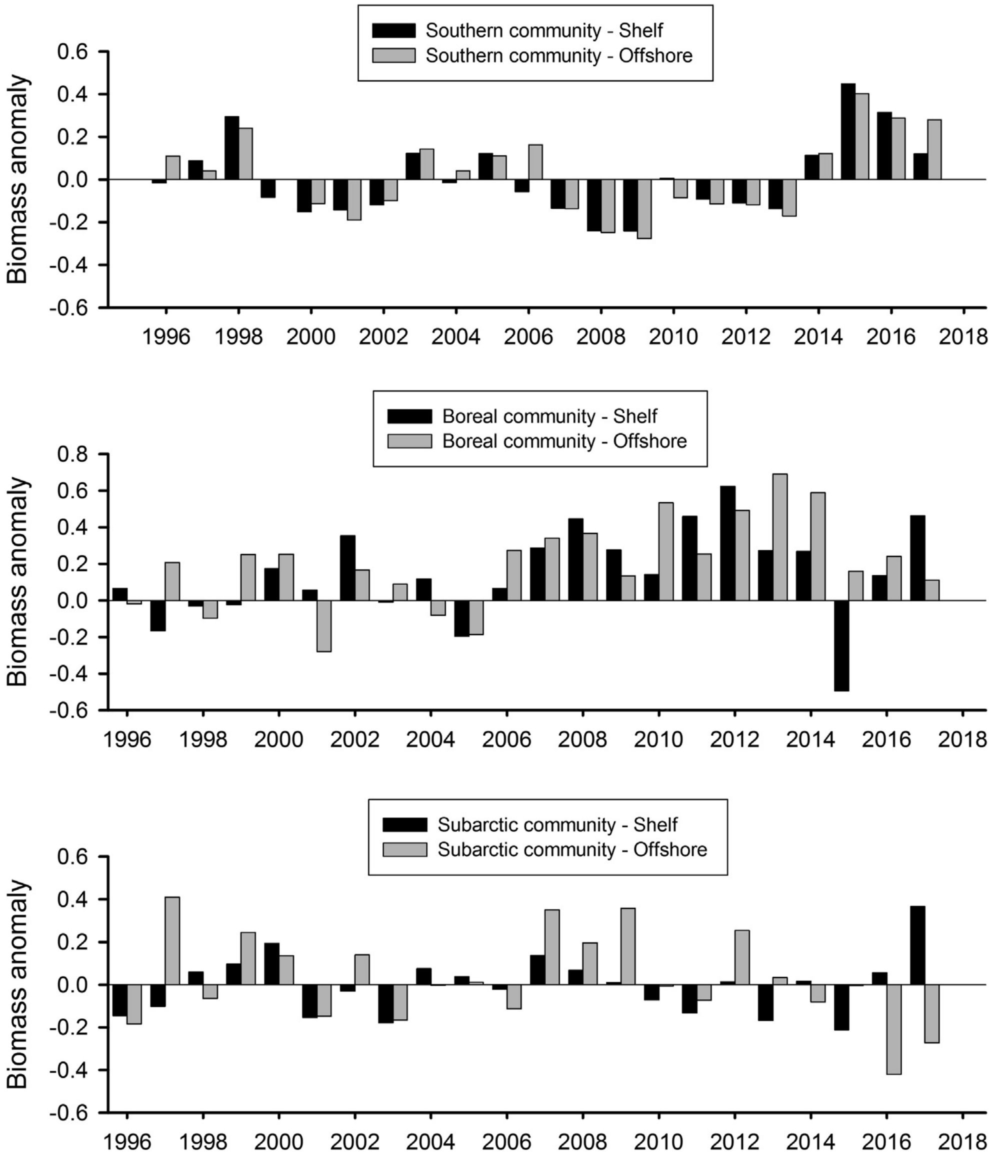

**Fig. 2.** Biomass anomalies (in g m$^{-3}$ of seawater) in continental shelf and offshore waters of each of the Northeastern Pacific Ocean's 'Southern' (top panel), 'Boreal' (middle panel), and 'Subarctic' (bottom panel) zooplankton (copepod) communities present in the zooplankton tows along the Northern Vancouver Island line in 1996–2017.

($F_{1,18} = 25.06$, $p < 0.001$) and NPGO ($F_{1,18} = 7.95$, $p = 0.01$), but unrelated to the MEI ($F_{1,18} = 0.68$, $p = 0.42$).

