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Euphausiids in the diet of a North Pacific seabird: annual and seasonal variation and the role of ocean climate

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ABSTRACT: Across the California Current System (CCS), euphausiid crustaceans are important prey for many vertebrate predators, including the seabird Cassin's auklet *Ptychoramphus aleuticus*. However, the effects of ocean climate on euphausiid biology, and their consequences for predators, remain poorly understood. Over a 13 yr period (1996 to 2008), *Euphausia pacifica*, *Thysanoessa spinifera* and *T. inspinata* cumulatively averaged about 35% of the annual biomass in the nestling diets of auklets at Triangle Island, but there was marked inter-annual variation. Whereas ocean climate had little influence on the amounts of *E. pacifica* or *T. inspinata* delivered, diets included more *T. spinifera* if spring sea-surface temperatures in the previous year had been lower. Cold conditions might facilitate the production of a strong annual cohort, thus increasing adult biomass in the following year. Within seasons, the amount of *E. pacifica* in diets declined with date, and the decline was consistent across both warm- and cold-water years. In contrast, diets were especially rich in both *Thysanoessa* spp. late in the provisioning period in warm-water years, when the harvest of *Neocalanus cristatus* declined dramatically due to a temporal mismatch between the auklet predator and this copepod prey. Both the annual nestling survival rate and the mean fledging masses of Cassin's auklets were tightly correlated to the amount of *N. cristatus* in their diets, and for fledging mass there was a further small, additive effect of increased amounts of *T. inspinata*. Results of the present study add new insight into effects of ocean climate on euphausiid biology in the northern CCS, and their potential consequences for population processes of an important euphausiid predator.

KEY WORDS: Auklet · Diet · Euphausiids · Ocean climate · Prey-switching

INTRODUCTION

Studies of marine ecosystem dynamics have been at the forefront of the research agenda investigating the biological consequences of climate variation (Stenseth et al. 2004). Climate-driven changes in the distribution, phenology and abundance of low trophic level organisms can have cascading effects within marine food webs, with consequences for the population dynamics of species at higher trophic levels (Anderson & Piatt 1999, Edwards & Richardson 2004, Richardson 2008). Studies on the demographic and behavioural responses of marine birds often provide clear signals of the mechanisms by which variation in ocean climate alters trophic pathways (Aebischer et al. 1990, Durant et al. 2003, Piatt et al. 2007). Studies of zooplanktivorous seabirds may be especially informative, because they feed on organisms within a low and narrow trophic range that often respond strongly and predictably to environmental variation (Springer & Roseneau 1985, Bertram et al. 2001, Sydeman et al. 2001).

As a group, euphausiid crustaceans play important yet often underappreciated roles in many marine food webs (Reid et al. 2004, Richardson 2008). Across the California Current System (CCS), for example, the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* are important prey for many vertebrate predators (Brodeur & Pearcy 1992, Ainley et al. 1996,

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in which year was included in a strongly supported model, I regressed the annual mean proportion of that euphausiid against the mean spring sea-surface temperature (SST) in the current year (x) and in the previous year ($x - 1$), and compared the relative support for these 2 models against that for a null model. To be consistent with previous work (Bertram et al. 2001, Hipfner 2008), I used the April mean SST measured at the lighthouse at Pine Island, ~100 km to the east of Triangle Island. Note that SST at Pine Island accurately gauges water-column temperature due to deep tidal mixing (Bertram et al. 2001); furthermore, throughout the 13 yr study period, April mean SSTs accorded very well with general accounts of oceanographic variation for the broader region (Mackas et al. 2007, DFO 2008), and correlated strongly with means in May (r = 0.86) and June (r = 0.80), when auklet provisioning peaks.

(2) For each euphausiid species in which session was included in a strongly supported model, I plotted the mean proportion delivered in each of the 5 sampling sessions, pooled across all years, to describe the overall seasonal pattern of delivery of each species. To account for inter-annual variation (i.e. a year effect), I calculated for each species the grand mean proportion delivered across all sessions within each year, set that annual grand mean value to zero, and then converted all raw data points within each year to deviations from the annual mean. Thus, raw data consisted of the deviations from the zero-centred mean for each of the 13 yr.

(3) For each euphausiid species in which the year × session interaction term was included in a strongly supported model, I subdivided all years into those falling within cold periods (1999 to 2002 and 2007 to 2008) and within warm periods (1996 to 1998 and 2003 to 2006), using the same zero-centred raw data. To allow for a visual comparison, I plotted the seasonal patterns of delivery in cold years versus warm years.

