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Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations

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ABSTRACT: We report on historical (1978 to 1982) and more recent (1996 to 2000) variation in the nestling diet of Cassin's auklet *Ptychoramphus aleuticus* breeding at Triangle Island (southern) and Frederick Island (northern), British Columbia, Canada; these islands are influenced by the California and the Alaska Current ecosystems, respectively. Ocean climate conditions off the British Columbia coast varied tremendously between 1978 and 2000. At both colonies, the nestling diet was composed largely of copepods and euphausiids, with fish contributing substantially in some of the warmer years at Triangle Island. The copepod *Neocalanus cristatus* was the single most important prey item at both colonies, and Stage V copepodites dominated in all sampling periods. We used a recently published temperature-dependent phenology equation to estimate the timing of peak biomass of *Neocalanus* near Triangle and Frederick Islands. During warm water years (such as 1996 and the El Niño of 1998), the timing and duration of *N. cristatus* availability in surface waters near Triangle Island was early and limited (mismatched) in contrast to cooler years (such as 1999 and 2000), when this prey was available to birds throughout the breeding season (matched). We argue that Cassin's auklet nestling diet data reflect the temperature-related timing of *Neocalanus* prey availability to seabirds in surface waters. Our results support the argument that inadequate overlap of prey availability and predator breeding (i.e. temporal trophic mismatch) is more likely on Triangle Island, where zooplankton peaks often occur earlier and are narrower, than on Frederick Island, where prey peaks are later and more protracted. Poor reproductive performance is the biological consequence of such trophic mismatch for Cassin's auklet. If the frequency of El Niño-like events increases and if ocean temperatures rise in the future, we predict an increase in the frequency of trophic mismatch events in the northeast Pacific Ocean.

KEY WORDS: Copepod availability · Ocean temperature · Match-mismatch · Seabirds · Cassin's auklet

INTRODUCTION

Reports of ocean climate change on upper trophic level predator (e.g. seabirds) populations are becoming more frequent throughout the Northern Hemisphere as sea surface temperature (SST) variability

increases and extremes are recorded (e.g. North Sea: Proffitt 2004; North Atlantic: Sandvik et al. 2008; Norway: Durant et al. 2003; Canadian Arctic: Gaston et al. 2005; Newfoundland: Montevecchi & Myers 1997; California: Sydeman et al. 2006, Lee et al. 2007; British Columbia: Gjerdrum et al. 2003, Hedd et al. 2006;

Alaska: Anderson & Piatt 1999, Springer et al. 2007). In several cases, authors have sought to explain climate-related variation in reproductive performance of marine birds by examining phenology of breeding and prey availability and the possibility of matches and mismatches in seasonal timing (e.g. Bertram et al. 2001, Hedd et al. 2002, Durant et al. 2005, 2007, Suryan et al. 2006, Hipfner 2008, Gaston et al. 2009).

In the northeast Pacific Ocean, researchers invoked the match-mismatch hypothesis to explain failed reproduction in warm ocean years (1996 and 1998) for Cassin's auklets *Ptychoramphus aleuticus* on Triangle Island, British Columbia, Canada (Bertram et al. 2001, Hedd et al. 2002). They argued that in warm years there was less temporal overlap between the parental provisioning period and availability of a key prey species, *Neocalanus cristatus*, in surface waters. Hipfner (2008) tested the predictions of the match-mismatch hypothesis and found strong support for the explanation of Bertram et al. (2001) using a more recent and extensive time series (1996 to 2006) for Cassin's auklet on Triangle Island. Hipfner (2008) further 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 world's largest Cassin's auklet population on Triangle Island.

The strong mismatches between *Neocalanus* prey availability and the timing of Cassin's auklet reproduction at Triangle Island reflect the geographic range of the prey, the highly seasonal life cycle of the prey, and the temperature-dependent nature of the seasonal peak and duration of prey availability. *N. cristatus* is a 'subartic copepod' and is not found as prey on Cassin's auklet colonies in California and Mexico because those colonies lie well below the southern limit to the geographic extent of *Neocalanus* spp. (Batten et al. 2003). The copepod prey are highly seasonal in surface waters (where they are available to Cassin's auklet to a depth of 40 m [mode]; Burger & Powell 1990) because of their distinctive life history strategy and annual life cycle. The copepod nauplii migrate from mesopelagic depths (400 to 2000 m) to feed and grow and then disappear from surface waters when they reach the final copepodite stage (cV) to migrate back to the deep sea zones and a prolonged dormancy (Mackas et al. 1998, 2004, 2007). In the northeast Pacific, total mesozooplankton biomass and productivity are strongly dominated by the large-bodied calanoid copepods of the genus *Neocalanus* (Mackas et al. 2007). As a consequence of their life history strategy as 'interzonal migrants' combined with their dominance of the regional mesozooplankton biomass, the annual peak of total mesozooplankton biomass in the upper layers of the subarctic Pacific is intense and may be very narrow in duration (Mackas & Tsuda 1999).

Latitudinal differences in the timing of *Neocalanus* copepod prey biomass peaks are expected based on regional temperature differences in the northeast Pacific. For *N. plumchrus*, monthly sampling using a continuous plankton recorder revealed that the timing of peak biomass (when 50% of the population consists of copepodites at Stage cV) occurs about 5 wk earlier at the southernmost (40° N) part of the range than at the northernmost part (Bering Sea), with intermediate areas having intermediate timing (Batten et al. 2003). Mackas et al. (2007) further observed that the latitudinal range of developmental timing is at least as large, and probably larger, than was originally reported by Batten et al. (2003) and developed a new predictive temperature-dependent phenology equation for the northeast Pacific. The phenology equation demonstrates that

'variability of *N. plumchrus* life cycle timing is associated very strongly, and approximately linearly, with cumulative anomalies of upper-ocean temperature during the season in which the copepods are feeding and growing in the near-surface layer' (Mackas et al. 2007, p. 238, Fig. 8b).