### 3.2. *Oceanographic influences on the diets fed to Cassin's Auklet nestlings*

Like the zooplankton community from which it was drawn, there was marked interannual variation in the composition of diets delivered to nestling Cassin's Auklets on Triangle Island over the 22 years of study (Fig. 4). In terms of biomass, the diet was dominated by two groups: ~40% copepods on average (annual range ~15–70%,), and ~35% euphausiids on average (annual range ~10–75%); by number, food loads consisted of ~56% copepods and ~28% euphausiids on average. A total of 28 species of copepods was recorded, the majority (18) in just a single year each, but almost all of the copepod biomass (> 99%) was comprised of just one species, *N. cristatus*. A maximum of eight species of copepods was recorded in any single year, with one exception: in 1998, which featured the strongest El Niño event during the period of this study, 16 species of copepods were included in diets, ten of them only in 1998. In terms of zoogeographic affinities, diets included two 'Subarctic' copepods (*N. cristatus* in all years, *N. plumchrus* in nine years), all three 'Boreal' copepods (*Calanus marshallae* in 10 years, *Pseudocalanus mimus* and *Acartia longiremis* in three years each), and five 'Southern' copepods (*Mesocalanus tenuicornis* in 1996*, Paracalanus parvus, Calocalanus styliremis,* and *Clausocalanus lividus* in 1998, and *Clausocalanus arcuicornis* in 2016).

The auklets' diets also included a total of five species of euphausiids, but almost all of the euphausiid biomass (> 98%) was comprised of just three species: *T. spinifera*, *T. inspinata*, and *E. pacifica*. All three of those euphausiids were recorded in all 22 years of study, except that *E. pacifica* was absent in 2016. The other euphausids recorded were *T. gregaria*, which was present in six years (2003–2006, 2016, and 2017), and *Nematocellis difficilis*, present only in 2002. Both of these euphausiids are more representative of the warmer waters of the Central and Southern CCS and the North Pacific Gyre (Brinton, 1962; Brinton and Townsend, 2003). Decapods (average 3%), amphipods (average 2%) and larval fish (average 12%) made up the bulk of the rest of the diets. Among the larval fish, only *Sebastes* spp. was present in all years.

The Principal Components Analysis varied along two primary axes that described 87.9% of the variation in individual food loads. The first principal component (PC1) describes variation on a copepod vs.

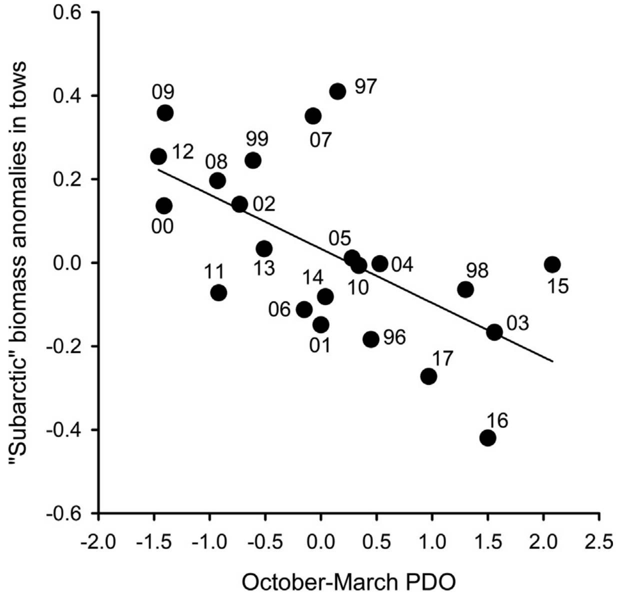

**Fig. 3.** Biomass anomalies (in g $m^{-3}$ of seawater) for the 'Subarctic' zooplankton community in zooplankton tows at offshore stations along the Northern Vancouver Island line in relation to the Pacific Decadal Oscillation in the preceding 1 October to 31 March period in 1996–2017.