(4) I tested whether there was a discernible fitness benefit for the auklets in including more of any of the 3 euphausiid species in nestling diets (as a secondary prey item, after *Neocalanus cristatus*). As fitness measures, I used the proportion of nestlings that survived the period from hatching to fledging in each year, and their mean fledging mass. I tested the relative support for each of a series of 4 explanatory GLMs: (1) *Neocalanus cristatus* + *N. cristatus*^{2}, (2) *N. cristatus* + *N. cristatus*^{2} + *Euphausia pacifica* + *E. pacifica*^{2}, (3) *N. cristatus* + *N. cristatus*^{2} + *Thysanoessa spinifera* + *T. spinifera*^{2} and (4) *N. cristatus* + *N. cristatus*^{2} + *T. inspinata* + *T. inspinata*^{2}. I included both linear and quadratic terms, to account for curvilinearity in the relationship with fledging mass.

RESULTS

Ocean climate variation

Relative to the long-term (1937 to 1995) average, mean April SSTs measured at Pine Island were very warm from 1996 through 1998, near average from 1999 to 2002, warmer than average from 2003 to 2006, then cool again in 2007 and 2008 (Fig. 1). Thus, the oceanographic periods described by others are evident in these SST data (Mackas et al. 2007, DFO 2008). Note that the present study spanned 2 transitions from generally warm to generally cool periods and 1 transition from a cool to a warm period.

Neocalanus cristatus in diets

Across the 13 yr, *N. cristatus* was the dominant prey item in the diets of Cassin's auklet nestlings, averaging 39.4% of biomass (range: 21.3 to 60.6%). As expected, *N. cristatus*

Euphausiids in the diets of auklet nestlings

Species composition and age ratios

Considering all species combined, euphausiids comprised an average of 35.1% of the biomass in the diets of auklet nestlings across the 13 yr. The most abundant species was *Thysanoessa spinifera* (average: 15.6% of biomass), followed by *T. inspinata* (average: 9.7%) and *Euphausia pacifica* (average: 9.3%). Only 2 other species of euphausiids were recorded: 1 food load collected on 28 May 2002 contained a very small amount of adult *Nematoscelis difficilis* and small amounts of adult *T. gregaria*

For all 3 euphausiid species, the best-supported AIC*c* model included year. In the case of *Euphausia pacifica* and *Thysanoessa inspinata*, the yearly variation was not linked to the ocean climate parameter examined: compared to AIC*c* models that included the mean April SST in the current year and in the previous year, only the null model was strongly supported, and it received at least 3.3 times the weight of either climate model (Table 2). In contrast, the best-supported model for *T. spinifera* was April SST in the previous spring (Table 2): diets were richer in *T. spinifera* in years that followed a year with lower spring SSTs (Fig. 5).

Seasonal variation

was explained most parsimoniously by the proportion of *Neocalanus cristatus* in their diets: offspring were more likely to survive, and they fledged heavier, in years in which they received more of this copepod. For survival, no model that included any of the 3

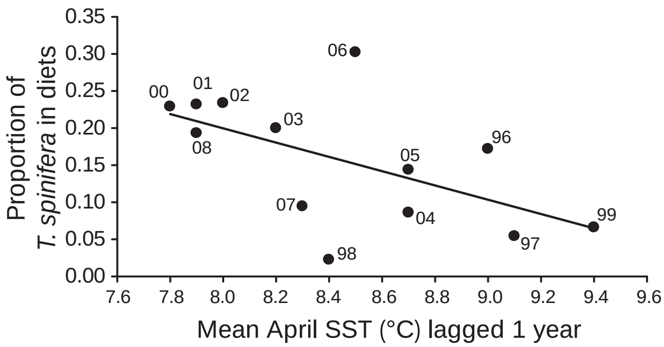
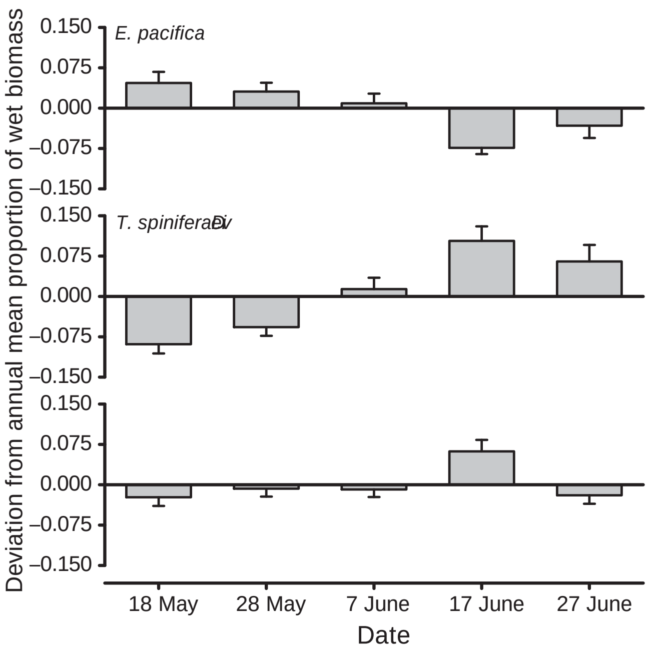


Fig. 5. *Ptychoramphus aleuticus*. The mean annual proportion of biomass comprised of *Thysanoessa spinifera* in food loads delivered by Cassin's auklet to nestlings in relation to April sea-surface temperature (SST) in the previous year. Numbers beside data points refer to the year in which euphausiids, not SST, were measured



euphausiid species received support, while for fledging mass, the model including *Thysanoessa inspinata* in addition to *N. cristatus* also received strong support (AIC*c* ≤ 2.0). Thus, there was no evidence that increased amounts of euphausiids in diets increased survival probabilities, but there was evidence of a meaningful, additive effect on fledging mass for greater amounts of *T. inspinata* as a secondary prey item (Fig. 8).