Within the northeast Pacific Ocean, British Columbia, Canada, occupies a pivotal position from an oceanographic perspective, because the North Pacific Current bifurcates off its coast forming the Alaska Current to the north and the California Current to the south. Associated with these major currents are 3 oceanographic domains, the downwelling domain in the north, the upwelling domain in the south, and the transitional domain in the central coast (Ware & McFarlane 1989; Fig. 1). The Queen Charlotte Sound, in the transitional domain, also 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 & Welch 2005).

Higher local adult annual survival of Cassin's auklets at Frederick Island, in the northern downwelling domain, than at Triangle Island, at the northern boundary of the California Current Ecosystem in the upwelling domain, indicates that British Columbia is a key location for the detection and investigation of latitudinal variation in oceanographic influences on upper trophic level predator demographics in the northeast Pacific (Bertram et al. 2005). Moreover, in striking contrast to Triangle Island, there have been no reports of reproductive failures on Frederick Island from historical reports (Vermeer 1985) or more recent comparisons (1994 to 1998, 2000 cited in Bertram et al. 2005).

In the present study we contrast inter- and intra-year nestling diets of Cassin's auklets on Triangle and Fred-
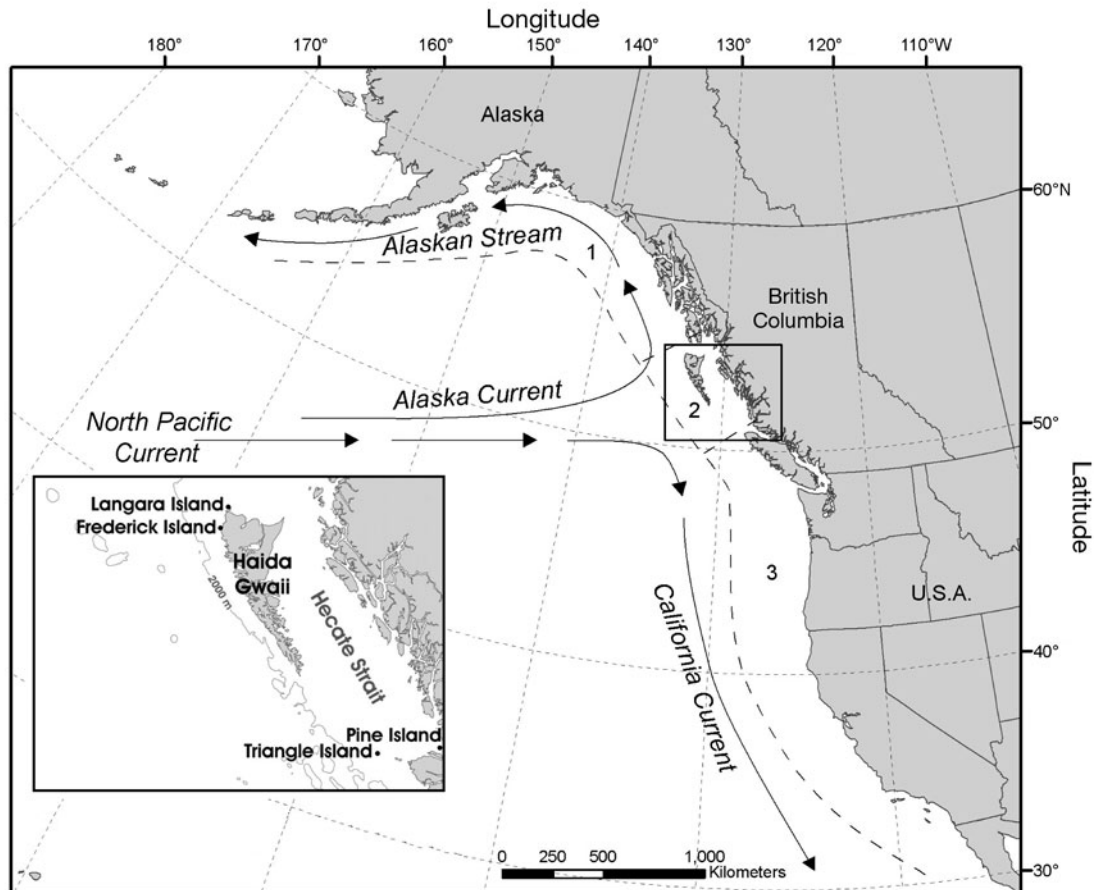
Fig. 1. Study sites, major currents, and oceanographic domains (adapted from Ware & McFarlane 1989). (1) Coastal downwelling domain; (2) transition zone; (3) coastal upwelling domain. Note that the north-south location of the bifurcation of the North Pacific Current varies between years (see Freeland & Cummins 2005 and also Batten & Freeland 2007). The 2000 m isobath and locations of Langara Island and Pine Island light stations are also shown in the inset

erick Islands and look for evidence of trophic mis-matches at both colonies to explore contributions of diet composition to the observed inter-colony variation in vital rates. We investigate mismatch events of *Neocalanus cristatus* using the new equation of Mackas et al. (2007) to estimate the timing of peak biomass in relation to the amount of *N. cristatus* in the nestling diet in the late chick-rearing period. The study period encompasses a natural experiment before, during, and after the large 1997-1998 El Niño Southern Oscillation (ENSO; Wolter & Timlin 1998) and subsequent La Niña events, enabling us to examine their influences on the diets of upper trophic level seabirds in the oceanographically distinct domains in northern and southern coastal British Columbia. Our results show how mismatches have not been observed on Frederick Island and how the geographic distribution and temperature-dependent life cycle of the prey predispose the Triangle seabird colony to trophic mismatches in warm years.

MATERIALS AND METHODS

SST records. We obtained monthly SST records from Pine Island (50° 35' N, 127° 26' W, in keeping with previous work by Bertram et al. 2001 and Hedd et al. 2002) and Langara Island (54° 09' N, 133° 02' W) light stations (www.pac.dfo-mpo.gc.ca/sci/OSAP/data/SearchTools/Searchlighthouse_e.htm). Consistent with previous work on Cassin's auklet diet in British Columbia (e.g. Bertram et al. 2001, Hedd et al. 2002), we plotted average SST for the month of April to reflect ocean conditions that affect prey availability.