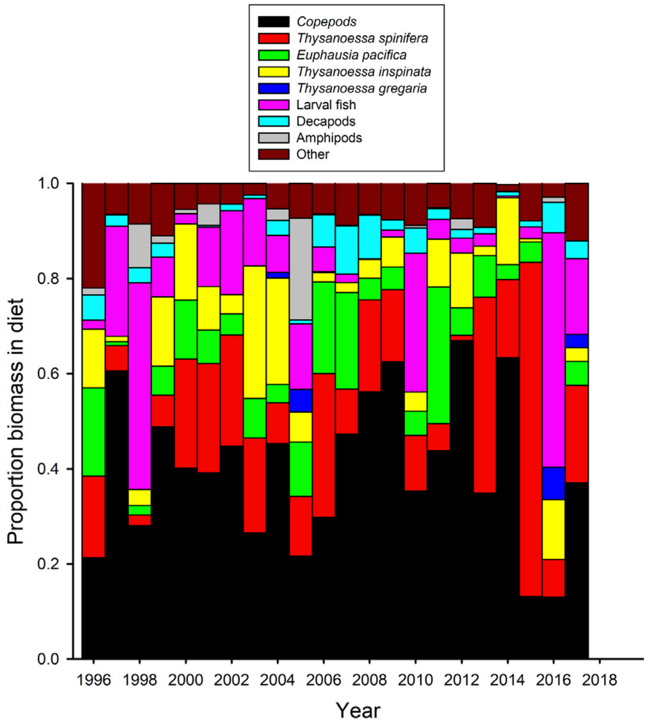

**Fig. 4.** Annual variation in the diets fed to nestling Cassin's Auklets on Triangle Island, British Columbia in 1996–2017. All 931 individual food loads collected (14–50 per year) were weighted equally, regardless of their size or completeness. Note that the 'Subarctic' copepod *Neocalanus cristatus* made up virtually all (> 99%) of the copepod biomass included in diets.

euphausiid axis with more negative scores being associated with more copepods (almost entirely *Neocalanus cristatus*). The second principal component (PC2) describes variation on a copepods-plus-euphausiids vs. larval fish axis, with more negative scores being associated with more copepods-plus-euphausiids and less larval fish (Table 1).

**Table 1**
Loadings and variance explained by the first two principle components describing the prey composition of food loads fed to nestling Cassin's auklets on Triangle Island between 1996 and 2017.

| Prey type | PC1 | PC2 |
|---|---|---|
| Copepods | −0.755 | −0.374 |
| Euphausiids | 0.651 | −0.531 |
| Amphipods | 0.014 | 0.068 |
| Decapods | 0.006 | 0.060 |
| Larval Fish | 0.082 | 0.755 |
| Other | 0.002 | 0.021 |
| Variance explained (%) | 56.1 | 31.9 |
| Cumulative variance explained | – | 88.0 |

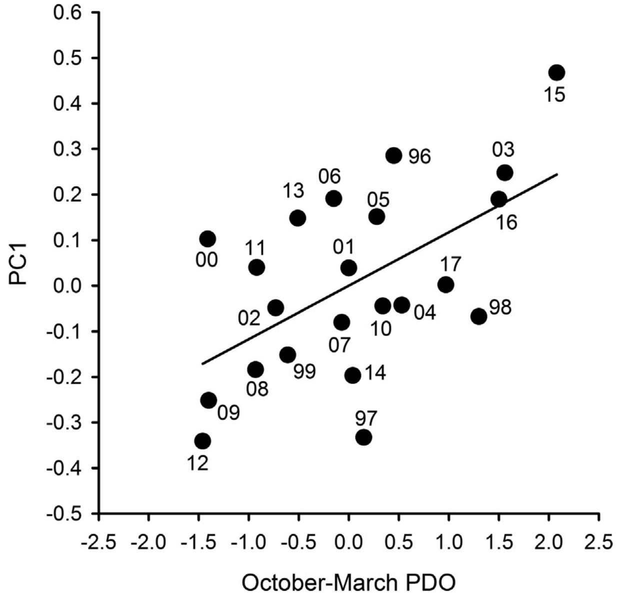

**Fig. 5.** Mean annual PC1 scores, which describe variation on a copepod vs. euphausiid axis, for diets fed to nestling Cassin's Auklets on Triangle Island, British Columbia, in relation to the Pacific Decadal Oscillation in the preceding October to March period in 1996–2017.

Combined, the PDO, MEI and NPGO over the preceding period from 1 October to 31 March explained 39% of the annual variation in the average PC1 scores ($F_{3,18} = 3.86, p = 0.03$). Average PC1 scores were positively related to the PDO ($F_{1,18} = 9.19, p = 0.007$), but unrelated to the MEI ($F_{1,18} = 1.55, p = 0.23$) and the NPGO ($F_{1,18} = 0.47$, $p = 0.50$). PDO alone explained 33% of the annual variation in the average PC1 score ($R^2 = 0.33, F_{1,20} = 9.73, p = 0.005$) (Fig. 5), indicating that there was greater biomass of copepods and lower biomass of euphausiids in Cassin's Auklet nestling diets when the PDO was in its cold-water, negative phase. PC1 was also negatively related ($R^2 = 0.37$, $F_{1,20} = 11.73, p = 0.002$) to the biomass anomaly of *N. cristatus* in the NVI zooplankton tows (Fig. 6), but not to the biomass anomalies of any of the three primary euphausiid prey in the tows ($R^2 = 0.06$ for *T. spinifera*, 0.02 for *T. inspinata*, and 0.09 for *E. pacifica*, all $p > 0.15$).

