

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

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 'subarctic 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-

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 *Thysanoessa 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 compar-

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 par-

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

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

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*

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