Study sites. While both study sites are among the outermost western islands on the coast of British Columbia and are located near the continental shelf break (200 m), they are influenced by different oceanographic domains (Fig. 1). Triangle Island (51° 52' N; 129° 05' W), at the northern end of the California Current Ecosystem, is in the coastal upwelling domain. It is the largest seabird colony in British

Columbia and contains the largest Cassin's auklet breeding colony in the world (540 000 pairs in 1989; Rodway et al. 1990). This windswept and effectively treeless island is the outermost island of the Scott Island chain, 45 km WNW of Cape Scott at the northern tip of Vancouver Island. It has been protected since 1971 as an ecological reserve by the province of British Columbia and is closed to the public (Anne Vallée Triangle Island Ecological Reserve, www.env.gov. bc.ca/bcparks/eco_reserve/anne_er.html).

Frederick Island (53° 56′ N, 133° 11′ W) lies approximately 2 km off the northwest coast of Haida Gwaii (Queen Charlotte Islands). The colony had approximately 90 000 pairs of nesting Cassin's auklets in 1980 (Rodway 1991, Rodway et al. 1994). Frederick Island is largely forested, and the vegetation is described by Rodway et al. (1994). The island is part of Duu Guusd Tribal Park and is protected as a Wildlife Habitat Area (Frederick Island, 6-037) for ancient murrelets *Synthliboramphus antiquus* and Cassin's auklet by the province of British Columbia (http://www.env.gov.bc.ca/cgi-bin/apps/faw/wharesult.cgi?search=number&select=6&number=037&submit=Search)

Nestling diet data. We used historical published records (Vermeer 1985) and available raw data files to reconstruct prey sampling from Triangle Island (1978, 1979, 1980, 1981, 1982) and Frederick Island (1980, 1981). More recent prey sampling was conducted from 1996 to 2000 in West Bay on Triangle Island (see Bertram et al. 2001) and also on Frederick Island from 1996 to 1998 and in 2000 (Table 1). Diet samples were collected by capturing incoming parents using a barrier net ('pheasant net'). We assisted adult birds to regurgitate the meals intended for nestlings by massaging the gular pouch while the beak was suspended over a pre-weighed sample container. The wet mass of sample was determined. We then added 10% formalin (buffered with borax to prevent degradation of invertebrate body parts) in sea water to each container to preserve the meal for identification and enumeration. Approximately 10 samples were collected every 10 d during a fixed time frame during the chick-rearing period at each colony. Timing of hatching is positively correlated on the 2 colonies ($\rho = 0.9$, $p = 0.004$, $n = 7$, A. Harfenist unpubl.) and occurs about 1 wk earlier on Triangle than on Frederick Island, so diet sampling began on 18 to 19 May (Period 1) on Triangle and on 27 May to 3 June (Period 2) on Frederick Island.

Diet analyses: assumptions and corrections. Species composition is reported as % wet mass in order to compare more recent samples with historical data (Vermeer 1985). For both the general and specific diet composition, % mass was expressed as a % of identified prey. We assumed that the proportions of identifiable and unidentifiable items were distributed similarly for all major prey species. The mass of euphausiids in the historical samples (1978 to 1982) was corrected because of the digested euphausiid category, which did not exist for the more recent samples. The mass of digested euphausiids was added, by species, according to the proportion of euphausiids identified in the corresponding sampling period. The euphausiid *Thysanoesa longipes* in the historical samples (1978 to 1982) is the same species as identified as *T. inspinata* in the more recent samples. Finally, the inter-annual comparisons were limited to samples collected between mid-May and the end of June (Periods 1 to 5), as these data were available for both colonies in most years.

Is *Neocalanus* prey phenology reflected in nestling diets? We investigated the relationship between the percentage of *N. cristatus* in Period 5 (26 June to 4 July, when the most data were available for comparison in the late chick-rearing stage), and the timing of peak biomass of *N. plumchrus* near Triangle and Frederick Islands using a newly available temperature-dependent phenology equation for the British Columbia continental margin (date of max biomass = $-0.16x + 169$, where x is degree-days relative to a 6 degree baseline, i.e. sum $[x–6]$ from Days 1 to 92 between 1 March and 31 May; Mackas et al. 2007, D. Mackas pers. comm.). Although no similar equation is available for *N. cristatus*, it is known that *N. cristatus* is available in surface waters longer and has a broader stage/age at any given date later and for longer in the season than *N. plumchrus* (D. Mackas pers. comm.) and thus can potentially overlap more extensively with Cassin's auklets during the incubation and chick-rearing periods. It is reasonable that both *Neocalanus* species demonstrate latitudinal variation in the timing of peak biomass and that differences in the peak timing of *N. cristatus* between colonies and years would be similar for *N. plumchrus* but with a greater potential capacity for temporal persistence. We used SYSTAT 10.2 for all analyses.

RESULTS

April SSTs

Within each year, the average April SST was always higher near Triangle Island (Pine Island light station) than near Frederick Island (Langara Island light station; Fig. 2). There was large inter-annual variation in the average April SSTs; however, temperatures rose and fell in unison on Langara and Pine Islands. The 1990s were generally warm, and 1998 was one of the warmest years on record near both colonies. SSTs dropped precipitously in 1999 and 2000 near both colonies.

Nestling diet composition

Overall, the diet of Cassin's auklet at both Triangle and Frederick Islands was dominated by 2 types of crustacean prey (copepods and euphausiids) and fish (Fig. 3). During Periods 1 to 5 in all years, these prey together contributed 89 to 99% by overall mass (Fig. 3). Three other types of crustaceans including carideans, brachyurans, and amphipods occurred frequently in the diet (Fig. 3 and Tables S1 & S2 in the Supplement, available at www.int-res.com/articles/suppl/m393p199 _app.xls), but in general they contributed little by mass.

Annual-level variation

While copepods, euphausiids, and fish comprised the bulk of the diet of Cassin's auklet, the relative contribution of these prey groups varied widely between sites and among years (Fig. 3). Overall, however, copepods were the predominant prey. At both sites and in all years, a single species, *Neocalanus cristatus*, in particular Stage cV, contributed > 99% to biomass of copepods in the diet.