The three oceanographic variables, PDO, MEI and NPGO, combined, explained 55% of the annual variation in the average PC2 scores ($F_{3,18} = 7.29, p = 0.002$). Average PC2 score were positively related to the MEI ($F_{1,18} = 15.05, p = 0.001$), but unrelated to the PDO ($F_{1,18} = 1.13, p = 0.30$) or NPGO ($F_{1,18} = 0.02, p = 0.90$). MEI alone explained 53% of the annual variation in the average PC2 score ($F_{1,20} = 22.55, p = 0.0001$) (Fig. 7) indicating that there was greater biomass of zooplankton (copepods + euphausiids) and lesser biomass of larval fish in nestling diets when MEI was in its cold-water, negative phase (i.e., La Niña). That positive relationship was largely driven by the two strongest El Niño events, 2016 and 1998, two years in which larval fish made up nearly 50% of the diets fed to Cassin's Auklet

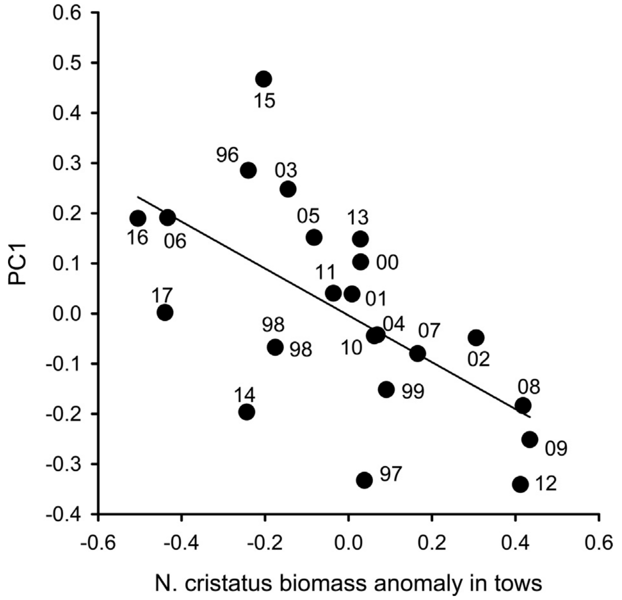

**Fig. 6.** Mean annual PC1 scores, which describe variation on a copepod vs. euphausiid axis, for diets fed to nestling Cassin's Auklets on Triangle Island, British Columbia, in relation to the biomass anomaly of *Neocalanus cristatus* in zooplankton tows at offshore stations along the Northern Vancouver Island line.

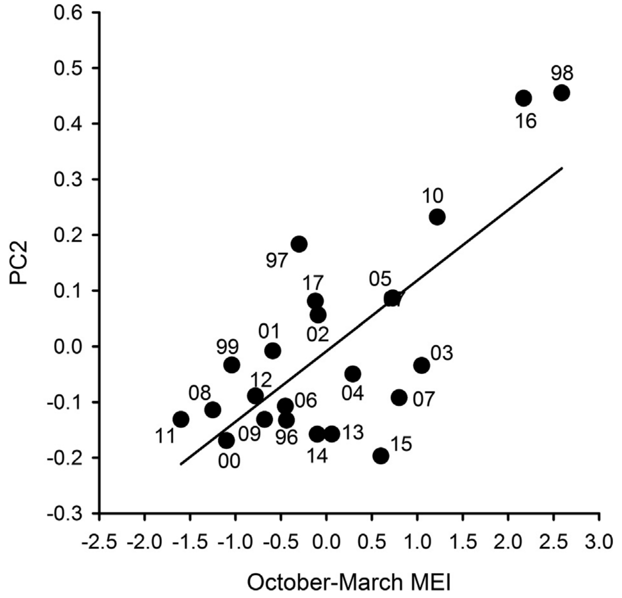

**Fig. 7.** Mean annual PC2 scores, which describe variation on a copepod-plus-euphausiid vs. larval fish axis, for diets fed to nestling Cassin's Auklets on Triangle Island, British Columbia, in relation to the Multivariate ENSO Index in the preceding October to March period in 1996–2017.

nestlings (Fig. 4).