DISCUSSION

Recent work, updated here through 2008, has shown that the ocean climate in spring strongly influences the composition of the diets fed by Cassin's auklet *Ptychoramphus aleuticus* parents to their offspring at Triangle Island (Bertram et al. 2001, Hedd et al. 2002). In particular, nestling diets tend to be richer in the subarctic copepod *Neocalanus cristatus* during cold oceanic years, when the springtime period of residency of late-stage *N. cristatus* copepodites in near-surface waters is delayed and prolonged (Mackas et al. 2007). This results in greater temporal overlap between the auklets' offspring-provisioning period and the period when the copepods are available to them. The auklets forage for *N. cristatus* along and seaward of the continental shelf break west of Triangle Island (Boyd et al. 2008), and they breed more successfully in years in which their diets include more *N. cristatus* (Hipfner 2008).

Euphausiids in the diets of auklet nestlings

Species composition and age ratios

The present study shows further that the 3 euphausiid species *Euphausia pacifica*, *Thysanoessa spinifera* and *T. inspinata* cumulatively form the major secondary prey items fed to Cassin's auklet nestlings at Triangle Island. Only 2 other euphausiids were recorded in diets in small amounts: *T. gregaria* (in 3 yr) and *Nematoscelis difficilis* (in 1 yr). Oceanic warming is widely expected to cause shifts in the distributions of zooplanktonic species (Richardson 2008), and in the northspecific differences in local oceanography, which determine the rate of advection of juveniles out of the birds' foraging range (Adams et al. 2004). The greater

the less abundant *Thysanoessa spinifera* than the more abundant *E. pacifica* (Tanasichuk 2002).

Fitness correlates of euphausiids in diets

The amount of *Neocalanus cristatus* in their diets previously was found to be the key factor affecting yearly variation in the percentage survival and mean fledging masses of Cassin's auklets at Triangle Island (Hipfner 2008). In both cases, this remains the most parsimonious explanation with the addition of 2 more years. There was little additive benefit of including more of either *Euphausia pacifica* or *Thysanoessa spinifera* on either fitness measure, despite that increased amounts of *T. spinifera* in diets previously were linked to higher growth rates (Abraham 2008). However, there was a relatively small additive effect on fledging mass (but not survival) of including more *T. inspinata*. This euphausiid increased dramatically in nestling diets in the middle of June in warm years, at the time when auklets ceased delivering *N. cristatus*. Unfortunately, there is almost no information on the ecology of *T. inspinata* in the northern CCS, and that precludes an assessment of what factors ultimately influence its availability to Cassin's auklets. It appears, however, that SST does not have a strong effect.

Implications for Cassin's auklets in the northern CCS

The bulk of the global population of Cassin's auklets breeds in the Scott Islands archipelago, off the coast of British Columbia (Rodway 1991). In this region, ocean climate strongly influences the birds' demography (Bertram et al. 2001, 2005, Hipfner 2008, Morrison 2009, Hipfner et al. in press). An adequate supply of *Neocalanus cristatus* appears to be critical for successful breeding by Cassin's auklets in this system, and a warming ocean is likely to result in more frequent and more severe temporal mismatches between the auklet predator and the copepod prey.

In the southern and central CCS, where *Euphausia pacifica* and *Thysanoessa spinifera* are their most important prey (Abraham & Sydeman 2004, Adams et al. 2004), all Cassin's auklet populations are relatively small and in precipitous decline due to ocean warming (Lee et al. 2007, Wolf et al. 2009). While euphausiids, in general, are less important to auklets in the northern CCS, there was some fitness benefit associated with including more *T. inspinata* in diets, but no overt benefit associated with including more of *E. pacifica* or *T. spinifera*. However, compared to *Neocalanus cristatus*, the effect of *T. inspinata* was small. Thus, there appears to be nothing presently available in the northern CCS to replace the predictable and high-quality prey item *N. cristatus* in feeding the very large Cassin's auklet populations in the Scott Islands. If true, then we can expect that continued warming of the marine environment around this archipelago will have strong deleterious effects on these large populations. Continued monitoring of this and other seabird populations in the CCS will be important as we attempt to document and understand changes to marine ecosystem functioning as a result of future climatic warming.

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