Triangle Island

At Triangle Island, copepods predominated the diet in both 1997 (63%) and 1999 (56%), euphausiids pre-
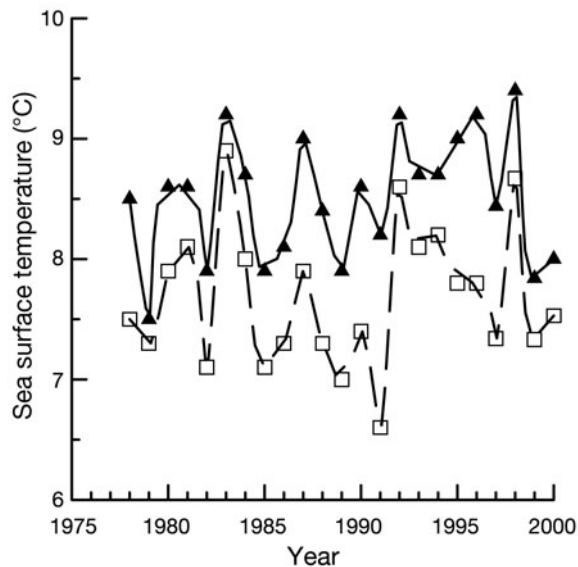

Fig. 2. Average April sea surface temperatures for Pine Island (▲) and Langara Island (□) during the study period. Note that temperatures vary over time in unison and are always warmer on Pine Island in the south than on Langara Island in the north of coastal British Columbia. Data are from www.pac.dfo-mpo.gc.ca/sci/OSAP/data/SearchTools/ Searchlighthouse_ e.htm

dominated in 1980 (49%), 1981 (53%), 1996 (62%), and 2000 (57%), and fish were the most important prey consumed in 1998 (46%). Three species of euphausiids (*Euphausia pacifica, Thysanoessa spinifera*, and *T. inspinata* [earlier identified as *T. longipes*]) were taken by Cassin's auklets, with both adult and juvenile age classes identified for the *Thysanoessa* spp. Adult *T. spinifera* comprised >25% of the diet at Triangle in 1980, 1981, and 2000, while in 1996, *E. pacifica* contributed 24% by mass. In 1996, adult *T. spinifera* and juvenile *T. inspinata* also contributed >10% to the diet, while in 2000, *E. pacifica* and adult *T. inspinata* also each contributed >10% by mass.

Fish were the predominant prey at Triangle only in 1998, but they also contributed 30% to the diet in 1997. Fish were highly digested at both sites and, in general, this component of the diet has been poorly documented (Tables S1 & S2). In all, 5 fish families were identified at Triangle. By mass, the rockfishes *Sebastes* spp. were the most important of the fish prey, with flatfishes Pleuronectidae and Irish lords *Hemilepidotus* spp. contributing significantly in some years. Rockfishes accounted for all fish identified at Triangle in 1997 and 50% of those identified in 1998. The flatfishes and Irish lords each comprised an additional 10% of the diet in 1998. Fish from the family Cottidae were identified in the diet at Triangle only in 1999, when they occurred in 26% of samples.

Carideans, amphipods, and brachyurans often occurred frequently, and sometimes in large numbers, at Triangle (Fig. 3, Table S1), but these groups generally made minor contributions. Exceptional were 1996 when unidentified brachyuran (crab) megalops contributed 4% to the diet, and 1998, when 7% of the diet consisted of amphipods, largely *Vibilia propinqua*.

Frederick Island

The diet of Cassin's auklet at Frederick Island was also highly variable among years (Fig. 3, Table S2). Copepods were again the most important prey overall, dominating the diet in 1980 (48%), 1981 (48%), and 1998 (51%).

Euphausiids were the most important prey at Frederick in 1996 (59%) and 2000 (52%), while in 1997, copepods (46%) and euphausiids (44%) contributed similarly to the diet. In years when euphausiids were important, it was largely adult *Thysanoessa spinifera* that were consumed. They contributed 46% to the overall diet in 1996, 30% in 1997, and 35% in 2000. *Euphausia pacifica* was important in 2000 only, when it contributed 10% by mass.