### 3.3. Annual variation in the growth of Cassin's Auklet nestlings

The mean mass of nestling Cassin's Auklets at 25 days of age varied by a factor of nearly 2 among years (~80–150 g). Nestling diet (annual average PC1 and PC2 scores combined) explained 39% of the variation in annual mean nestling mass ($R^2 = 0.39$, $F_{2,19} = 6.19$, $p = 0.009$). Mean mass at 25 days of age was negatively related to the average PC2 score (Fig. 8; $F_{1,19} = 9.90$, $p = 0.005$), indicating that nestlings grew more quickly when their diets included more copepods-plus-euphausiids and less larval fish. Mean mass at 25 days of age also tended to be negatively related to the average PC1 score (Fig. 8; $F_{1,19} = 3.56$, $p = 0.07$), suggesting that nestlings also grew more quickly in years in which their diets were richer in copepods and poorer in euphausiids. That latter relationship is strengthened ($F_{1,18} = 6.38$, $p = 0.02$) with the exclusion of the data from 2010, an extreme data point in the 22-year dataset and a year in which few chicks survived to fledge.

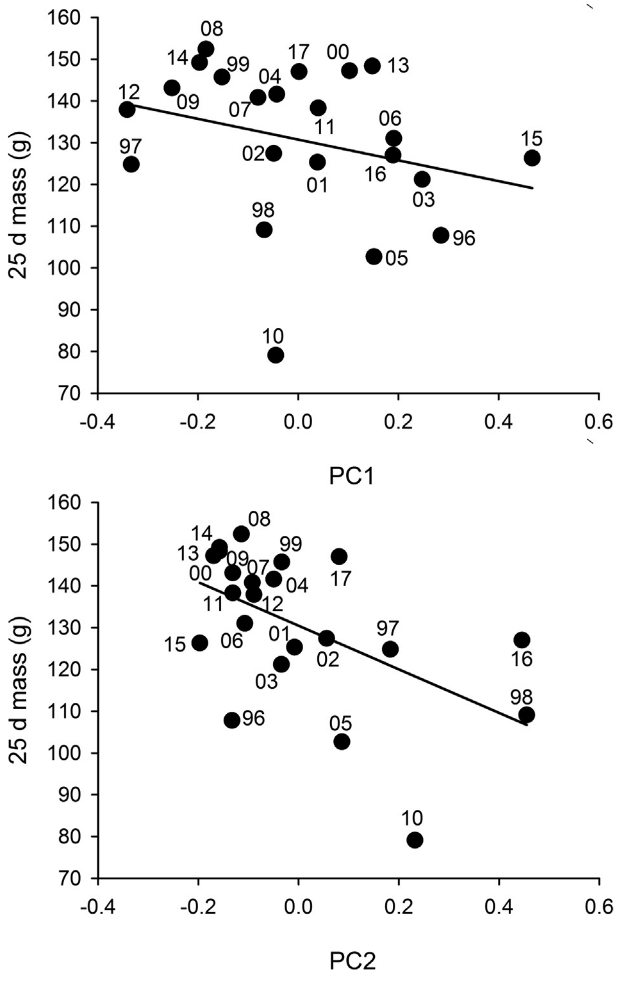

**Fig. 8.** Growth rates of nestling Cassin's Auklets (indexed by mass at 25 d of age) on Triangle Island, British Columbia in relation to diets as gauged by Principal Components analysis. PC1 describes variation on a copepod vs. euphausiid axis; PC2 describes variation on a copepod-plus-euphausiid vs. larval fish axis.

## 4. Discussion and conclusions

### 4.1. Oceanographic influences on the zooplankton community

As found in previous studies (Mackas et al., 2001), the biogeographic affinity of the zooplankton community present in waters of the Northern California Current System off the coast of British Columbia, Canada, exhibited substantial variation over the 22-year period of this study. Much of the variation could be attributed to basin-scale oceanographic processes. The relationship with the Pacific Decadal Oscillation was strongest: a suite of copepods representative of the North Pacific Ocean's 'Subarctic' zooplankton community (Miller et al., 1984) was more abundant in offshore waters in cold-water, PDO-negative years, while a suite of copepods representative of the 'Southern' zooplankton community was less abundant. Neither the MEI nor the NPGO had significant relationships with the relative abundance of the 'Subarctic' group, but the 'Southern' zooplankton group also was less abundant in NPGO positive years. None of the PDO, MEI or NPGO influenced the abundance of the 'Boreal' zooplankton community present in offshore waters.

A strong relationship between 'Subarctic' copepods and the PDO was expected, because in PDO-negative years, elevated southward wind stress moves a cold, subarctic water mass equatorward into the Northern California Current System (Fisher et al., 2015). 'Subarctic' copepods are advected within this water mass (Bi et al., 2011; Keister et al., 2011; Liu et al., 2015), and in addition, slower development and elevated survival of *Neocalanus* copepods dictate that the period when late-stage copepodites are resident in near-surface waters is both later and more prolonged in cold years (Mackas et al., 1998). Low biomass of 'Southern' copepods in those PDO-negative years was also expected (Batten and Walne, 2011). But while a strong relationship between PDO and the biogeographic affinities of the zooplankton community was expected, the weak relationship observed with ENSO was not. Previous studies have found that El Niño events often result in concurrent increases in zooplankton with southerly biogeographic affinities and decreases in those with northerly affinities (Mackas et al., 2004). There are several possible explanations for the discrepancy. Notably, ENSO-associated changes in the zooplankton community of the NCCS can be dampened unless the ENSO event is strong (Fisher et al., 2015), the community responses tend to be weaker in the offshore waters than over the continental shelf (Mackas and Galbraith, 2002), and the responses tend to decline in strength toward the Transition Zone with the Alaska Current System (Mackas et al., 2004).

### 4.2. Oceanographic influences on diet and growth of Cassin's Auklet nestlings

Like the preyscape from which it was drawn, the composition of the diets fed to nestling Cassin's Auklets on Triangle Island was highly variable from year to year. In cold-water, PDO-negative years, the auklets delivered more copepod prey to nestlings, while at the same time delivering fewer euphausiids. Virtually all ($>$ 99%) of the copepod biomass was comprised of a single species, *Neocalanus cristatus*, a large-bodied, lipid-rich copepod, and one of the diagnostic species of the North Pacific Ocean's 'Subarctic' zooplankton community (Miller et al., 1984). As in earlier studies (Vermeer, 1985; Bertram et al., 2001), *N. cristatus* was the primary prey in this study, averaging 40% of the diet by mass in the 931 food loads collected over all 22 years; euphausiids – consisting largely (98%) of adults and juveniles of three species, *Thysanoessa spinifera*, *T. inspinata* and *Euphausia pacifica* – formed a nearly equal proportion (35%) of dietary biomass.

Mackas et al. (2001) noted that there was a mirror-image relationship between the relative abundance of two euphausiids (*T. spinifera, E. pacifica*) and the 'Subarctic" copepods off the coast of British Columbia through the 1990s. Therefore, the tendency for the auklets to trade-off between those two major prey types could have been a passive consequence of opposing patterns of availability over the range of PDO values. However, the evidence derived by comparing percentage biomass of *N. cristatus* and the three primary euphausiids in diets (prey selected) to their biomass anomalies in zooplankton tows (prey available) suggested that in trading-off between the two prey types, the birds were responding to variation in the abundance of copepods, not euphausiids. A previous study also found that Cassin's Auklets on Triangle Island increased their harvest of euphausiids late in warm-water years as the availability of *N cristatus* declined; in cold-water years, they continued to feed on *N. cristatus* (Hipfner, 2009). It appears then that Cassin's Auklets actively selected *N. cristatus* over euphausiids as prey to deliver to nestlings. Selection of *N. cristatus* over euphausiids appeared to have fitness benefits, because it resulted in faster growth rates.

Evidence from stable isotope analyses conducted over four years included in this study (2002–2005) suggested that the targetting of *N. cristatus* by Cassin's Auklets involves a change in foraging behaviour. While incubating eggs, at which time they had only themselves to feed, the adult auklets foraged in less $^{13}$C-depleted, presumably more neritic waters, but then shifted to more $^{13}$C-depleted, presumably more oceanic waters, when they had both themselves and their nestlings to feed (Hipfner et al., 2014). Least (*Aethia pusilla*) and Crested (*A. cristatella*) auklets, close relatives of Cassin's Auklet (Smith and Clarke, 2015), also changed prey types before vs. after their chicks hatched in three years, from diversified diets to diets dominated by single prey types: *Calanus finmarchicus* for Least Auklets, and *Thysanoessa* spp. for Crested Auklets (Bédard, 1969). GPS tagging studies could track these stage-specific changes in foraging habits, but have not yet been carried out on incubating Cassin's Auklets; the GPS tagging work completed to date does, however, complement 3 years of VHF radio-tagging (Boyd et al., 2008) in placing provisioning auklets in deep, cold water mainly seaward of the continental shelf break (Domalik et al., 2018).