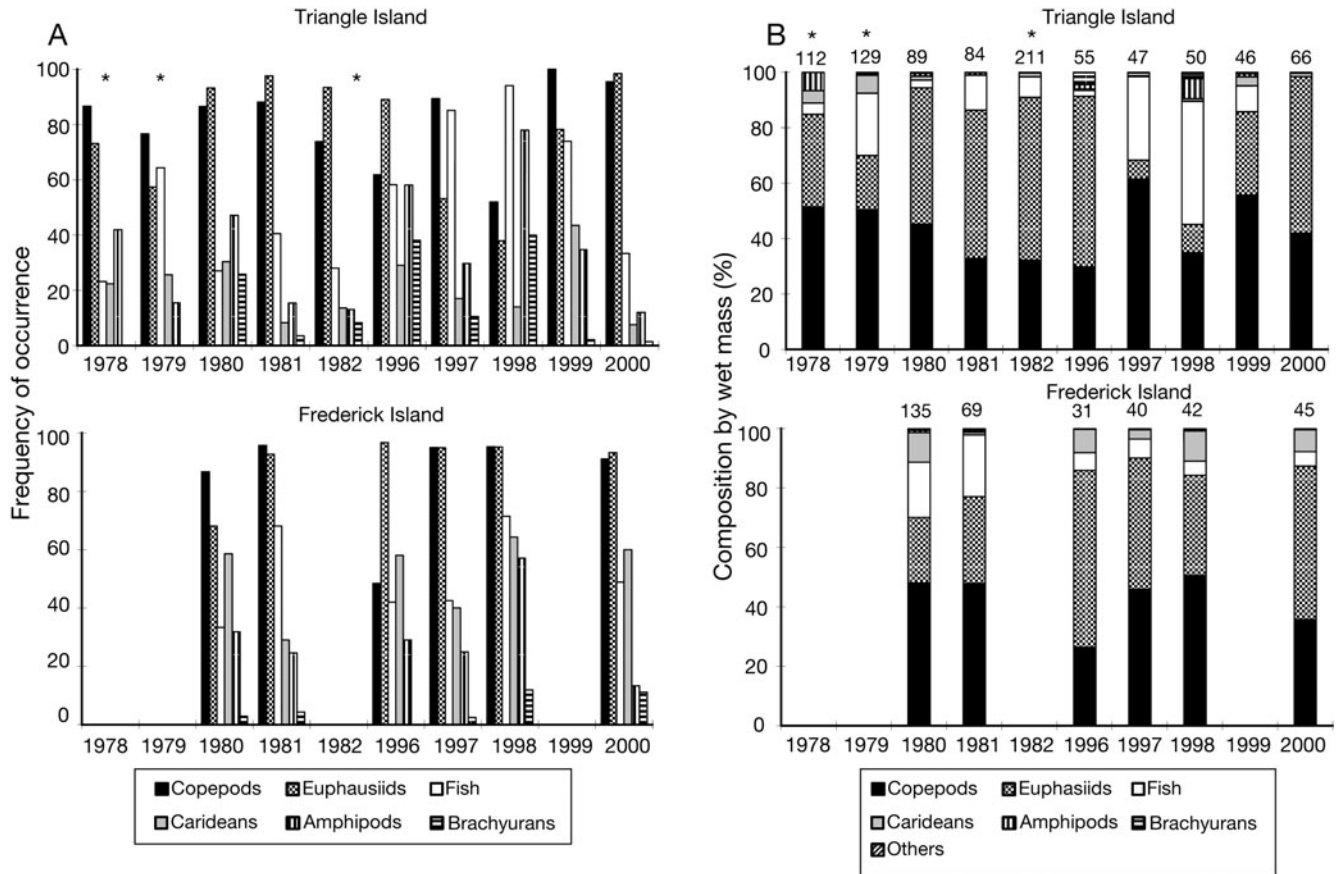Unlike at Triangle, fish was never the annually predominant prey group at Frederick, but were significant

Fig. 3. *Ptychoramphus aleuticus.* Annual trends in the general composition of Cassin's auklet diet at Triangle and Frederick Islands between mid-May and the end of June expressed as (A) percent frequency of occurrence, and (B) percent by wet mass for the 6 major prey classes. Years indicated with an asterisk (1978, 1979, and 1982 at Triangle Island) are from Vermeer (1985) and include data from late May to the end of July. The number of samples examined each year is indicated above the bar

during the 1980s, contributing 19% by mass in 1980 and 21% in 1981. The species consumed in these years, however, were unidentified. Since 1996, fish have contributed only ~5% yr^{-1} to the diet at Frederick Island, and in 1998 and 2000, largely rockfishes (>4% in 1998, 3.5% in 2000) and Irish lords (1% in 2000) were consumed (Table S2).

Unlike at Triangle, carideans (shrimps and mysids) were important to the nestling diet at Frederick, where they contributed >7% by mass in 4 of 6 yr. The bulk of the carideans were *Pandalopsis dispar*, and *Pandalus* spp. At Frederick, amphipods and brachyurans occurred frequently, but they never contributed >1% by mass (Table S2).

Within-year variation

Apart from high dietary variation among years, at both sites there were substantial within-year changes in diet composition (Fig. 4) that appeared to be driven

by availability of copepods. At Triangle, copepod occurrence in the diet generally peaked early in the breeding season (mid-May to early June, Periods 1 to 3), and its importance then declined through to fledging. The seasonal persistence of copepods, however, showed substantial variation among years (Fig. 4). In 1996 and 1998, for example, copepods had almost or completely disappeared from the diet at Triangle by late June (Period 5), while in 1980, 1981, and 1999, copepods were delivered to chicks until mid-July. Late-season sampling in 1980, 1981, and 1999 was particularly instructive, demonstrating that regardless of the level of seasonal dominance, copepods do eventually disappear from the diet, presumably coincident with cV migration to depth (Bertram et al. 2001). The temporal window of copepod availability to Cassin's auklets therefore varies among years, and also presumably between the breeding sites. At Frederick, the timing of copepod availability either begins later and/or it extends through the season as in 1980, 1981, and 1998 when copepods persisted in the diet at
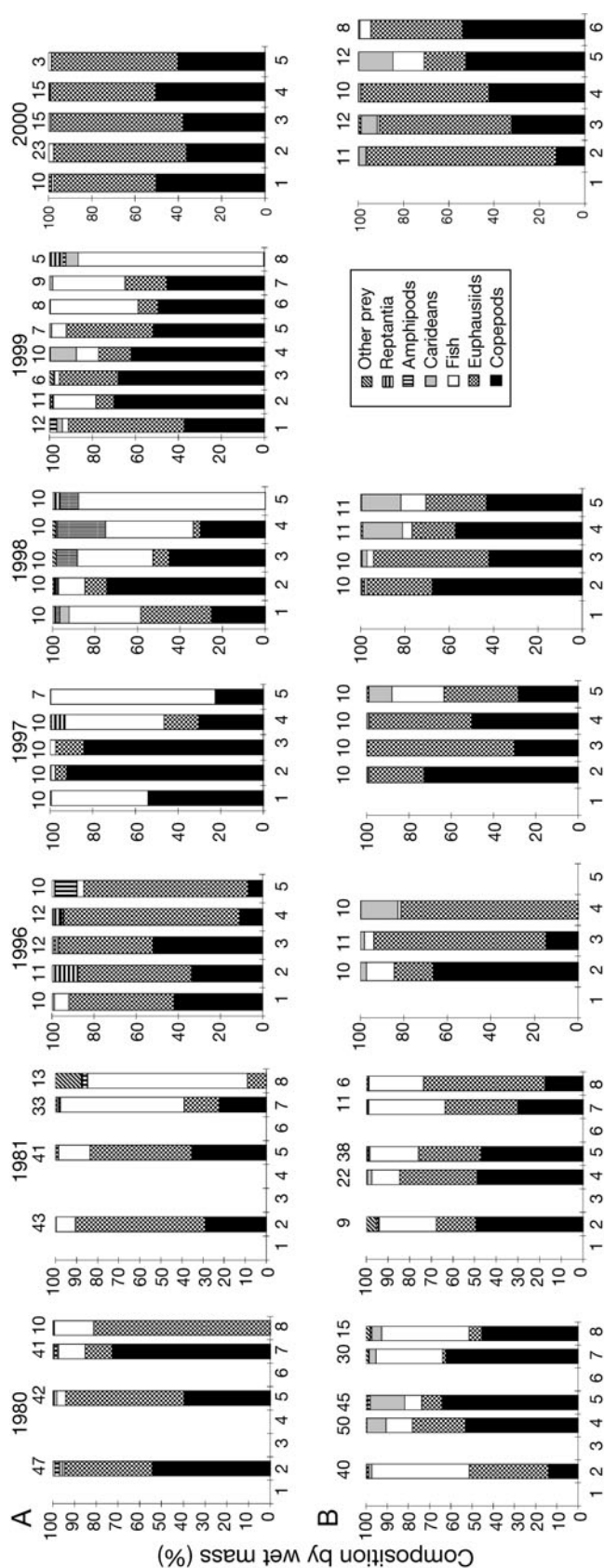
Fig. 4. *Ptychoramphus aleuticus*. Within-year trends in the general composition of Cassin's auklet diet at (A) Triangle and (B) Frederick Island expressed as percent composition by wet mass. Data are summarized and blocked by period within each year as follows: Period 1 = 18–19 May; 2 = 27 May–03 June; 3 = 7–10 June; 4 = 12–19 June; 5 = 26 June–4 July; 6 = 8 July; 7 = 13–20 July; 8 = 21–30 July. The number of samples examined in each period is indicated above the bar