It is striking nonetheless that *N. cristatus* comprised virtually all ($>$ 99%) of the copepod biomass delivered to nestling Cassin's Auklets, especially given how variable the representation of that copepod was in diets: as high as ~70% of total biomass in 2012 (the most PDO-negative year in this study), but as low as ~15% of biomass at the height of "The Blob" (Bond et al., 2015) in 2015 and during the strong El Niño event of 2016 (both strongly PDO-positive years). Large calanoid copepods dominate mesozooplankton biomass in the subarctic North Pacific Ocean (Mackas et al., 2007), yet two of the major co-occurring calanoids, the 'Subarctic' *N. plumchrus* and the 'Boreal' *Calanus marshallae*, present in diets in 9 and 10 of the 22 years respectively, were never present in more than trace amounts.

In the colder waters of the Bering Sea, all of *N. cristatus*, *N. plumchrus*, *N. flemingeri*, and *C. marshallae* can be important prey of provisioning Least Auklets (Springer and Roseneau, 1985; Hunt and Harrison, 1990; Dorresteijn et al., 2012), the other species especially in years when *N. cristatus* is less available (Gall et al., 2006). Temporal and spatial issues may be factors underlying the paucity of those other calanoids in Cassin's Auklet diets in the NCCS: compared to *N. cristatus*, *N. plumchrus* copepodites are resident in near-surface waters for a shorter period of time each year, and *C. marshallae* is more abundant over the continental shelf than in the offshore waters (Mackas and Coyle, 2005; Mackas et al., 2007). We propose that the singular focus on *N. cristatus* over other apparently suitable prey types explains why the majority (~70%) of the global population of Cassin's Auklets breeds on a small number of large colonies ($>$ 50,000 breeding pairs), including Triangle Island, scattered along British Columbia's outer coast (Rodway and Lemon, 2011). At these outer-coast colonies, the birds have easy access to waters seaward of the continental shelf break, where the 'Subarctic' copepods make up ~50–75% of total copepod biomass (Mackas et al., 2004). *N. cristatus* was the most important prey item in nestling diets at Frederick Island (Vermeer, 1985; Bertram et al., 2009), the only outer coast colony other than Triangle where diets have been examined.

While marine conditions associated with the phase of the PDO had the strongest relationship with the biogeographic affinity of the zooplankton community of the NCCS, and thus the prey available to and taken by Cassin's Auklets breeding on Triangle Island, there was a secondary influence of the MEI. Specifically, nestling diets included less *N. cristatus* and euphausiids but more larval fish when MEI was in its positive, warm-water phase (El Niño). Increased biomass of larval fish over zooplankton in diets was linked to lower offspring growth rates. That association between the MEI and nestling auklet diets was most apparent in the two years with the strongest El Niño conditions, 1998 and 2016, when larval fish made up nearly 50% of the biomass of diets, and copepods and euphausiids occurred at low or very low levels (euphausiids were nearly absent altogether in 1998). Several 'Southern' copepod species were taken by the auklets only in those years, and those same copepods also appeared in unusually large numbers in zooplankton tows conducted off the coast of British Columbia in 1998 (Zamon and Welch, 2005).

### 4.3. Regional comparison of oceanographic influences on Cassin's Auklet

One of the more interesting messages to emerge from our study concerns the contrasting manner by which basin-scale climatic processes influenced the productivity of a single species in different oceanic domains. Wolf et al. (2009) studied productivity of Cassin's Auklets at three colonies spanning the CCS (San Benito Island off Baja California, plus Farallon and Triangle islands) over six years (2000–2005) and found that local factors, especially sea-surface height, had the most pronounced effects on the birds' productivity; basin-scale climatic processes, specifically ENSO, served to homogenize productivity system-wide to some degree. We found that the primary mode of climatic influence differed between the latter two colonies: at Triangle Island, in the NCCS/Transition Zone, oceanographic conditions associated with the PDO and secondarily with the ENSO had the strongest influence on Cassin's Auklet diet and productivity, whereas at the Farallon Islands in the CCCS, ENSO (to the mid-1990s) and then NPGO (since the mid-1990s) were more influential (Schmidt et al, 2014). The contrast between the two colonies can be attributed to latitudinal differences in the prey base, and linked to ocean transport, temperature, and phenology.