Frederick after they had disappeared on Triangle. In 2000, a cooler year in the time series, occurrence of *Neocalanus cristatus* increased during Periods 1 to 5 on Frederick Island while remaining stable on Triangle Island.

Latitudinal differences in the effects of prey phenology on nestling diet are evident from the relationship between peak biomass timing of *Neocalanus* near Triangle and Frederick Islands and the representation in the nestling diet in the late chick-rearing period (Fig. 5). A significant positive relationship between percentage *Neocalanus* in the nestling diet and the timing of peak biomass exists on the southern island (Triangle Island: $y = 2.23x - 260.73$, $R^2 = 0.919$; $F_{1,5} = 56.78$, p < 0.01), but was not detected on the northern island (Frederick Island: $y = -0.22x + 76.99$, $R^2 = 0.02$; $F_{1,3} = 0.06$; p > 0.8). The paucity of *Neocalanus* late in the nestling diet period on Triangle Island in the years of 1996 and 1998 indicates a mismatch with the prey phenology in those warm spring years.

As copepods are a preferred prey item for Cassin's auklet in British Columbia, both the overall importance and seasonal timing of other prey presumably vary in accordance with copepod availability. At Triangle, either fish or euphausiids became generally more important in the diet through the season as copepods disappeared (Fig. 4). Euphausiids supplemented the diet in 1996 and 2000, but the species involved in each year were different (Fig. 6). In 1996, *Euphausia pacifica* was consumed early followed by a mix of adult and juvenile *Thysanoessa spinifera* and juvenile *T. inspinata* as the season progressed. In 2000, *E. pacifica* was less important, and adult *T. spinifera* and both adult and juvenile *T. inspinata* figured prominently. In the absence of copepods at Frederick, the diet consisted largely of euphausiids and fish in the 1980s, and mainly euphausiids from 1996 to 2000 (Fig. 6). Carideans were also important late in the breeding season during some years in the 1990s (Fig. 4). *T. spinifera* was the dominant euphausiid delivered to chicks at Frederick Island; adult *T. spinifera* early in the season were replaced later in some years by juveniles (Fig. 6). 1981 was notably different, when largely juvenile *T. inspinata* were delivered to chicks from the end of June.
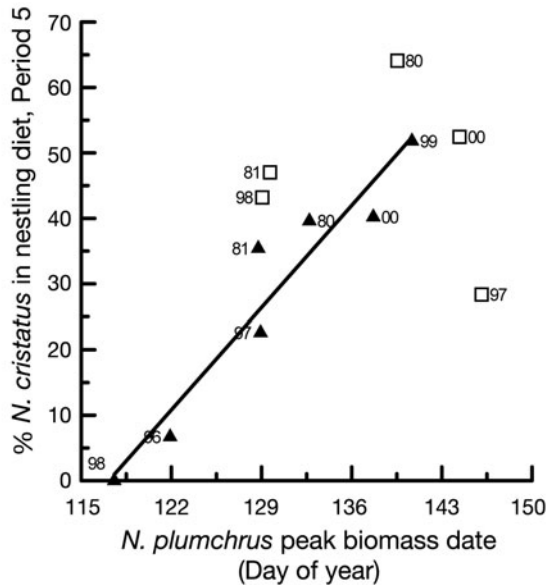
Fig. 5. *Neocalanus cristatus* and *N. plumchrus*. Prey phenology effects on predator diet show latitudinal differences related to variation in SST. The percentage of *N. cristatus* in Cassin's auklet nestling diet in Period 5 (26 June to 4 July, *y*) versus the predicted date of peak biomass of *N. plumchrus* based upon the temperature-dependent phenology equation of Mackas et al. (2007, see 'Materials and methods'). We drove the phenology equation using SST data from Pine Island light station (for Triangle Island) and from Langara light station (for Frederick Island). A significant positive relationship exists on the southern island (Triangle Island; (▲): $y = 2.23x − 260.73$, $R^2 = 0.919$; $F_{1,5} = 56.78$, p < 0.01), but was not detected on the northern island (Frederick Island; (□): $y = −0.22x + 76.99$, $R^2 = 0.02$; $F_{1,3} = 0.06$; p > 0.8). The figure highlights the fact that Cassin's auklet nestling diet on Triangle Island is mismatched with the phenology of *Neocalanus* copepod prey in the early sprin years of 1996 and 1998 in our time series

Copepod variety

While *Neocalanus cristatus* dominated the copepod portion of the diet, 24 copepod species were identified in the diet of Cassin's auklet in British Columbia; 21 species at Triangle Island and 12 species at Frederick Island (Tables S1 & S2). Other copepods occurred frequently in some years, and sometimes in relatively large numbers, but they always contributed little by mass (Tables S1 & S2). In general, copepod diversity was high at both sites during the 1998 El Niño; occurrence of *Calanus marshallae* (Stage cV) and *Pseudocalanus mimus* was >10% at Triangle Island and *N. plumchrus* (Stage cV), *Paracalanus parvus*, *Pseudocalanus* spp., *Oithona similis*, and *Cyclopoid* spp. each occurred in >10% of samples at Frederick Island (Tables S1 & S2). Copepod diversity was also relatively high at Triangle Island in 1999, when *Pseudocalanus* spp. occurred in 22% of samples.

Other prey species

Seventeen species or groups of amphipods were identified: 16 at Triangle Island and 11 at Frederick Island (Tables S1 & S2). Amphipods occurred frequently and often in large numbers, but they always contributed negligibly by mass. Three species, *Themisto pacifica*, *Brachycelus crusculum*, and *Vibilia propinqua*, occurred frequently (i.e. in >15% of samples in at least 1 year) at both sites while *Brachycelus* spp., *Hyperoche medusarum*, and *Primno abbysallis* also occurred frequently in the diet during some years at Triangle Island.

DISCUSSION

Peak timing and duration of availability of *Neocalanus*

Together, copepods and euphausiids contributed >89% to the diet of Cassin's auklet nestlings on both Triangle and Frederick Islands in all years of the study. Our findings confirm and extend historical observations from 1978 to 1982 (Vermeer 1981, 1985, Vermeer et al. 1985) and also offer new insights into latitudinal patterns of temporal variation in the timing of *Neocalanus* prey availability in surface waters and its association with ocean climate variability.

Our results are consistent with the idea that the diet of nestling Cassin's auklets in British Columbia reflects the temporal availability of *Neocalanus cristatus* prey within the foraging range of the colony (10 to 90 km on Triangle, Boyd et al. 2008). *N. cristatus* is a highly profitable prey item that is linked to rapid nestling growth (Bertram et al. 2001, Hedd et al. 2002, Hipfner 2008), and thus its dietary occurrence should reflect regional availability of Stage cV copepodites in surface waters.

We argue that the opportunity for a temporal mismatch between Cassin's auklet provisioning and *Neocalanus* prey timing has a latitudinal component and is greater on Triangle Island than on Frederick Island in warm years such as 1996 and the El Niño event of 1998 (which are both known years of reproductive failure on Triangle Island but not on Frederick Island; Bertram et al. 2001, 2005). Note that it is not only the timing of the peak of, but also the duration of, the *Neocalanus* availability in surface waters that affects foraging Cassin's auklet parents. In warm years, the biomass peak of *Neocalanus* is early and narrow in duration, whereas in cooler years, the biomass peak is later and broader in duration (Mackas & Galbraith 2002, Batten & Mackas 2009, this Theme Section). We argue that within a warm year, the peak will be early and narrow on Triangle Island, but farther north around Frederick
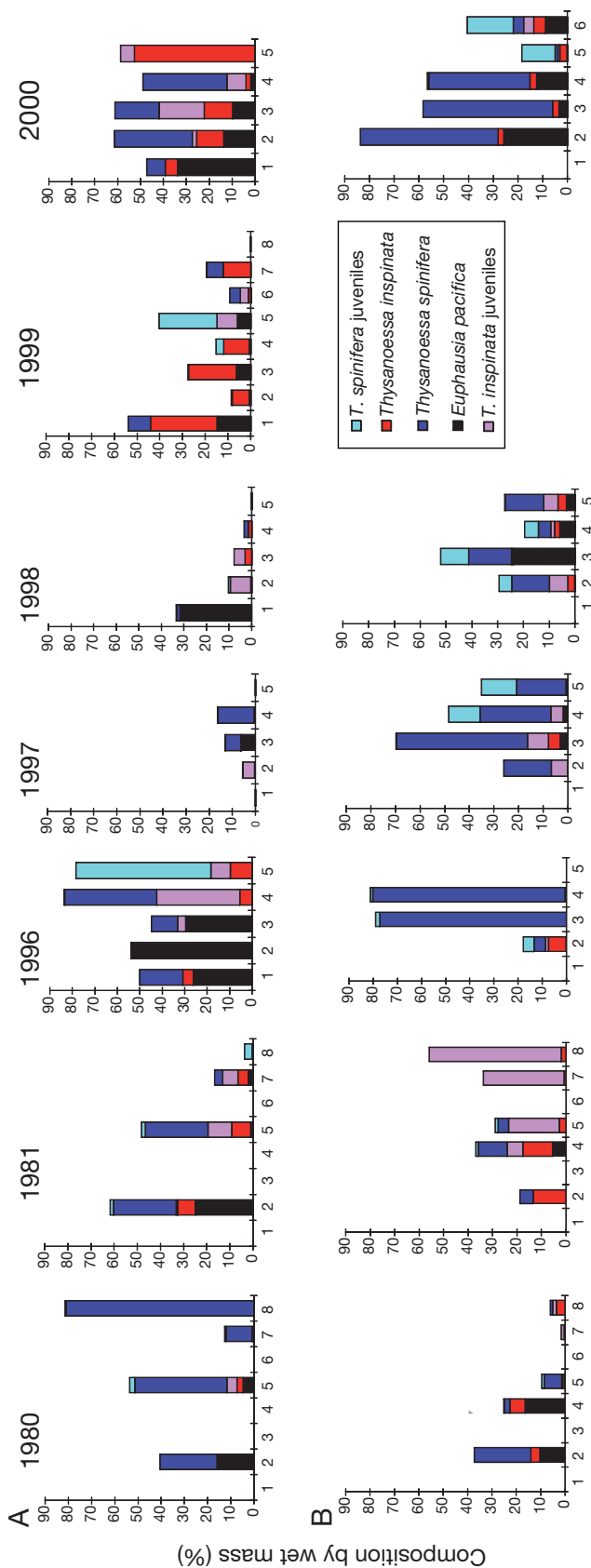
Fig. 6. *Ptychoramphus aleuticus*. Annual trends in the species composition of the euphausiid portion of the diet at (A) Triangle and (B) Frederick Islands, expressed as percent composition by wet mass. Note that the maximum *y*-scale value is 80 %. Data are blocked by period as in Fig. 4

Island, the peak will be later and more protracted. Poor reproductive performance is the biological consequence of a trophic mismatch for Cassin's auklet.