The range of the 'Subarctic' copepods, including *N. cristatus*, extends further south during PDO negative years due to strong equatorward flow of a subarctic water mass into the NCCS (Keister et al., 2011; Bi et al., 2011; Liu et al., 2015). That, we have argued, combined with a longer seasonal period of residency in surface waters due to slower development and higher survival of *Neocalanus* copepodites in cold water (Mackas et al., 1998), accounts for the relationships between PDO and diet and productivity of Cassin's Auklets on Triangle Island. But the 'Subarctic' copepods were uncommon in the CCCS on surveys that ranged as far south as 39°N, including in two PDO-negative years (Batten and Walne, 2011). That latitude is north of the Farallon Islands (37°42′ N), where the PDO was found to have little influence on the auklets' productivity (Schmidt et al., 2014).

Rather than northern copepods, the euphausiids *T. spinifera* and *E. pacifia* are the primary prey of Cassin's Auklets in the Central and Southern CCS (Ainley et al., 1996; Sydeman et al., 2001). Those two euphausiids typically combine to form ~80% of nestling diets on colonies in California (Abraham and Sydeman, 2004; Adams et al., 2004; Manugian et al., 2015), where both ENSO and NPGO have strong effects on euphausiid populations. Positive ENSO conditions (i.e., El Niňo) are associated with weak coastal upwelling (Jacox et al., 2015), and the presence of a warm-water zooplankton community (Lilly and Ohman, 2018) with reduced abundance of cold-water euphausiids (Schroeder et al., 2014; Lindegren et al., 2018). Positive NPGO conditions are linked to a 1–2 month advance in the onset of upwelling, a more productive planktonic ecosystem through the spring and summer (Chenillat et al., 2012), and increased abundance of *T. spinifera* (Sydeman et al., 2013). *T. spinifera* is the primary prey for Cassin's Auklets at breeding colonies in California (Abraham and Sydeman, 2004; Adams et al., 2004). The effect of the NPGO on the timing of coastal upwelling is strongest south of latitude 38°N (Di Lorenzo et al., 2008), an area that includes waters around the Farallon Islands. Of note, both the variability and the influence of the NPGO have increased since the mid-1990s (Di Lorenzo et al., 2008; Sydeman et al., 2013), and that timing aligns with when that index began to exert strong influence on Cassin's Auklet productivity at the Farallones (Schmidt et al., 2014).

### 4.4. Conclusions

It is well established that climate-driven variation in the distribution, abundance and phenology of low trophic-level organisms can have cascading effects within marine food webs (Edwards and Richardson, 2004; Stenseth et al., 2004). Understanding these complex ecosystem dynamics is of vital importance, especially given ongoing climatic change. By quantifying a short chain of connected events over a multi-decadal time series (22 years) – from basin-scale oceanographic indices, to zooplankton community structure, to diet and productivity of a sentinel zooplanktivorous seabird, Cassin's Auklet – results of this correlational study provide mechanistic insights into ecological functioning within the offshore waters of the NCCS ecosystem. In particular, we highlight the importance of the large-bodied, lipid-rich, 'Subarctic' copepods to predators in the NCCS (Mackas et al., 2007; Liu et al., 2015). Future work should investigate how and to what extent oceanographic variation affects physiological processes in primary producers that determine their quality as prey to primary consumers – in particular the production of essential fatty acids (Miller et al., 2017). Our study also provides insight into the utility of seabirds as indicators of ecosystem processes in the NCCS.

Looking forward, projections from recent climate models indicate that increased coupling between the NPGO and PDO could lead to future increases in the magnitude and persistence of prolonged, multi-year marine heatwaves in the northeastern Pacific Ocean (Di Lorenzo and Mantua, 2016; Joh and Di Lorenzo, 2017). One such event, "The Blob" (Bond et al., 2015), resulted in widespread, mass mortality of hundreds of thousands of Cassin's Auklets in the fall and winter of 2014–2015 (Jones et al., 2018), and negatively affected productivity of the large aggregation of auklets breeding on Triangle Island. Other models predict that the frequency of extreme El Niňo events will increase in the future (Cai et al., 2014; Wang et al., 2017; Cai et al., 2018), and the two strongest El Niňo events during this study, in 1998 and 2016, had marked effects on diet and productivity of Cassin's Auklets on Triangle Island. Adult survival rates were also markedly reduced as a result of the 1998 event (Bertram et al., 2005; Morrison et al., 2011). One other recent climate model predicted that a warming ocean will drive declines in zooplankton density in pelagic ecosystems of the North Pacific Ocean through the 21st century, with concomitant declines in the carrying capacity of this marine system for predators (Woodworth-Jeffcoats et al., 2017). Should projections such as these play out, we can expect that there will be severe consequences not just for seabirds, including Cassin's Auklets, but for the structure and function of the entire marine ecosystems of the North Pacific Ocean.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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