Our data and analyses show that in the warm El Niño year of 1998, the peak of *Neocalanus* at Triangle Island was earlier (28 April) and diminished progressively to 0 during the chick-rearing period (mismatched) in marked contrast to Frederick Island where the peak occurred later (9 May) and persisted in the nestling diet at over 40 % wet mass throughout the nestling period (matched). In contrast to warm years, mismatches were not observed at either colony in cool years. During the cool ocean year of 2000, the peak dates were relatively late and close in time (18 May on Triangle and 24 May on Frederick), and *Neocalanus* copepods were available on both colonies throughout chick rearing. Note, too, that on Frederick Island in 2000, *N. cristatus* increased steadily in the nestling diet from 10 % in Period 1 to roughly 50 % in Period 5 of chick rearing. The gradual increase in *N. cristatus* in the nestling diet over time in 2000 likely reflects the growing availability of fully grown, oil-laden Stage cV copepodites in surface waters in this cool year.

Independent evidence from 2005 supports our conclusion that mismatches are more likely to occur on Triangle than on Frederick Island. In general, for British Columbia in 2005, SSTs were warmer than normal (DFO 2006). The seasonal timing of the peak copepod biomass was anomalously early off North Vancouver Island in 2005, and as in 1998, the *Neocalanus* copepods left the surface layer early in the season (Mackas et al. 2006). On Triangle Island in 2005, *N. cristatus* were scarce in the nestling diet (DFO 2006, Hipfner 2008, M. Hipfner pers. comm.), indicating a trophic mismatch.

As a result of the mismatch, only 8 % of nesting pairs were successful (Sydeman et al. 2006), and nestlings showed retarded development and overall poor production in 2005 on Triangle Island (DFO 2006, Hipfner 2008). In marked contrast, nestlings on Frederick Island in 2005 were developmentally robust (M. Hipfner pers. comm.), an indication that no trophic mismatch occurred in the northern region and that food web effects of the 2005 warm event were largely limited to the California Current Ecosystem (see Mackas et al. 2006, Sydeman et al. 2006).

Coho salmon growth and survival mirror the seabird patterns

Upper trophic level predators other than seabirds also show strong responses in production in relation

Table 1. *Ptychoramphus aleuticus.* Details of the sampling dates and the number of nestling diet samples collected from Cassin's auklet parents at Triangle and Frederick Islands, 1978 to 2000

Year	N	Sampling period
Triangle Island		
1978	112[a]	27 May – 25 July
1979	129[a]	27 May – 25 July
1980	140	27 May – 27 July
1981	130	28 May – 25 July
1982	211[a]	30 May – 28 July
1996	55	19 May – 28 June
1997	47	18 May – 28 June
1998	50	18 May – 28 June
1999	68	18 May – 27 July
2000	66	19 May – 29 June
Frederick Island		
1980	180	28 May – 23 July
1981	86	1 June – 30 July
1996	31	28 May – 18 June
1997	40	28 May – 28 June
1998	42	28 May – 28 June
2000	53	28 May – 8 July
	988	

[a]Raw data were unavailable for these years, but the annual values are included in Fig. 3 for completeness based upon Vermeer (1985)

to changes in zooplankton that are related to ocean climate (e.g. Mackas et al. 2007). Additional independent information on juvenile coho salmon *Oncorhynchus kisutch* growth rates also mirror the dichotomy of seabird responses to warm ocean years in northern and southern British Columbia. Growth rates of salmon in SE Alaska have been largely uniform ranging from 1.4 to 1.5 mm d^{-1} from 1998 to 2005. In contrast, on the west coast of Vancouver Island, growth rates were well below average in 1998 and were the lowest on record (<0.8 mm d^{-1}) in 2005 (Trudel et al. 2007). The variation in growth rates has also been positively linked to variation in survival and hence production (Trudel et al. 2003, 2007, Mackas et al. 2007). While juvenile coho salmon are largely piscivorous, the strong and similar pattern to Cassin's auklet suggests that bottom-up processes (cf. Ware & Thomson 2005, Frederiksen et al. 2006) influence production at higher trophic levels for both seabirds (see also Ware & McQueen 2006a,b) and salmonids (see also Roth et al. 2007, Sydeman et al. 2008). Poor availability of *Neocalanus* prey may indeed contribute to the observed poor year classes of Pacific sand lance *Ammodytes hexapterus* in warm years around Triangle Island (Hedd et al. 2006), and the poor recruitment could contribute to the poor growth of coho salmon, which are known to prey heavily upon sand lance (Brodeur & Pearcy 1990).

CONCLUSION

Rising global terrestrial and marine temperatures are forecasted based on global temperatures from 1850 to 2007 (www.metoffice.gov.uk/corporate/pressoffice/myths/2.html).

If warming continues and if predictions of more frequent ENSO events (e.g. Herbert & Dixon 2002) are realized, then we would expect to have more trophic mismatch events on Triangle Island, which is influenced by the California Current Ecosystem, than on Frederick Island in the cooler Alaska Current Ecosystem. Finally, recent work demonstrates that the average cohort widths of *Neocalanus plumchrus* in the northeast Pacific were significantly narrower in 2000–2007 than 1957–1965 (Batten & Mackas 2009). Narrowing of the duration of prey availability in surface waters, coupled with our diet observations, further supports the idea that the frequency of mismatches could increase on Triangle Island and possibly even occur for the first time on Frederick Island if prey cohort width becomes narrower in the future.

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